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Wetland Plant Influence on Sediment Ecosystem Structure and Trophic Function

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Wetland plant influence on sediment ecosystem structure and trophic function

A Dissertation submitted in partial satisfaction of the requirement for the degree
Doctor of Philosophy

in

Oceanography

by

Christine René Whitcraft

Committee in charge:

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University of California, San Diego
2007

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DEDICATION

This dissertation is in recognition of the many mentors, both academic and personal, who instilled in me a love of the outdoors, encouraged curiosity and exploration, and devoted their time and resources to develop both of those. I especially dedicate this to my parents, Wilfred and Susan Whitcraft, and my husband, Jonathan Pompa, who have provided amazing examples of what love, devotion, intelligence, and compassion can achieve.

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I can no other answer make, but, thanks, and thanks. ~William Shakespeare

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PUBLICATIONS

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ABSTRACT OF THE DISSERTATION

Wetland plant influence on sediment ecosystem structure and trophic function

by

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Doctor of Philosophy in Oceanography

University of California, San Diego, 2007

Professor Lisa A. Levin, Chair

Vascular plants structure wetland ecosystems. To examine mechanisms behind their influence, plants were studied under different scenarios of change: experimental manipulation of cover, invasion, and response to flushing regimes. I tested the hypothesis that wetland plants alter benthic communities through modification of abiotic factors, with cascading effects on microalgae and invertebrate communities. Major plant effects were observed in all systems studied, but the magnitude of, mechanisms behind, and exact consequences of plant alterations depended on the particular combination of physical and biological stresses within the habitat along the marine to terrestrial continuum. Manipulation of plant cover and light regime, combined with natural abundance isotope studies in a mid-elevation salt marsh of Mission Bay, CA revealed how two dominant plants, *Spartina foliosa* and *Sarcocornia pacifica* (formally *Salicornia virginica*), regulate light, temperature, and moisture, thereby influencing the abundance of benthic diatoms and the relative importance of microalgal-feeding invertebrates.

Tamarisk (*Tamarix* spp.), normally a freshwater invader that has recently colonized the salt marsh in Tijuana Estuary, was studied in 3 marsh zones with mensurative benthic assessment techniques and stable isotope enrichment experiments. Results demonstrate that this plant has (1) impacted the mid-marsh environment most, (2) accelerated salt marsh succession towards a more terrestrial environment by creating drier, less organic-rich sediments and an altered macroinvertebrate community (decreased densities of gastropods and marine oligochaetes, more insects) and (3) entered the food web through a broad range of invertebrate consumers.

Using similar approaches, the ephemeral seagrass, *Ruppia maritima*, abundant in lagoons during periods of inlet closure, was also shown to play a key trophic role in structuring wetlands in southern California. Results of faunal characterization and isotope enrichment studies within San Dieguito Lagoon suggest that food webs in these environments are driven by detrital and epiphytic production. Increased representation of detritivores in *R. maritima* habitats relative to unvegetated mudflat appears linked to animal feeding preferences and the ability of consumers to utilize *R. maritima*. In summary, this research developed several experimental methods by which to isolate structuring mechanisms of vascular plants in wetlands and allowed us to make generalizations across abiotic gradients in salt marsh ecosystems.

CHAPTER I

INTRODUCTION

Background

Vascular plants in both marine and terrestrial ecosystems structure the ecosystems in which they reside. We can learn a lot about these structuring mechanisms by studying plants under different scenarios of change: wrack deposition, invasion, restoration, experimental manipulation, and altered flushing regimes. What changes in an ecosystem when one plant species replaces another? What changes when plant cover disappears completely? In investigating these questions, I first examined how they had been pursued in terrestrial systems and then I focused on answering these questions for coastal wetland ecosystems.

On land, the role of plants in altering the physical environment is relatively well-understood, and our knowledge includes the effect of plants on above- and below-ground biota. We have a reasonable mechanistic understanding of these effects (Table 1.1). Although vascular plants are recognized as a structuring force in marine benthic communities, a mechanistic understanding of how this occurs has not been completely developed. The overall goal of my thesis is to bridge the gap between descriptive and predictive understanding of how plants affect wetland sediment communities by illustrating the mechanisms by which the plants modify their ecosystems.

In terrestrial communities, vascular plants act as the major modifiers of the physical environment, provide primary energy and nutrient sources, and form most of the structural environment for other organisms. The dominant species of vascular plant differs for each ecosystem, but from an early point, scientists have recognized that these

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plants determine the conditions under which all remaining species exist (Clements 1936). Plants influence microhabitat conditions and nutrient supply for other organisms at different trophic levels by root penetration and by production of litter and photosynthetic products (Gillison et al. 2003, Swift and Anderson 1993, Angers and Caron 1998). In forested ecosystems, vascular plants control the amount of light reaching the soil surface and thus influence forest succession (Aubin et al. 2000). In addition, it is well-documented that large trees shade smaller understory plants and soil surfaces, reducing temperature, wind speeds, and rainfall (Purves et al. 1995).

Although the influence of plants in structuring ecosystems is acknowledged in early and modern work, a significant portion of research treats the above-ground and below-ground systems as separate compartments in isolation from each other. Terrestrial literature mentions the need to understand the linkages between above- and below-ground biota (e.g. Hooper et al. 2000, van der Putten et al. 2001), and researchers have recently begun addressing this gap (Table 1.1). For example, Bardgett et al. (1998) demonstrate that plant herbivory affects the soil biota and decomposer food web by an alteration of root structure, carbon allocation, and nutrient supply. Work in grasslands also indicates that variation in plant cover because of various factors (herbivory, cutting, complete removal, conversion to agriculture) can affect abiotic parameters and thus control soil biota abundance and diversity (e.g. Ledeganck et al. 2003, Moon and Stiling 2002, Blomqvist et al. 2000). These changes in the belowground community also influence the success, abundance and diversity of the aboveground plant community and thus complete the feedback loop and influence ecosystem functioning (Setälä 2000, Setälä 2002). Although some marine work addresses the link between above- and belowground biota

(Snelgrove et al. 2000, Smith et al. 2000), work in the marine realm and specifically in salt marshes lacks a mechanistic understanding and research focus on the topic.

The marine literature does address the role of organisms as foundation species (Dayton 1975) and as ecosystem engineers (Jones et al. 1994, Crooks 2002). Familiar examples include kelp forests, mussel beds, seagrass meadows and coral reefs (Bruno and Bertness 2001). Research on marine intertidal systems also demonstrates that vascular plants have a dominant influence within their communities. Specifically, the presence of plants in coastal wetlands affects ecosystem-level processes such as hydrology, sedimentation rates, and nutrient cycling (Bertness 1988, Leonard and Luther 1995, Zipperer 1996, Levin and Talley 2000) (Table 1.2). Plants regulate marsh ecosystems directly through carbon and nutrient inputs and through 3-dimensional structure regulation of resources including nutrient filtering (Valiela et al. 2001). Plant shoots and detrital material partially fuel the salt marsh food web (Armstrong 1978, Peterson et al. 1985, Levin and Talley 2000). In addition, vascular plants stabilize the sediment and modify the amount and quality of light reaching the sediment. This light modification indirectly affects soil properties, such as temperature (Gallagher 1971, Bertness and Hacker 1994, Levin and Talley 2000) and algal growth (Lüning 1980, Seliskar et al. 2002). Critical salt marsh functions (such as nursery habitat provision, coastal stabilization, runoff filtration, and trophic support) are directly and indirectly tied to the presence of vascular plants (Gleason et al. 1979, Warren and Neiring 1993). Yet, the exact role of these plants in modifying the benthic environment and the consequences for sediment fauna are not well understood (Table 1.2).

Changing plant cover is one of the main sources of spatial heterogeneity in Pacific

coast salt marshes and can influence the abundance and diversity of benthic invertebrates (i.e. Costa and Davis 1992, Scatolini and Zedler 1996) (Table 1.2). Shifts in vegetation composition can cause large-scale ecosystem changes due to influence on soil characteristics, geomorphology, biogeochemistry, regional climate, and activity and distribution of other organisms (Eviner and Chapin 2003). Anthropogenic influences (e.g. development, human-mediated invasion) have demonstrated effects on benthic infaunal diversity in salt marshes, and certain disturbances can serve as large-scale experiments which advance an understanding of plant and benthic biota interactions. Specific examples of this disturbance include wrack deposition, changing flushing regimes (Zedler et al. 2001), invasion (Ayres et al. 2004, Neira et al. 2005), and restoration (Levin and Talley 2002), which are all known to alter the distribution of vascular plants in California wetlands.

Changes in coastal salt marsh and tidal flat ecosystems, such as creation or restoration of wetlands, large-scale invasions, or altered flushing regimes, provide an unprecedented opportunity to examine the factors influencing succession on much larger scales than might otherwise be possible. A major function of California salt marshes is trophic support for shellfish, fish and birds. Thus, the monitoring of trophic functions (food web architecture and complexity) helps us to understand temporal changes in ecosystem functioning of wetlands. I have used two approaches for addressing questions of trophic changes: (1) use of natural abundance, stable isotopic signatures to examine food web structure, and (2) isotopic enrichment experiments to trace the consumption of labeled vascular plant detritus. In **Chapter II**, I have combined plant and animal monitoring following manipulation of plant cover with natural abundance signatures

(δ^{13}C and δ^{15}N) of primary producers and lower consumers to identify changes in the base of the food web and animal trophic groups and to identify trophic complexity in different plant cover situations. Isotope enrichment experiments provide direct information about animal food sources and about trophic shifts in feeding mode. In **Chapters IV** and **VI**, I have traced the role of plant detritus in wetland food webs with isotope enrichment experiments. The results document the effectiveness of stable isotopes as a tool for evaluating trophic function and help us understand the successional trajectories for invertebrates and algae (and the associated food webs) in multiple wetlands through southern California.

Objectives

The overall objective of my thesis research was to develop a conceptual understanding (and model) (Figure 1.1, Table 1.3) of plant-benthic interactions in southern California wetlands. This model can be articulated as a series of hypotheses about the effects of altered light regime and aboveground plant structure. In my thesis research, I tested the hypotheses that changes in light regime due to loss of the plant canopy would directly alter (1) abiotic sediment properties such as redox potential, porewater temperature, porewater salinity, water content, (2) sediment properties such as grain size and organic matter content, (3) algal community composition, and (4) infaunal community parameters such as species richness, abundance and community composition. Additionally, I hypothesized that loss of the plant canopy could indirectly affect the infaunal community through (1) changes to the structure and composition of algal community or (2) changes to the abiotic parameters that make the soil environment more harsh.

This model was tested in three different southern California wetland systems that are subject to change: (1) a salt marsh in Mission Bay, CA (USA) where one native species, *Salicornia spp*. (pickleweed), is slowly replacing another, *Spartina foliosa* (Pacific cordgrass) and where restoration activities are underway; (2) a large estuary reserve (Tijuana River, CA, USA) where a renown riparian invader *Tamarix ramosissima* (tamarisk or saltcedar) has made its first full-scale appearance in a salt marsh; and (3) a lagoon in Del Mar, CA (USA) where episodic inlet blockage leads to loss of flushing and blooms of the seagrass, *Ruppia maritima* (widgeongrass). By addressing similar questions about plant effects in three systems and with plants of different architectures, I examined whether specific mechanistic plant-benthos interactions and processes are pervasive across systems, disturbance forms, or species.
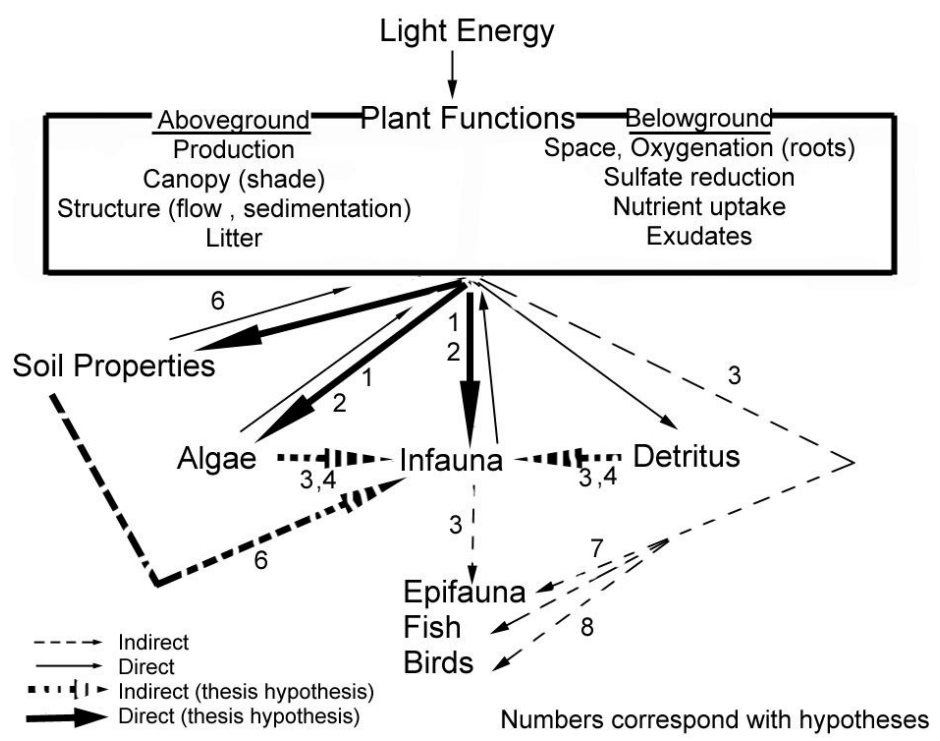
Figure 1.1: Plant canopy – benthos interaction model with mechanistic hypotheses (1-8) identified

Significance

Wetland systems are ideal for examining the forces that structure natural communities (Bertness and Yeh 1994). They have simple vascular plant communities with a relatively low diversity of species. Sharp physical gradients exist in intertidal habitats that allow detailed examination of abiotic factors that structure communities. Effects of plant community disturbance on abiotic sediment properties and on positive interactions between different plant species are well-documented (Bertness 1988, Bertness and Yeh 1994, Seliskar et al. 2002) as are ecosystem-level consequences of these disturbances. However, responses of below-ground invertebrates are less well known or in some cases, completely unaccounted for.

In addition to being ideal systems due to their structure, understanding how wetlands function is imperative to effectively managing them. A management strategy for wetland loss is restoration; a management strategy for invasion is eradication; a management strategy for coastal lagoons is construction of permanent jetties. Yet, the efficacy of all of these strategies remains uncertain. Existing studies reveal that generally, vascular plants exert structuring influence on the associated edaphic environment and macroinvertebrate assemblages with potential consequences for ecosystem functioning (Tables 1.2, 1.4, 1.5). Understanding how vascular plants affect the associated benthic community and the mechanisms driving these effects will provide valuable information for the conservation and management of these systems.

Due to the rapid rate of wetland decline worldwide, the time to ask these questions is now. Destruction of wetland habitat has significantly reduced the amount of wetlands across the country. During the pre-settlement era, the United States contained

approximately 390 million acres of freshwater and marine wetlands; 50% of this wetland area was lost between 1790 and 1980 (Dahl 1990). Individual state statistics reflect this trend; for example, in the Mississippi Delta, 100 km^2 of wetlands are lost per year (Day et al. 2000). Here in California, less than ten percent of the original area of coastal wetlands remains (Schoenherr 1992). In addition to loss of actual land area, wetlands are threatened by non-native species invasions that can also change plant cover and the structural characteristics that define the ecosystem itself (Vitousek 1990, Ruiz et al. 1999, Crooks 2002). The ecosystem-level consequences of this wetland reduction, especially in a low-diversity system such as a salt marsh, are unknown.

Scope of the dissertation

Restoration and changes in hydrology affect the distribution of the two dominant plant species in southern California marshes, *Spartina foliosa* and *Salicornia* spp.. Certain plant species, including Pacific Cordgrass, *Spartina foliosa*, cannot survive unless regular ocean flushing occurs (Bradshaw 1968, Zedler et al. 1992). Thus *Spartina foliosa* is absent from most lagoons that close periodically or from embayments where ocean flushing is restricted. When this species disappears, the endangered clapper rails that nest in stands of *Spartina* also disappear. It is not known whether there are other *Spartina*-dependent species whose distribution might be regulated by ocean flushing in this way. Polychaetes, molluscs and peracarid crustaceans are more common in better flushed or lower elevation *Spartina*-vegetated sediments, while insects and oligochaetes dominate *Salicornia*-vegetated habitat (Levin et al. 1998, Talley and Levin 1999, Levin and Talley 2000). In **Chapter II**, using clipping (structural) and light (shading) manipulations in two salt marsh vegetation zones (one dominated by *Spartina foliosa* and

one by *Salicornia virginica*), I hypothesized that both *S. foliosa* and *S. virginica* exert influence on abiotic sediment properties and thus have cascading impacts on the benthic algal and animal community.

<div align="center">**Invasion**</div>

Invasions by introduced plants are one of the most serious threats to global biodiversity today (e.g. - Heywood 1989, Lonsdale 1999, Gaskin and Schaal 2002). Although invasion is a natural process, the rate and mechanisms by which species are transported are anthropogenically altered, causing invasions to become a major conservation concern. Invasion affects all ecosystems, but the rate of invasion is increasing most quickly in wetlands (Posey 1988, Ruiz et al. 1997).

This thesis examines the consequences of *Tamarix* spp. invasion into Tijuana River National Estuarine Research Reserve (TRNERR). Considered one of United States' worst invaders (Stein and Flack 1996), tamarisk or salt cedar (*Tamarix* spp.) is an aggressive, woody invasive plant that has become established over 1.5 million acres of floodplains, riparian areas, and freshwater wetlands in the western United States (Stenquist 2000). Native to Eurasia and Africa, tamarisk was first introduced into North America in the early 1800s by nurserymen (Di Tomaso 1998). The westward spread of tamarisk was facilitated by use as windbreaks, shade cover, erosion control or ornamental plants (Neill 1985). The high intertidal, native pickleweed marsh of the TRNERR now supports dense stands of these salt-tolerant plants, which convert the salt marsh from a succulent-dominated canopy of less than 1 meter to a landscape dominated by stands of woody trees that can grow to over 3 meters tall. This invasion is described in **Chapter III**.

The effects of tamarisk invasions have been well-documented for stream riparian areas and include local alterations to the chemical and physical conditions as well as larger-scale effects of the entire invaded ecosystem (Table 1.4). Previous invasions in freshwater wetlands and riparian areas demonstrate that tamarisk increases salt deposition under the plants, decreases water velocity, and increases sedimentation while also causing declines in the water table due to its extremely high rate of evapotranspiration (from 0.1 – 0.4 cm per day) (i.e. Davenport et al. 1982) (Table 1.4). As a result of changes in local water tables, channel width reductions have occurred, causing a transformation of rivers away from natural desert riparian systems (Lovich et al. 1994, Lovich and de Gourvenian 1998, Lovich and Meyer 2002). Possibly as an indirect effect of the abiotic changes, *Tamarix*-invaded stands also support different plant communities compared to non-invaded stands (Carmen and Brotherson 1982, Griffen et al. 1989).

Most research indicates that areas invaded by tamarisk are much less valuable to wildlife, with the exception of honeybees and two species of doves (Brown and Trossett 1989, Frasier and Johnsen 1991); density, diversity and species richness of many organisms decrease in invaded areas (Kerpez and Smith 1987, Cohan et al. 1978). Yet, because the TRNERR invasion is the first foray of tamarisk into the marine realm, little is known about the impacts of tamarisk invasion into salt marshes. We hypothesized that tamarisk in the salt marsh will affect physical resources which could translate into community-level effects for marsh biota (Stevens 2000, Crooks 2002). As a short invasion note, **Chapter III** documents an extensive incipient invasion and modification of coastal salt marsh habitats by multiple species of trees and shrubs in the genus *Tamarix.* Extending the conclusions of **Chapter III**, **Chapter IV** uses a complete

randomized block design within three habitats to test the influence of tamarisk on abiotic environmental factors and the biotic community and to predict that this invasion hastens natural succession processes ("terrestrialization") along an elevation gradient. Utilizing litter dynamics techniques and stable isotope enrichment experiments, **Chapter V** evaluates the trophic consequences of invasion by tamarisk on detrital food chains in the TRNERR salt marsh.

Inlet status

The southern California coast is dotted with small coastal lagoons and embayments. Due to the Mediterranean climate of southern California, these lagoons have episodic freshwater input linked to rain events and receive significant inputs of energy, nutrients and organisms from the sea. While large embayments typically remain permanently open, smaller lagoons experience periodic closures which result from natural or anthropogenic activities that cause increased sediment deposition from the upland watershed (Conners et al. 1991, Callaway 2001) or from division of wetland habitats by roads and railroads (West 2001). Additionally, coastal buildup of sand or inland erosion of sediments that are transported down river can seal up openings to the ocean (Conners et al. 1991, West 2001). When lagoons are closed for extended periods, key species with life cycles dependent on ocean flushing may disappear. Once a lagoon is breached, the plants that thrived in closed water conditions (higher temperature, lower salinity) may also disappear. Loss of particular plant species, especially seagrasses, may cause loss of associated invertebrate communities and change in food web structure as many of these species structure their environments (Table 1.5).

Ruppia maritima L.. (widgeongrass) is an example of a plant species that thrives

in the closed lagoon state. It is a ruderal or opportunistic species with a broad environmental tolerance and a reportedly cosmopolitan distribution (Kantrud 1991, Johnson et al. 2003). Typically, *R. maritima* exists in marginal seagrass habitats or as a secondary species where other seagrasses dominate (Lazar and Dawes 1991, Johnson et al. 2003). *R. maritima* L. thrives in warmer temperature (upwards of 25 ºC) (Evans et al., 1986, Johnson et al. 2003) and in lower salinity water (Kantrud 1991, Koch and Dawes 1991). In absence of these warmer, more saline conditions, *R. maritima* frequently disappears (Williams et al. 2003).

In 2002, the San Dieguito Lagoon (SDL) inlet closed for 8 months. During this period of low salinity and increased temperature, *Ruppia maritima* became abundant, and large bivalves and gastropods disappeared from the lagoon (Levin et al., unpublished data). In Oct. 2002-March 2003, the SDL was breached after its extended closure. The breach initiated tide-induced fluctuations in salinity, temperature and dissolved oxygen. Tidal flats were dominated by *Ruppia maritima* in Oct. 2002 but were largely unvegetated (although covered with *Ulva* spp.) post-breach in late October and again in March 2003. **Chapter VI** explores the hypothesis that changes in the seagrass cover (*Ruppia maritima*) will affect the associated algal and infaunal communities and thus affect pathways of trophic support.

Chapter VII integrates the insights of each of the previous studies and compares among systems, among different architecture plants, and along a marine to terrestrial continuum. These comparisons extend the research beyond species-specific conclusions and thus advance our general understanding of the structural and mechanistic role of plants in wetland ecosystems.

Table 1.1: Effects of terrestrial vegetation on infauna in published literature.

Effects of Vegetation Alteration	Organisms Studied	Habitat type	Reference
Species number and density increased with increase in plant functional groups, Evenness was unaffected	Testate amoeba	Synthesized grasslands	Ledeganck et al. 2003
Plant species nor functional group diversity of plants had any effect, Legumes had lower root biomass, higher inorganic N and nitrate concentrations, and higher density and diversity of earthworms than grasses	Nematodes, Earthworms	Grassland Germany)	Gastine et al. 2003
Departures from historical disturbance (frequent fires, grazing) may result in greater abundances of introduced earthworms	Earthworms	Prairie (KS)	Callaham et al. 2003
Climate and soil parameters were significantly correlated with biodiversity	Nematodes	6 types of European grasslands	Eckschmitt et al. 2003
Correlations of species richness with mean canopy height, woody plant basal area, and plant species richness	Termites	Tropical forest (Sumatra)	Gillison et al. 2003
Different land uses affected the vertical distribution and dominant genera	Bacterivorous nematodes	Grasslands (Europe), Cropland (China), Desert (Israel)	Ou et al. 2005, Liang et al. 2005, Hanel 2003, Ilieva-Makulec 2000, Yeates et al. 2000, Sohlenius and Sandor 1987
Increased salinity increased density while reduction of parasitism had no effect. Higher densities of stem-borers reduced density of planthoppers	Salt marsh planthopper (*Pissonotus quadripustulatus*)	Salt marsh (Florida)	Moon and Stiling 2002

Table 1.1 (continued)

Effects of Vegetation Alteration	Organisms Studied	Habitat type	Reference
Abundance changed with plant type (i.e. mites greatest in shrublands, predators increased from grasslands to shrublands)	Collembola, Predacious mites, Spiders, Ants, Centipedes	Forest, Grassland prairies, Shrubland (Canada)	Ferguson 2001
Mass of soil organic layer (related to plant canopy composition and microbial food web) is major determinant of density	Collembola, Acarina	Deciduous and rainforests in Asia	Takeda and Abe 2001, Takeda 1987
Abundance of all organisms (except fungus feeding nematodes) increased steadily with increasing defoliation.	Omnivorous and fungus-feeding nematodes, echytaeid oligochaetes,	Greenhouse experiment with grassland species	Mikola et al. 2001a
Taller plants increase ant digging and mound formation, Decreases abundance of nematodes, Increased activity and mounding changes plant community	Yellow ants (*Lasius flavus*), Nematodes	Grassland	Blomqvist et al. 2000
Species abundance of belowground biota is correlated with diversity of plant species	Collembola, Acarina, Diplopoda	Artic-alpine	Rusek 2000
Changes in C allocation and root structure result in changes in invertebrate community, dependent on system	Microbial, Nematode	General	Bardgett et al. 1998
Conversion of land to agriculture reduces the diversity (partially due to differences in plant and litter biomass)	Collembola	Prairie (MI, IL)	Brand and Dunn 1998
Cultivated land maintains high diversity	Nematodes	Range in latitude of cultivated lands	Boag and Yeates 1998
Disturbance decreases species richness and abundance	Termites	Forest (East Malaysia)	Eggleton et al. 1997
Conversion of land to agriculture reduces the diversity	Termites	Deciduous forest (Cameroon)	Bloemers et al. 1997

Table 1.1 (continued)

Effects of Vegetation Alteration	Organisms Studied	Habitat type	Reference
Lower species richness and a lower number of native species in undisturbed ecosystems	Earthworms	Mexico, Peru, and India (Peruvian Amazonia)	Fragoso et al. 1997
Agricultural improvement decreases diversity	Nematodes	Pastures (New England)	Yeates and King 1997
Disturbance of soil through tillage reduces or elevates diversity of macrofauna but does not affect microfauna		Literature synthesis - Northern Swedish boreal forest zone	Wardle 1997
Decline in diversity (S, H', E) with vegetational diversity	Ants (ground-foraging)	Coffee plantations (Costa Rica)	Perfecto and Snelling 1995
Increase in abundance due to grazing (possibly due to increase of C from root death)	Bacterial-feeding nematodes, Root-feeding nematodes	Prairie Yellowstone)	Merrill et al. 1994
Increases in abundance following grazing as linked to availability of microbial food resources	Collembola (*Onychiurous procampatus*)	Semi-natural upland grasslands (UK)	Bardgett et al. 1993a,b,c
Disturbance from land use changes (chemical inputs, high human management) decreases species richness and abundance	Nematodes	Agricultural meadows (MI)	Freckman and Ettema 1993, Wasilewska 1997
Decline in diversity	Scarabaeid beetle	Coffee plantations	Nestel et al. 1993
Short-term increases in C input causes rapid increases in microbial communities		Barley field	Christensen et al. 1992
Diversity relocates under shrubs		Grasslands	Virginia et al. 1992

Table 1.1 (continued)

Effects of Vegetation Alteration	Organisms Studied	Habitat type	Reference
Disturbance of soil through tillage reduces abundance and diversity	Earthworms (Lubricid)	Farmland (New Zealand)	Springett 1992
Conversion of land to agriculture reduces the diversity	Nematodes		Lavelle and Pashanasi 1989
Increase in density on grazed or mowed prairie, Microarthropods were sensitive to C or N additions. Earthworms (native and introduced) and nematodes increased with C, not N.	Microarthropods, Earthworms, Nematodes	Grassland (Kansas)	Seastadt et al. 1988
Biomass reduced by mowing	Soil cicada nymphs	Tallgrass prairie	Seastadt 1985
Abundance increased in heavily-grazed areas versus ungrazed areas, Grazed areas facilitates gazing by belowground herbivores	Bacterial-feeding nematodes, Root-feeding nematodes	Prairie (SD)	Ingham and Detling 1984
Abundance reduced by heaving clipping	Bacterial-feeding nematodes	Glass house - blue gamma grass	Stanton 1983
Abundance increased in heavily-grazed areas versus ungrazed areas	Bacterial-feeding nematodes	Prairie (North America)	Smolik and Dodd 1983, Freckman et al. 1979
Reduced abundance in overgrazed areas by cattle and sheep	Nematodes	Prairie (North America)	Smolik and Lewis 1982, Hutchinson and King 1980

Table 1.2: Effect of plants on macroinvertebrate infauna in coastal salt marshes as documented in published literature

Effects of Vegetation Type on Infauna	Organisms Studied	Habitat Type	Reference
Epifauna specialists were affected by plant removal, whereas generalists were not. Abundance was significantly correlated with plant biomass, predation pressure, sediment changes on small spatial scales and freshwater on large scales	Benthic macro invertebrates	*Spartina alterniflora* marsh (vegetated *vs.* unvegetated) (Brazil)	Pagliosa and Lana 2005, Lana and Guiss 1991
Vegetated areas buffer harsh physical conditions (high temperature, soil hardness, organism heat stress and dehydration) via shading and provision of predation refugia, thus increasing abundance	Benthic macro invertebrates	High marshes and salt pans (GA, Argentina)	Nomann and Pennings 1998, Bortolus et al. 2002
With scarce plant cover, the macrofaunal assemblage had a lower proportion of oligochaetes and a higher proportion of insect larvae compared to assemblage in the mature marsh. As the vegetation expanded and the created marsh matured, the percentage of insect larvae decreased, and the percentage of polychaetes and amphipods increased.	Benthic macro invertebrates	Restored marsh system versus natural marsh system	Levin and Talley 2002, Moseman et al. 2004
Created *Salicornia* marshes had assemblages in between natural *Salicornia* marshes and natural *Spartina* marshes	Benthic macro invertebrates	*Spartina-* vs. *Salicornia-*dominated (CA)	Talley and Levin 1999
Species composition were different between marshes; More enchytraid oligochaetes in Pacific with more polychaetes and tubificid oligochaetes in Atlantic	Benthic macro invertebrates	*S. alterniflora* (Atlantic) vs. *S. foliosa* (Pacific) salt marshes	Levin et al. 1998
Abundance and species composition were affected by salinity and energy, not vegetation zone.	Polychaetes	*S. alterniflora* marsh vs. mangroves (Brazil)	Lana et al. 1997
Development of infaunal community corresponds with replacement of *S. alterniflora* with *S. robustus*	Benthic macro invertebrates	3 created marshes of different ages (SC)	Posey et al. 1997

Table 2.1 (continued)

Effects of Vegetation Type on Infauna	Organisms Studied	Habitat Type	Reference
Spartina marsh food web is more complex than in *Salicornia* marsh. *Spartina* was the major food source for fish & macroalgae for invertebrates; in the other system, algae, *Salicornia*, & POM	Fish, invertebrates	*Spartina*-dominated vs, *Salicornia*-dominated (CA)	Kwak and Zedler 1997
S. foliosa supports greater densities of polychaetes while *Salicornia spp.* supports more gastropods, isopods and tubificid oligochaetes	Benthic macro invertebrates	*Spartina*-dominated vs, *Salicornia*-dominated (CA)	Levin et al. 1997
Higher density and greater trophic diversity in *S. virginica* marsh	Benthic macro invertebrates	*Salicornia virginica* marsh, *Schoenoplectus robustus* marsh (NC)	de Szaley and Resh 1996
Food webs differ, Reduced species richness and abundance, skewed population toward young animals, and dominance by species with early reproductive maturity with reduced flushing	Fish, benthic macro invertebrates	open estuary (Tijuana) vs. usually closed estuary (Los Penasquitos)	Nordby and Zedler 1991
Higher densities in *Juncus* marshes attributed to lesser root densities	Carolina marsh clam (*Polymesoda caroliniana*)	3 tidal marshes (*S. alterniflora, S. cynsuroides,* and *Juncus roemerianus*) (NC)	Capehart and Hackney 1989

Table 1.3: Hypotheses from Model of Plant–Benthos Interactions
(*Hypotheses to be tested in dissertation*)

Number from Figure 1.1	Alternative Hypotheses	Explanation
1	*Changes in light regime or structure due to plant canopy loss will alter abiotic or algal properties.*	*Abiotic properties (redox potential, light levels, temperature, salinity, water content), Algal properties (biomass, community composition)*
2	*Changes in aboveground plant structure due to plant removal will alter the infaunal community directly.*	*Plant Structure / Water Flow*
3	*Changes in algal community or detritus production (as food sources) will alter the infaunal community which will propagate through to higher trophic levels.*	
4	*Changes to the algal mat structure will alter the infaunal community*	*Algal Structure (refuge from predation, abiotic alterations)*
5	Alterations to the infaunal community will change feedback loops to plants or change existing community.	Feedback Loop to Plants
6	*Changes in light regime or structure will affect soil properties.*	*Soil Properties (grain size, organic matter)*
7	Changes in light regime and structure will affect epifauna and fish indirectly through loss of refuge from predation and loss of egg substrate	Effect on Epifauna, Fish
8	Changes in light regime and structure will affect birds indirectly through loss of refuge from predation, loss of nesting	Effect on Birds (predation refuge, nesting site)

Table 1.4: Effects of *Tamarix* spp. on native habitat as documented in published literature.

Effect of Tamarisk	Habitat Type	Location	Reference
Decreased densities of native pupfish, exotic snails and increased density of exotic crayfish due to increased shading and reduced algal cover	Freshwater stream	Mojave Desert, NV	Kennedy et al. 2005
Caused food web shift from autochthonous production to allochthonous leaf litter, Altered decomposition through influence on litter quality	Freshwater stream	Mojave Desert, NV	Kennedy and Hobbie 2004
Species richness of birds did not suffer provided structural diversity of plant community remains unchanged by invasion	Freshwater river	Muddy River, NV	Fleishman et al. 2003
Reduces density of cicadas due to lack of heterogeneity in canopy	Freshwater lake	Bill Williams River, AZ	Ellingson and Andersen 2002
Decreases water supply and lowers local water tables which has put western pond turtles at risk	Freshwater river	Mojave River, CA	Lovich and Meyer 2002
Alters food web due to altered food quality of leaf litter, Different macroinvertebrate composition (lower α-diversity), Lowered arthropod abundance	Freshwater Stream	Wet Beaver Creek, AZ	Bailey et al. 2001
Effect on arthropod uncertain although an abundant surface-active arthropod community is present under tamarisk	Freshwater river	Rio Grande, NM	Ellis et al. 2000
Increased sedimentation, Decreases in width and depth of water channels	General	n/a	Zaveleta 2000
Traps sediments, Reduces channel width of rivers, Makes sediment more xeric, Lowers water tables, Alters riparian systems from ambient	Freshwater river	Mojave River, CA	Lovich et al. 1994, Lovich & de Gouvenain 1998

Table 1.4 (continued)

Effect of Tamarisk	Habitat Type	Location	Reference
Diverse and abundant arthropod community	Freshwater	Bosque del Apache	Mund-Meyerson 1998
Decreases forest litter and litter production, Available litter decreases after flooding compared to native habitats	Freshwater river	Rio Grande, NM	Ellis et al. 1998
Reduces native woody and herbaceous plant cover	Freshwater river	Mojave River, CA	Engel-Wilson and Ohmart 1978, Hughes 1993, Lovich et al. 1994, Weeks et al. 1987
Reduced avian density and diversity	Freshwater river	Lower CO River	Anderson et al. 1997, Cohan et al. 1978, Shrader 1977
Gophers do utilize tamarisk in mounds and possibly as food	Freshwater river	Owens Valley, CA	Manning et al. 1996
Equal water use to other native species under ample water availability. Lowered water table.	Freshwater Stream	Virgin River, NV	Sala et al. 1996
Species richness of birds did not differ, but composition varied	Freshwater river	Rio Grande, NM	Ellis 1995
Decreases in small mammal abundance (Increased after eradication)	Freshwater river	Lower CO River, AZ	Andersen 1994
Outcompetes native plants due to dripping salt from lateral roots, Depletes surface water	General		Duncan 1994

Table 1.4 (continued)

Effect of Tamarisk	Habitat Type	Location	Reference
Reduces density of native birds and reptiles, Shifts understory vegetation to salt-tolerant plants, Reduces diversity of understory plants	Freshwater river	Finke River, Australia	Griffen et al. 1989
Equal or higher avian density in tamarisk invaded stands	Freshwater river	Upper CO River	Brown 1987
Equal or higher avian density in tamarisk invaded stands	Freshwater river	Rio Grande, TX	Hunter et al. 1985, 1988
Stabilize soils and desalinize soil through salt excretion	Freshwater lake	Sebkhet Kelbia, Tunisia	Goldsmith and Smart 1982
Depletes surface water, Changes plant community to rabbit-footgrass (ephemeral species) from saltwort, Makes infested sites more xeric	Freshwater lake	Utah Lake, UT	Carmen and Brotherson 1982
Stabilizes sediment, making stream channels immobile and frequently narrower with increased water flow	Freshwater river	various areas through SW United States	Graf 1978, Friederici 1995, Kerpez and Smith 1987
Lowers water tables due to increased water use relative to native plant species			Van Hylckama 1970

Table 1.5: Effects of *Ruppia* and other seagrasses on infaunal communities as documented in published literature.

Effects of Vegetation	Organisms Studied	Habitat Type	Reference
Abundance of shredders was significantly related to biomass of *R. cirrhosa*	Crustaceans (*Gammarus aequicauda, Idotea chelipes, Sphaeroma hookeri*)	Lagoon (Tunisia)	Cassagranda et al. 2006
Birds consume *R. maritima* in all seasons	Flamingos and waterfowl (coots, ducks)	Fish ponds (SW Spain)	Rodriguez-Perez and Green 2005
Greater abundance of fish in *R. maritima* beds	Pipefish (Syngnathidae)	Lagoon (S. Brazil)	Garcia et al. 2005
Abundance increased in vegetated vs. non-vegetated areas (*Potamogeton pectinatus* L., *R. cirrhosa*)	Gastropod (mud snail, *Hydrobia ventrosa*)	Lagoon (Tunisia)	Cassagranda et al. 2005
Abundance increased at localities with submerged vegetation (*R. maritima*)	Fish (mojarras, Gerreidae)	Lagoon (Mexico)	Castillo-Rivera et al. 2005
Species richness and abundance increased in clear, macrophyte-dominated wetlands (*Ruppia, Lepilaena, Lamprothamnium*)	Macroinvertebrates	Lakes (coastal, SW Australia)	Strehlow et al. 2005
Sediment characteristics (oxygen, grain size, compaction) controlled structure of polychaete community more than seagrass species (*R. cirrhosa* vs. *Cymodocea nodosa*)	69 taxa of polychaete species	Bay (Canary Islands)	Brito et al. 2005
Greater abundance of shrimp in *R. maritima* and *Halodule wrightii* beds	4 shrimp species (*Farfantepenaeus* spp.)	Lagoon (Mexico)	Perez-Castaneda and Defeo 2004
Multiple covarying factors controlled abundance and composition of seagrass communities, not just presence/absence	8 decapod and 4 fish species	Bay (NC)	Hovel et al. 2002

Table 1.5 (continued)

Effects of Vegetation	Organisms Studied	Habitat Type	Reference
Different abundance and composition on *Ruppia* vs. macroalgae and *Syringodium filiforme* seagrass, Lower abundance of most epifauna	Motile epifauna (dominated by pericarid crustacea)	Bayou (FL) - macroalgae vs. seagrass	Knowles and Bell 1998
Higher densities in vegetated areas, Certain crustaceans higher abundance in salt marsh	Nekton (crustaceans, fishes)	Estuary (TX): salt marsh, seagrass, unveg	Rozas and Minello 1998
Diversity lowest in *Ruppia* and exotic milfoil, Total abundance was higher in *Ruppia* and milfoil, Perhaps due to spatial and temporal differences in resource utilization	Fish	Bay (LA)	Duffy and Baltz 1998
Abundance inside and outside the *Ruppia* bed changed according to species, Low water transparency and lack of predation determined structure of assemblages	Fish	Lagoon (Patos, Brazil)	Garcia and Veira 1997
Densities increased with *Ruppia magacarpa* cover due to protection from predation and food	Macroinvertebrates	Lagoon (Australia)	Platell and Potter 1996
Different composition on *Ruppia* vs. *Potamogeton pectinatus*, Epiphytic biomass less on *Ruppia*, Benthic biomass greater beneath *Ruppia*, Indirect effects of salinity (plant loss) affects invert biomass	Epiphytic and benthic macroinvertebrates	Oligo- and mesosaline lake (WY)	Wollheim and Lovvorn 1996
Lowest abundance in *Ruppia* pools (due to low DO at night?)	Macroinvertebrates	Marsh complex (MA)	Heck et al. 1995
Pintails consumed primarily Chironomidae and *Ruppia* nutlets	Water fowl	Evaporation ponds (CA)	Euliss and Jarvis 1991
Two macroinvertebrate species graze on *R. cirrhosa*, contributing to microbial colonization and decomposition	Amphipods (*Gammarus aequicauda, Sphaeroma hookeri*)	Lab experiment	Menendez et al. 1989, Menendez & Comin 1990

Table 1.5 (continued)

	Organisms Studied	Habitat Type	Reference
Prawns fed with Ruppia showed the poorest growth, Survival was 65% with decaying and 59% with live *Ruppia*	Giant tiger prawn (*Penaeus monodon*)	Lab experiment	Primavera and Gacutan 1989
Fish predation was not effective on invertebrates in the *Ruppia* due to physical complexity of environment	Fish, macro benthic and epiphytic invertebrates	Pond (NC)	Gilinsky 1984
Birds consumed *Ruppia cirrhosa* (up to 20% of biomass consumed) and associated invertebrates. Crustaceans also consumed decomposed *Ruppia*.	Coot (*Fulica atra* L.), Flamingo, Amphipods (*Gammarus* spp.), Isopods	Brackish pond (TX)	Verhoeven 1980
Not *Ruppia* Specific (General Seagrass)	**Organisms Studied**	**Habitat Type**	**Reference**
Epiphytes on *Posidonia oceanica* L. are essential component of diet for urchins	Urchins (*Paracentrotus lividus*)	Ocean (NW Mediterranean)	Tomas et al. 2006
Dominant consumer species (listed next column) grazed on *Zostera marina* and associated epiphytes while others (*Batillaria cumingii, Macoma incongrua, Rupitapes philippinarum, Pullucina pisidium*) did not indicate consumption of either	Gastropods (*Littorina squalida, Homalopoma sangarense*),	Inlet (Sea of Japan)	Kharlamenko et al. 2001
Densities were greater on mangrove roots surrounded by seagrass (*Zostera mucronata*) than patches without seagrass, Explained by greater recruitment to shaded areas	Spirorbid polychaetes (*Neodexiospira* spp.)	Mangroves (S. Australia)	Saunders and Connell 2001
Greater taxa diversity in vegetated *vs.* open water habitat, Bottom substrate type was an important determinant of abundance and biomass.	Macro benthic invertebrates	Lakes (FL)	Schramm and Jirka 1989
Similar composition on all macrophytes regardless of architecture, abundances varied by plant species, Species richness was higher and abundances were lower on seagrass vs. macroalgae	Epifaunal crustaceans	Subtropical seagrass meadow (FL)	Lewis 1987

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CHAPTER II

REGULATION OF BENTHIC ALGAL AND ANIMAL COMMUNITIES BY SALT

MARSH PLANTS: IMPACT OF SHADING

Abstract

Plant cover is a fundamental feature of many coastal marine and terrestrial

systems and controls the structure of associated animal communities. Both natural and

human-mediated changes in plant cover influence abiotic sediment properties and thus

have cascading impacts on the biotic community. Using clipping (structural) and light

(shading) manipulations in two salt marsh vegetation zones (one dominated by *Spartina*

foliosa and one by *Salicornia virginica*), we tested whether these plant species exert

influence on abiotic environmental factors and examined the mechanisms by which these

changes regulate the biotic community. In an unshaded (plant and shade removal)

treatment, marsh soils exhibited harsher physical properties, a microalgal community

composition shift towards increased diatom-dominance, and altered macrofaunal

community composition with lower species richness, a larger proportion of insect larvae

and a smaller proportion of annelids, crustaceans, and oligochaetes compared to shaded

(plant removal, shade mimic) and control treatment plots. Overall, the shaded treatment

plots were similar to the controls. Plant cover removal also resulted in parallel shifts in

microalgal and macrofaunal isotopic signatures of the most dynamic species. This

suggests that animal responses are seen mainly among microalgae grazers and may be

mediated by plant modification of microalgae. Results of these experiments demonstrate how light reduction by the vascular plant canopy can control salt marsh sediment communities in an arid climate. This research facilitates understanding of sequential consequences of changing salt marsh plant cover associated with climate or sea-level change, habitat degradation, marsh restoration or plant invasion.

Introduction

Vascular plants have major structuring roles in both marine and terrestrial ecosystems (Clements 1936, Bruno and Bertness 2001). On land, the role of plants in altering the physical environment is well-understood, and ecologists are working towards a detailed understanding of how plants affect the complete sediment system (e.g. Swift and Anderson 1993, Hooper et al. 2000). Although vascular plants are recognized as a structuring force in coastal benthic communities (Bertness 1991a,b, 1992, Snelgrove et al. 2000, Smith et al. 2000, Bortolus et al. 2002), a detailed mechanistic understanding of plant-animal relationships has not been developed, especially for salt marshes. For coastal wetlands, it is known that the presence of plants affects ecosystem-level processes such as hydrology, sedimentation rate, and nutrient cycling (Bertness 1988, Leonard and Luther 1995, Levin and Talley 2000). Plant shoots and detrital material partially fuel the salt marsh food web (Peterson et al. 1985, Levin and Talley 2000, Levin et al. 2006). In addition, vascular marsh plants modify the amount and quality of light reaching the sediment, thus affecting temperature (Gallagher 1971, Bertness and Hacker 1994) and algal growth (Lüning 1980, Seliskar et al. 2002). On a larger scale, critical salt marsh functions, such as nursery habitat provision, coastal stabilization, runoff filtration, and trophic support, are directly and indirectly tied to the presence of vascular plants

(Gleason et al. 1979, Warren and Neiring 1993).

Experimental work has shown that plant community disturbance affects abiotic sediment properties and positive interactions between different plant species (Bertness 1988, 1991a,b, 1992, Bertness & Callaway 1994). However, few studies have experimentally studied the responses of benthic algae and below-ground invertebrates to plant disturbance (Pagliosa and Lana 2005). Comparing a restored and an adjacent natural wetland system in southern California, Levin and Talley (2002) inferred the influence of vascular salt marsh vegetation on the rate and trajectory of macrofaunal recovery. They observed that during early succession when the marsh had little plant cover, the macrofaunal assemblage had a lower proportion of oligochaetes and a higher proportion of insect larvae as compared to the assemblage in the neighboring mature marsh. As the vegetation expanded and the created marsh matured, the percentage of insect larvae decreased, and the percentage of polychaetes and amphipods increased. Similar trajectories have been observed in other southern California systems (Talley and Levin 1999, Moseman et al. 2004). Our study was designed to experimentally identify the mechanisms behind the observed macrofaunal community changes and to test whether this trajectory occurs under small-scale disturbance scenarios.

Thus, we designed field manipulations of light levels and structure to explore the role of above-ground vegetation in determining environmental conditions, and algal and macrofaunal diversity. These manipulative experiments tested the hypotheses that (1) modification of plant cover would alter environmental conditions and microalgal assemblages, (2) these environmental and algal modifications would lead to changes in the abundance and composition of the macrofaunal community, (3) structure and light

removal would have differing effects, and (4) plant effects on algal and macrofaunal communities would be equivalent for the dominant grass (*Spartina foliosa*) and succulent (*Salicornia virginica*) species in southern California. We predicted that plant influence on benthos should be especially strong in the arid Mediterranean climate regime characteristic of southern California relative to wetter Atlantic systems, where much related research has been conducted (i.e. New England & Southeast, USA). Describing the functional role of plants in salt marsh ecosystems is crucial to ecological understanding and highly relevant to conservation issues associated with restoration, invasions, marine reserves and biodiversity maintenance.

Materials and Methods

The Mediterranean climate of southern California with mild, wet winters and warm, dry summers supports two dominant vascular plant species within the salt marsh environment; pickleweed (*Salicornia virginica*) and Pacific cordgrass (*Spartina foliosa*). *Salicornia virginica* dominates in mid-marsh habitat and under conditions of episodic inlet closure, while *Spartina foliosa* occupies the low marsh zone and requires regular flushing; it disappears in the absence of ocean water influx (Zedler et al. 1992). The research was conducted in the 6.5-ha Kendall Frost Mission Bay Marsh Reserve, an intertidal salt marsh in the NE corner Mission Bay, San Diego, CA (32° 47' 35" N, 117° 13' 00" W) where both plant species co-occur.

Experimental Design: To determine mechanisms by which plants influence sediments, algae and macrofauna, we conducted parallel experiments in adjacent *S. foliosa*- and *S. virginica*-dominated habitats. Within the marsh, eight experimental blocks were established in patches of *S. foliosa* (at least 90 percent cover) growing with

other mixed vegetation (*Salicornia* spp*., Batis maritima*), and eight blocks were

established in existing patches of *S. virginica* (again at least 90 percent cover). Three

different 1m^2 treatments were created within each vegetation type: (1) absence of plant

cover and structure (clipped, unshaded), (2) absence of plant structure (clipped, shaded),

and (3) control (unclipped, no shade manipulation). Hereafter, these will be referred to as

unshaded, shaded and control treatment plots, respectively. In the unshaded and shaded

treatment plots, all species present in the plot (*S. foliosa, S. virginica* etc.) were clipped at

the soil surface, leaving belowground biomass intact. These two treatments were

maintained by weekly clipping for the duration of the study (6 months). The clipped

plant roots continued to resprout and require clipping, indicating that the plants remained

alive belowground and suggesting limited decay of underground plant matter.

S. *foliosa* plant removal treatments were maintained from May 2002 until May

2003; *S. virginica* treatments were maintained from May 2004 until May 2005. Weekly

maintenance included removal of detrital material trapped on shade cloth and/or chicken

wire over treatments. Sampling (details discussed below) took place 3 mo. and 6 mo.

after establishment of the treatment plots. Plant habitat elevations, measured for each

plot using an automatic level (CST/Berger SAL series), were on average 0.3 m lower in

the *S. foliosa* plots (2.00 $\pm$ 0.03 m below mean low water) than in the *S. virginica* plots

(2.27 $\pm$ 0.15 m below mean low water).

Light measurements, made immediately prior to clipping in May, revealed that

natural plant cover reduced incident light by approximately 94% in *S. foliosa* patches

(94.1% $\pm$ 2.1%) and 85% in *S. virginica* patches (85.7% $\pm$ 5.0%) (*S. foliosa* > S.

virginica, χ^2=17.396, P<0.0001). Shaded treatments, designed to mimic light reduction,

had a set of four poles suspending a chicken wire frame and a 90% reduction shade cover

(two layers of 70% reduction shade cloth) over the plot. To equalize experimental

artifacts, unshaded and control treatment plots also had a set of four poles suspending

only chicken wire, allowing light to penetrate to the ground. Light measurements were

made on a cloudless day using a QSL – 100 Laboratory Quantum Scalar Irradiance Meter

(4pi sensor, Biospherical Instruments Inc.) in each replicate. Ambient light readings were

taken immediately preceding light measurements under the canopy, and all light readings

were an average of three measurements.

Measurement of abiotic and sediment properties: Within each treatment plot, soil

salinity of the top 0.5 cm ($\pm$ 1 psu) was measured weekly by squeezing porewater from

the sediment surface through a Whatman No. 1 qualitative grade filter onto a hand-held

salinity refractometer. Temperature ($\pm$ 0.1ºC) at 2 cm depth was measured weekly using

a portable Ingold Mettler-Toledo digital thermometer. Water content of the top 0.5 cm

was determined at 3 mo. and 6 mo. by weight loss after drying a known volume of

sediment (Buchanan 1984). Redox potential was measured at 3 mo. and 6 mo. at 1-cm

depth with a portable Mettler Toledo mV-meter. These mV readings were corrected to

the standard hydrogen electrode value by adding 207 mV (Giere et al. 1988). Redox

potential has been used to indicate the degree of oxygenation in wetland soils (Gambrell

and Patrick 1978) and is known to be influenced by wetland plant rhizomes (Lovell

2002). One sediment core (4.8 cm diameter x 6 cm) was collected within each treatment

plot at 3 mo. and 6 mo. for analysis of particle size and organic matter content using

methods of Neira et al. (2005). Belowground plant detrital biomass (dry mass) was

calculated by removing all plant detritus (> 300 μm) from macrofaunal cores (4.8 cm

diameter x 6 cm), drying the material at 60 ºC, and weighing it on an analytical balance.

Algae collection and analysis: In each treatment plot at 3 mo. and 6 mo., separate cores were taken for chlorophyll a (0.95cm^2 x 5mm) (a proxy for microalgal biomass) and for analysis of algal pigments by High-Performance Liquid Chromatography (HPLC) (0.56cm^2 x 5mm) to indicate microalgal functional group composition and diversity (Cariou-LeGall & Blanchard 1995). Once back in the laboratory, chlorophyll a was extracted with 90% acetone, and the concentration was determined spectrophotometrically (Plante-Cuny 1973). Pigment separation was conducted according to Janousek (2005). For HPLC data presented, detector outputs (mV) were converted to mass (ng, µg) of pigment using pigment-specific calibrations generated independently with purified pigment material (Janousek 2005).

Macrofauna sampling: At 3 mo. (August) and 6 mo. (November), macrofaunal cores were taken in each treatment plot using a cylindrical push core (4.8 cm diameter, 18.1 cm^2) inserted to a depth of 2 cm. We selected a 4.8-cm diameter core to target macrofauna typically in the 1-2 mm size range, recognizing that this is likely to exclude megafauna, such as large clams or crabs. This core size is consistent with published literature on macrobenthos from this and nearby marshes (Levin et al. 1998, Talley and Levin 1999, Levin and Talley 2002, Levin and Currin 2005). Most (78 – 89%) of the macrofauna in southern California *S. foliosa* marshes is found in the top 2 cm of sediment (Levin et al. 1998). Cores were preserved (unsieved) in 8% buffered formalin with Rose Bengal. For macrofaunal quantification, the core sediments were washed through a 0.3 mm mesh. The animals retained were sorted under a dissecting microscope at 12x magnification, identified to the lowest taxonomic level possible, counted, and stored in

70% ethanol. Most insects collected were larvae; identifications of these were at the family level only. For other organisms, identifications were to species level, although putative names were used in some cases. The biomass of each species was measured on an analytical balance as wet mass (nearest 0.01 mg) after rehydrating the organisms in water and then blotting on a Kimwipe for ≈ 30 s. Wet weight was assessed to avoid variability associated with previous ethanol storage. The error incurred for repeated measurements of wet mass, assessed for representatives of four phyla, was less than ± 4 % (C. Whitcraft, unpublished). Storage in ethanol for 1-2 years will have reduced actual biomass, but differences among treatments are considered valid.

Stable isotope analysis: Stable isotopic analyses were used to assess (a) whether signatures of the primary producers change with plant cover, (b) which consumer species rely on microalgae as a food source (i.e., species whose signatures track changes in microalgae caused by treatments), and (c) whether microalgae grazers are influenced by changing plant cover more than other feeding groups (detritivores, predators, or plant grazers). Samples of sediment organic matter, microalgae, macroalgae and macrofauna were collected in March 2005 in the *S. virginica* habitat within each treatment using collection methods described above and were analyzed for $\delta^{13}C$ and $\delta^{15}N$ signatures. $\delta^{15}N$ signatures were analyzed statistically for differences among treatments as discussed below but revealed no significant patterns so results are not included in this paper.

Microalgae were collected using density centrifugation with ludox (colloidal silica) (Currin et al. 1995), providing a pure algal sample (devoid of sediment). Macrofaunal invertebrates were sieved on a 0.3 mm mesh, sorted live, and identified to species. All animals were kept alive in seawater and allowed to evacuate guts for up to 24

hours. Animal material was washed in Milli-Q® water and frozen in combusted vials

(500 °C for 4 hours) or tin boats until analysis. Larger organisms were removed from the

shell or carapace, dried at 65°C and then ground with a mortar and pestle. All samples

were treated with Pt Cl$_2$ to eliminate inorganic C. Isotopic composition of animal and

algal samples was analyzed using a PDZ Europa 20-20 mass spectrometer connected to

an elemental analyzer (PDZ Europa ANCA-GS, Northwich, UK). Stable isotope

abundance is expressed in parts per thousand in a ratio of heavy to light isotope content

(^{15}N:^{14}N or ^{13}C:^{12}C). Working standards, sucrose and ammonium sulfate, were δ^{13}C =-

23.83‰ vs. Vienna Pee Dee Belemnite Standard or δ^{15}N = +1.33‰ vs. air N$_2$. Typical

sample precision is better than 0.1‰.

Statistical Analysis: All univariate tests were conducted with JMP 5.1 statistical

software (SAS Institute, NC, USA). Data were tested for normality, and square root or

log$_{10}$ transformed as needed prior to analysis. If no transformation yielded normal data,

nonparametric Wilcoxon tests were utilized. Comparisons of abiotic, sediment, and algal

properties, macrofauna percent composition, and macrofauna species-level density and

biomass data among treatments were conducted with one-way ANOVAs or

nonparametric Wilcoxon tests followed by *a posteriori* Student's t-tests. Whole core

measurements of species richness and diversity (Simpson's D [$D=1/\sum P_i^2$]) were

calculated from count data, and comparisons among treatments were conducted using

one-way ANOVAs or nonparametric Wilcoxon tests, again followed by *a posteriori*

Student's t-tests. Relationships among abiotic and biotic factors were analyzed for

significance using Spearman's Rho. Species were used as replicates for analyses of

treatment effects on stable isotope (δ^{13}C) signatures in one-way ANOVAs and Wilcoxon

nonparametric tests with *a posteriori* Student's t-tests. We present as significant the increase in microalgae $\delta^{13}C$ signatures in plant removal treatments (P=0.082) because power analysis shows that with 4 additional samples, P would have been 0.05. In figures and text, one standard error about the mean is presented for all data unless otherwise noted.

Multivariate analyses were conducted on macrofaunal count and biomass data (both 4th root transformed) using Primer 5 (Plymouth Marine Laboratory, Clarke 1993, Clark and Warwick 1994). Analyses are based on Bray-Curtis similarity indices (Clarke 1993). Pairwise comparisons of overall community similarity were made using Analysis of Similarity, ANOSIM.

Results

Abiotic sediment properties: Light reduction was significantly greater in the shaded and control treatments relative to the unshaded treatments (*S. foliosa*, unshaded $36.8 \pm 8.0\%$, shaded $82.9 \pm 3.0\%$, control $94.1 \pm 2.1\%$; χ^2=12.12, P=0.002) (*S. virginica*, unshaded 14.7 ± 4.5 %; shaded 85.0 ± 3.9 %, control 85.7 ± 5.0 %; χ^2=13.12, P=0.014). Prior to experimentation, no differences existed among *S. foliosa* treatments with respect to salinity (ANOVA, $F_{2,21}$=0.21, P=0.811), temperature (Wilcoxon, χ^2=2.61, P=0.272), nor among *S. virginica* treatments with respect to salinity (ANOVA, $F_{2,21}$=0.38, P=0.687), temperature (ANOVA, $F_{2,28}$=0.03, P=0.968), or redox potential (Wilcoxon, χ^2=1.36, P=0.508). Redox potential in *S. foliosa* plots was not measured before establishment of experiment. Following removal of plants, the unshaded treatment plots in *S. foliosa* and *S. virginica* habitats demonstrated consistently higher temperatures and porewater salinities compared to the shaded or control treatment plots over the duration

of the experiment (Figure 2.1). The unshaded treatment plots had lower water content

relative to the shaded and control treatment plots in both *S. foliosa* and *S. virginica*

habitats (3 months, *S. foliosa*, $F_{2,21}$=3.86, P=0.038; 6 months, *S. virginica*, χ^2=9.78,

P=0.008).

Prior to treatment establishment, the standing stock of belowground plant detritus

did not differ between *S. foliosa* (13,800 $\pm$ 1,400 g/m^2) and *S. virginica* (11,015 $\pm$ 3,000

g/m^2) habitats (Wilcoxon, χ^2=0.89, P = 0.345). Neither the removal of shade nor the

removal of aboveground plant structure was associated with any soil organic matter or

particle size changes during the experiment (Table 2.1a,b). Redox potential

measurements were extremely variable among *S. virginica* blocks and treatments and did

not demonstrate treatment effects. The redox data (unshaded: mean = -7.5, range= -165

to 116; shaded: mean= -34.4, range= -222 to 111; control: mean= -40.5, range= -262 to

126) indicate that the soils in unshaded and shaded treatments did not become more

reduced than control sediments.

Algal community: Prior to treatment establishment, there were no treatment

differences in sediment chl *a* concentrations (all values in µg/g sediment) for both *S.*

foliosa (unshaded = 167.0 $\pm$ 35.5, shaded = 272.4 $\pm$ 50.2, control = 266.6 $\pm$ 91.7) and *S.*

virginica habitats (unshaded = 53.0 $\pm$ 11.6, shaded = 54.3 $\pm$ 12.5, control = 53.72$\pm$ 12.5)

(Wilcoxons: *S. foliosa*, χ^2=1.40, P=0.498, *S. virginica*, χ^2=0.05, P=0.978). After 3 and 6

months, the *S. foliosa* treatment plots had greater chlorophyll *a* concentrations than *S.*

virginica plots (ANOVA, 3 mos., $F_{1,46}$ = 79.57, P<0.0001) (ANOVA, 6 mos., $F_{1,45}$ =

32.93, P<0.0001). The removal of plant cover did not alter chlorophyll *a* concentrations

in any habitat or season (Table 2.1a,b). All pigments that are indicative of a single

functional group were tested for significant difference among treatments, but only

significant pigment data is presented. The HPLC pigment data at 3- and 6-months

suggest a shift from a cyanobacteria-dominated to a more diatom-dominated community

in the unshaded treatments. Microalgal communities in the unshaded treatment plots

exhibited increased fucoxanthin pigment concentrations at 3 months in the *S. foliosa*

habitat and decreased zeaxanthin pigment concentrations at 3 months in the *S. virginica*

habitat (Figure 2.2), indicating diatom and euglenoid abundance increases and

cyanobacteria abundance decreases relative to shaded and control treatment plots.

Macrofaunal community response: Macrofauna in the upper 0-2 cm exhibited

similar responses across habitats and seasons so all results are summarized together

below with details of season and habitat type given in Tables 2.1a,b & 2a,b, and

Appendix A. Relative to the shaded and control treatment plots, unshaded treatment

plots exhibited a reduction in species richness (Wilcoxon, *S. foliosa*, unshaded < shaded

and control, P=0.0006 after 3 months), decreased density of organisms (Wilcoxon,

unshaded < shaded and control, P<0.05 at 3 mos., both habitats), reduced biomass

(Wilcoxon, *S. foliosa*, unshaded < shaded and control, P=0.05 after 3 mos.), and altered

macrofaunal community composition based on count and biomass data (ANOSIM,

unshaded ≠ shaded and control, P<0.05 in all seasons and vegetation zones except *S.*

virginica after 6 months). Density, biomass, and richness changes in unshaded treatment

plots involved a significant loss of amphipods (*Corophium* spp., species of Gammaridae),

loss of tubificid oligochaetes, and an increase in insect larvae (Figure 2.3, Tables 2.2a,b,

Appendix 2.1).

We observed relationships between temperature, salinity, water content and

macrofaunal density and diversity when seasonal data were pooled within vegetation zone. Increases in temperature and salinity for both vegetation zones and decreases in water content for *S. virginica* were correlated with decreased macrofaunal density (Figure 2.4 a,b,c,d,f). Although these are significant regressions, the r^2 values for several of the relationships are very low with slopes close to zero (Figure 2.4 b,f,h,i) . Increased temperature in *S. virginica* habitat and increased salinity for both vegetation zones were correlated with decreased macrofauna species richness (Figure 2.4 g,h,i,j). A positive correlation was found between chl *a* and macrofauna density in the *S. virginica* habitat after 3 mo. (r^2=0.167, P=0.047).

Stable isotope analysis: Among the three primary, non-vascular plant food sources available to macrofauna (sediment organic matter (SOM), benthic microalgae, and the macroalgae, *Ulva* spp.), only benthic microalgae demonstrated significant change in $\delta^{13}C$ with experimental treatment (Table 2.3). There was a 2-3 ‰ increase in $\delta^{13}C$ of microalgae in the unshaded and shaded treatment plots after 11 months ($F_{2,21}$=2.83, P=0.082) (Figure 2.5a). Averaged signatures of all macrofauna within shaded and unshaded treatment plots mimicked the shift in microalgae signatures, with significantly enriched $\delta^{13}C$ values compared to the control treatment plot ($F_{2,84}$=7.79, P=0.0008) (Figure 2.5b). Among invertebrate groups, $\delta^{13}C$ signatures of oligochaetes and insects in the shaded and unshaded treatment plots also mimicked this $\delta^{13}C$ enrichment (oligochaetes: $F_{2,11}$=4.02, P=0.049; insects: χ^2=7.79, P=0.012), indicating a probable reliance on microalgae as a primary food source. Crustaceans and polychaetes exhibited no shift in $\delta^{13}C$ signatures among treatments (crustaceans: $F_{2,3}$=0.15, P=0.869; polychaetes: $F_{2,2}$= 1.48, P=0.403) (Figure 2.5c). Most invertebrate species exhibiting

shifts in δ^{13}C signatures were those with significant changes in overall density and biomass in the unshaded treatment plots, suggesting that microalgae influenced abundance responses. In the unshaded treatment plots, organisms that increased in abundance (insects) were more enriched in δ^{13}C (resembling the microalgal signatures) compared to organisms that decreased in abundance (crustaceans) or showed no shift (polychaetes, molluscs) (Figure 2.5d). Oligochaetes were the exception with declines in density but clear δ^{13}C enrichment. Finally, comparison of the taxa by feeding group revealed differentiation of δ^{13}C signatures in the unshaded treatment plots; microalgal grazers had more enriched signatures relative to the detritus and plant grazers ($F_{3,8}=8.24$, P=0.008) (Figure 2.5e).

Discussion

Our manipulative experiments provide direct evidence that plant-animal interactions mediated by soil and algal properties are important structuring forces in southern California salt marshes. We show that plant cover influences the micro-habitat of the sediment by controlling the amount of light reaching the sediment surface, and that these changes in key abiotic environmental factors appear to induce changes in the sediment biotic community. Such changes can occur as quickly as 3 months after plant cover loss.

In the absence of shading, removal of plant cover induced higher soil temperature, increased porewater salinities, and lower water content, most likely due to the increased sun exposure and subsequent evaporation. These changes are analogous to conditions seen in unvegetated patches or plant-removal experiments in New England salt marshes (Bertness 1991b) and to naturally occurring conditions observed in bare patches in

Mission Bay (Janousek 2005). However, none of the studies mentioned above considered the effect of these alterations on the associated macrofaunal communities. In this study, these significant physical alterations were correlated with changes in macrofaunal density, biomass, and species richness.

Algal mats beneath the marsh plants experienced community composition shifts (increased diatom abundance or decreased cyanobacteria abundance) in the absence of shade. While these changes are complex, other experiments in riverine and forested areas have demonstrated similar shifts away from diatom-dominated communities under low light intensity, with green algal communities dominating under higher light intensities (Lamberti et al. 1989, Franken et al. 2005). In addition to the dramatic shifts in the physical environment, the changes in the microalgae, which are a crucial food source for marsh consumers (Kwak and Zedler 1997, Moseman et al. 2004), represent a second important potential mechanism by which plant cover affects macrofaunal community dynamics.

The plant-induced changes in environmental conditions and in microalgal communities were correlated with changes in the macrofauna community composition, richness, and diversity (Figure 2.4). In both seasons, the macrofauna in unshaded treatments resembled communities seen in newly restored *S. virginica* (de Szalay et al. 1996) and *S. foliosa* (Levin and Talley 2002) salt marshes in southern California; as plant cover increases, oligochaetes, crustaceans, and polychaetes increase, and insects decrease in representation (Talley and Levin 1999, Levin and Talley 2002, Moseman et al. 2004). Similar compositional shifts in the macrofaunal community were observed in our experiments conducted in both grass- and succulent-dominated marsh habitats,

reinforcing the generic role of plant cover in ameliorating harsh physical conditions in a manner essential to the development and maintenance of a natural sediment ecosystem (Bertness and Hacker 1994).

In our experiment, redox, belowground plant structure, and detrital biomass did not differ among treatments. The fact that redox values did not become more reduced in the plant removal treatments indicated little degradation of remaining belowground plant material during the experiment. However, higher photosynthetic oxygen inputs in the unshaded treatments may have masked some degradation. In restored, invaded or degraded systems where plant community shifts involve a dramatic canopy loss or conversion to vegetated area, belowground root biomass and detritus will also change. Such alterations have the potential to drive large trophic shifts through alterations to the detritivore food supply (Levin et al. 2006) and space limitation (Brusati and Grozholz 2006).

Our results provide a mechanistic understanding of the plant-induced shifts in abiotic and biotic factors and also inform us about controlling factors in this particular marsh environment. Changes in physical properties due to changing light regimes appear to mediate changes in the sediment biotic community. Several other plant effects that may be important in structuring the benthic ecosystem were not studied, such as the effects of plants on detrital food supply, on predators or on flow regime (Leonard and Luther 1995, Nomann and Pennings 1998, Neira et al. 2006). However, the Mission Bay marsh system has low hydrodynamic energy, potentially reducing the importance of plant structure effects on flow and elevating the importance of light and evaporation as structuring agents.

Stable isotopic techniques have recently been used to assess trophic succession in created and invaded salt marshes (Currin et al. 2003, Moseman et al. 2004, Levin et al. 2006). The enriched $\delta^{13}C$ isotope values seen in the unshaded and shaded treatment plots relative to the control plots have several possible explanations. Typically, heavier $\delta^{13}C$ values in microalgae are indicative of faster photosynthetic rates (increased light) accompanied by carbon limitation, increased cyanobacterial content, less utilization of remineralized plant matter, higher salinity, or less nitrogen fixation (Beardall et al. 1998, Raven et al. 2002). In this experiment, unshaded treatment plots had increased salinity and algal community shifts. However, because the $\delta^{13}C$ enrichment was observed in the shaded and unshaded treatment plots (Figure 2.5), it is more likely that the enrichment is due to the influence of above-ground plant structure rather than light.

The isotope data provide two potential explanations for plant-induced shifts in macrofaunal abundances. In the absence of aboveground plant structure and shade (unshaded treatments), algal mat samples shifted to more diatom-dominated communities, and fresh detrital food sources were reduced by removal of aboveground biomass. Detrital grazers such as amphipods and oligochaetes decreased overall. Insect larvae, typically microalgal grazers, increased in abundance and exhibited an isotopic shift similar to that of the microalgae (Figure 2.5). These results support a major role for microalgae in structuring animal response to changing plant cover. These plant-canopy-induced changes in microalgae and macrofauna can have effects that extend to higher trophic levels. For example, structural differences in macrofaunal communities between natural and created systems have been shown to translate to higher trophic levels by altering foraging patterns of fish (Moy and Levin 1991).

Much research has been focused on the role of interspecific interactions, facilitation, and subsequent zonation among vascular plant species within the salt marsh environment (Bertness 1991a, 1991b, 1992, Pennings et al. 2005). Equally important to consider is plant facilitation and zonation of the sediment system for sessile or limited-mobility invertebrates. Many of the early studies mentioned above that revealed plant effects on edaphic factors such as substrate redox potential and salinity were conducted within New England salt marshes. Studies in Brazilian marshes have identified changes in macrobenthos associated with plant biomass, detrital input, grain size, predation pressure, sediment organic matter, and freshwater input (Lana and Guiss 1991, Pagliosa and Lana 2005). In southern California where there are significantly higher salinities and less predictable redox than in these other systems due to a Mediterranean climate, our studies emphasized the importance of the light reduction function of plants. Halophytes generally occur at higher tidal elevations in the southern California marshes compared to Atlantic marshes. Although the exact mechanisms behind observed macrobenthos changes may differ, comparison with studies in the high marshes/salt pans of Georgia and Argentina reveals complementary mechanisms behind changes in plant-animal interactions. Studies by Nomann and Pennings (1998) and Bortolus et al. (2002) demonstrated the ability of plants to buffer harsh physical conditions (high temperature, soil hardness, organism heat stress and dehydration) via shading and provision of predation refugia. We predict that these salt marsh plant effects on the benthic ecosystem should be especially strong at lower latitudes, higher-temperatures, and in arid regions, such as southern California.

Our experiments demonstrate that the light reduction function provided by the

vascular plant canopy is crucial to maintaining the natural biotic community of southern California salt marsh sediments. Although the connection has been made between light intensity and associated consumers (Nomann and Pennings 1998, Franken et al. 2005), this research isolates the strong relationship between plant-mediated light regime and sediment-dwelling organisms in coastal wetlands. These results highlight the probability that any anthropogenic change influencing plant density, cover, height, or growing season will alter salt marsh algal and animal assemblages via light regulation.

Whitcraft, C. R. and L. A. Levin. in press. Regulation of benthic algal and animal communities by salt marsh plants: impact of shading. The dissertation author was the primary investigator and author of this paper.
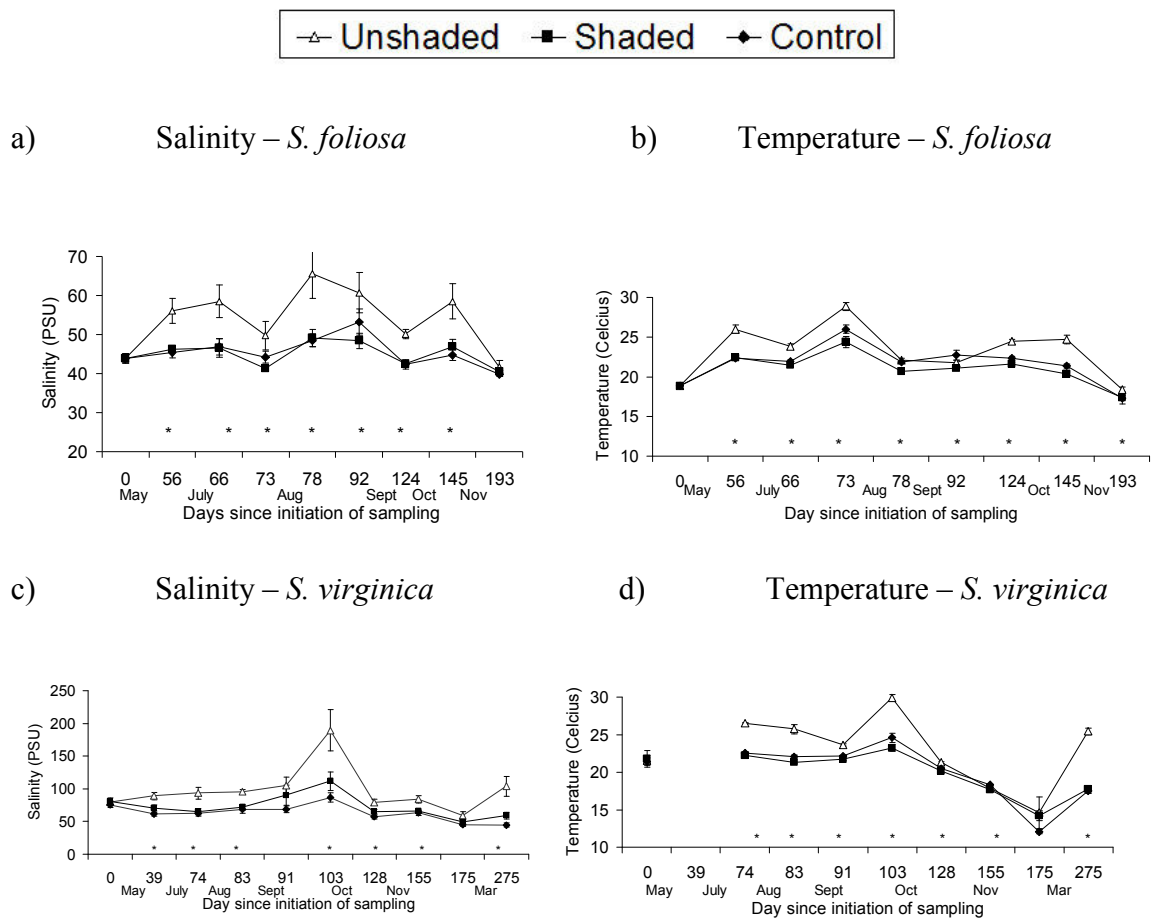
Figure 2.1: Mean (± 1 SE) porewater salinity and temperature of upper 2 cm of sediment in 3 treatments in *S. foliosa* & *S. virginica* treatment plots. Values designated with asterisks indicate that unshaded treatment values are significantly different from shaded & control treatment values (Wilcoxon rank sum, P<0.05).

Figure legend: □ Unshaded ⊞ Shaded ■ Control
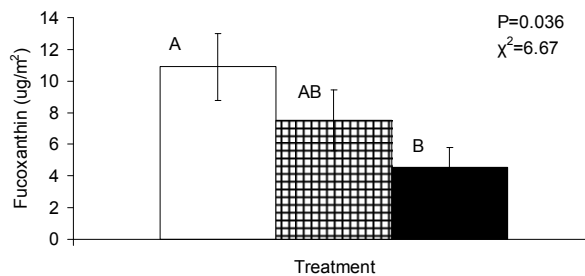
a) *S. foliosa* – 6 months

b) *S. virginica* – 3 months
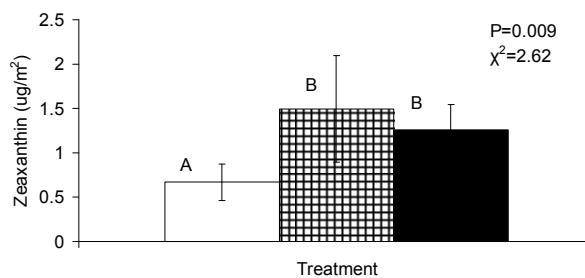
Figure 2.2: Pigment abundance a) fucoxanthin in *S. foliosa*, 6 months and b) zeaxanthin in *S. virginica*, 3 months as determined through High-Performance Liquid Chromatography: only significant (P<0.05) results are shown. Graphs indicate a shift in importance of diatoms in unshaded treatment plots relative to control and shaded treatment plots.
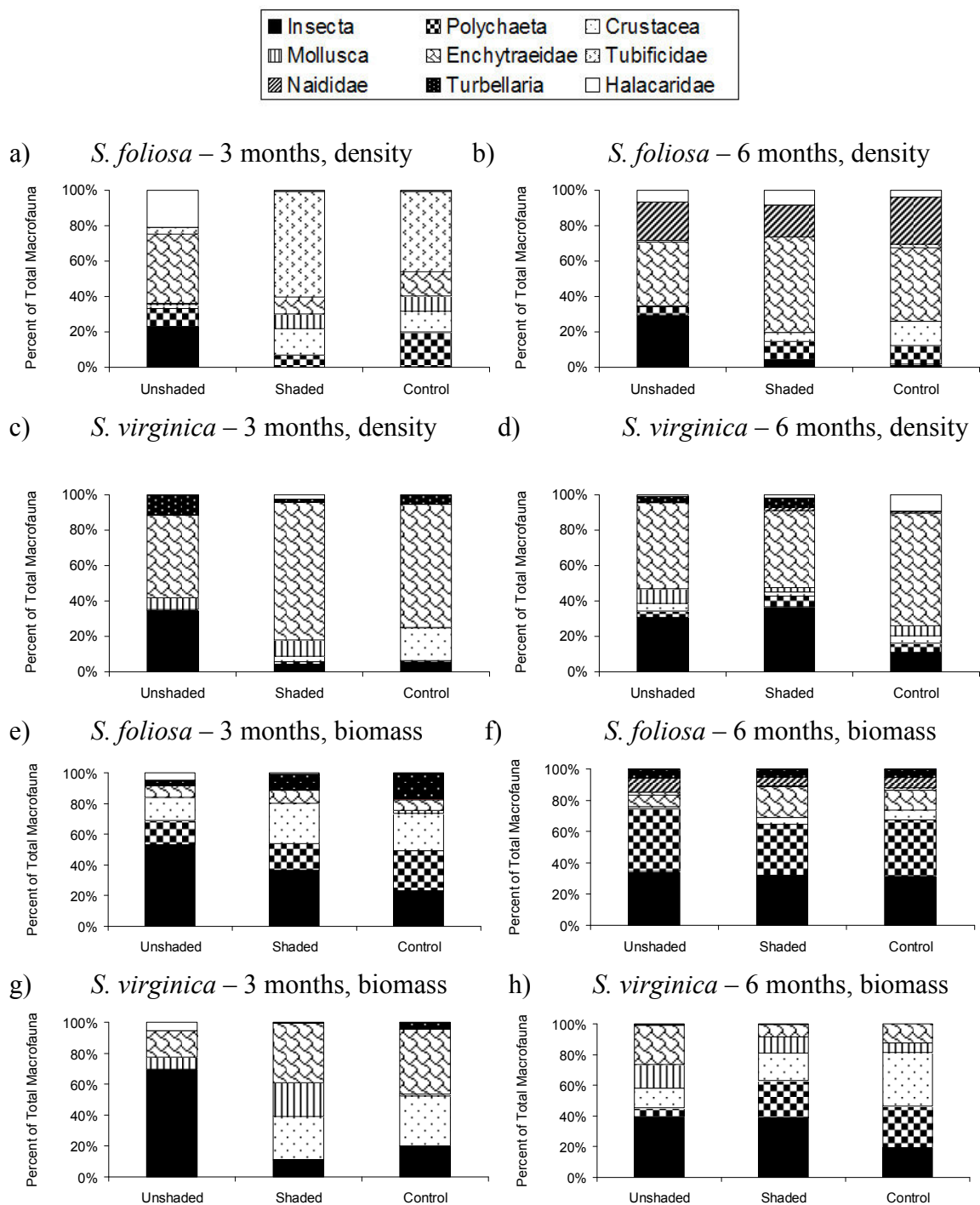
Figure 2.3: Macrofaunal community composition (based on counts: a-d, based on biomass: e-h) in three treatments 3 and 6 months after experiment initiation: unshaded (absence of plant cover & structure), shaded (absence of plant structure), and control (plants intact) in *S. foliosa* and *S. virginica* treatment plots. Note: Enchytraeidae, Tubificidae, and Naididae are Oligochaeta.
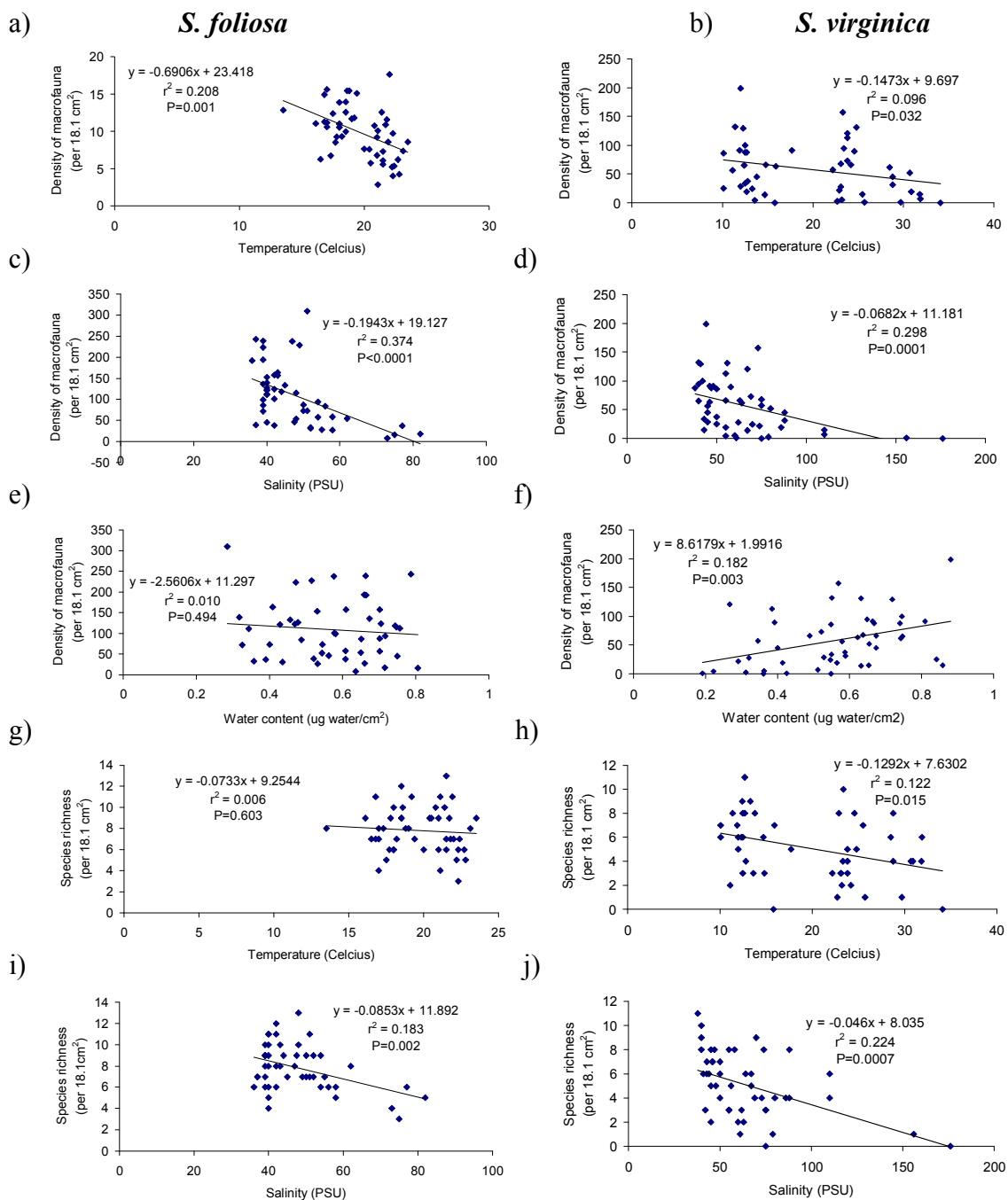
Figure 2.4: Regressions showing relationships between temperature (a,b), salinity (c,d), water content (e,f) and macrofauna density (no. / 18.1 cm^2) & between temperature (g,h), salinity (i,j), and macrofaunal species richness (# of species / 18.1 cm^2). Analyses were pooled across treatments and seasons.

Figure 2.5: Stable isotope signatures (δ^{13}C) of sediment, microalgae, macroalgae and selected macrofauna in *S. virginica* habitat, 11 months after treatment initiation. Natural abundance δ^{13}C values are given for a) macrofaunal food sources, b) total macrofauna, c) major macrofaunal taxa, d) macrofauna grouped by response to unshaded treatment, and e) macrofauna feeding mode. Letters indicate *a posteriori* differences among treatments (P<0.05) in δ^{13}C values.

Table 2.1. Comparison of responses to unshaded, shaded, and control treatments by sediment properties, abiotic physical parameters, and the algal community after 3 months (August) and 6 months (November) in a) *S. foliosa* and b) *S. virginica* habitat. Mean (± 1 SE) noted. Superscripted letters indicate *a posteriori* differences among treatments (P < 0.05).

a)

Spartina foliosa

Property	3 month					6 month				
	unshaded	shaded	control	X^2_2 or $F_{2,21}$ value	P value	unshaded	shaded	control	X^2_2 or $F_{2,21}$ value	P value
Grain size (% mud)	93.6 (3.3)	97.0 (1.2)	96.6 (0.9)	X^2=1.19	0.553	94.5 (2.8)	96.2 (3.7)	98.1 (1.1)	X^2=0.79	0.659
Organic matter (%)	30.2 (5.7)	31.4 (4.3)	32.6 (4.8)	X^2=0.47	0.793	29.2 (4.7)	30.6 (6.1)	31.4 (2.3)	X^2=2.45	0.334
Salinity	50.1 (1.2)[a]	42.5 (0.8)[b]	42.4 (1.2)[b]	$F_{2,21}$=13.06	0.002	41.6 (1.8)	40.5 (1.1)	39.9 (0.5)	$F_{2,21}$=0.25	0.882
Temperature (° C)	24.4 (0.3)[a]	21.6 (0.1)[b]	22.3 (0.2)[b]	$F_{2,21}$=17.75	0.0001	18.4 (0.3)[a]	17.3 (0.3)[b]	16.8 (0.6)[b]	$F_{2,21}$=7.16	0.028
Water content (g / core)	0.64 (0.03)[a]	0.62 (0.05)[a]	0.48 (0.04)[b]	$F_{2,21}$=3.86	0.038	0.58 (0.06)	0.57 (0.04)	0.55 (0.05)	$F_{2,21}$=0.08	0.927
Redox (Eh)	19 (63.08)	-25.63 (65.81)	-27.63 (82.95)	X^2=0.38	0.829	-84.50 (46.82)	-162.63 (39.22)	-151.04 (49.33)	$F_{2,21}$=0.87	0.435
Chl a (µg / g sediment)	305.6 (92.6)	346.6 (107.8)	214.4 (53.2)	X^2=1.1	0.560	334.2 (91.5)	283.7 (95.3)	185.2 (33.8)	X^2=1.58	0.454
Fucoxanthin (µg/cm²)	4.32 (0.64)	5.26 (1.53)	4.74 (0.59(	X^2=0.42	0.811	10.90 (2.11)[a]	7.53 (1.91)[ab]	4.55 (1.24)[b]	X^2=2.08	0.021
Density (# / 18.1 cm²)	35.3 (21.2)[a]	120.3 (23.5)[b]	64.9 (17.5)[b]	X^2=0.39	0.0006	123.1 (17.5)	133.8 (23.5)	174.6 (21.2)	X^2=2.95	0.229
Species richness / 18.1 cm²	5.50 (0.57)[a]	8.88 (0.58)[b]	8.50 (0.89)[b]	X^2=10.1	0.0006	7.75 (0.53)	7.50 (0.7)	8.75 (0.80)	X^2=1.06	0.587
Biomass (mg / 18.1 cm²)	7.57 (3.50)[a]	21.42 (5.76)[b]	22.13 (7.75)[b]	X^2=5.96	0.050	1139.61 (640.15)	11.31 (2.73)	26.75 (5.59)	X^2=4.34	0.114
Diversity (Simpson's D)	0.58 (0.09)	0.62 (0.06)	0.69 (0.07)	X^2 = 1.23	0.539	0.58 (0.04)	0.53 (0.08)	0.48 (0.06)	X^2 = 1.46	0.482

Table 2.1 (continued)

b)

Salicornia virginica	3 month					6 month				
Property	unshaded	shaded	control	X^2_2 or F value	P value	unshaded	shaded	control	X^2_2 or $F_{2,21}$ value	P value
Grain size (% mud)	92.1 (4.9)	93.0 (4.0)	92.7 (3.6)	$\chi^2 = 1.65$	0.513			no data		
Organic matter (%)	29.8 (2.4)	28.5 (2.8)	30.4 (3.1)	$\chi^2 = 2.19$	0.293			no data		
Salinity	79.4 (5.1)[a]	65.0 (3.7)[b]	57.0 (2.8)[b]	$F_{2,21}=8.2$	0.002	59.1 (5.9)	49.3 (2.9)	44.8 (1.9)	$F_{2,21}=5.24$	0.070
Temperature (°C)	21.3 (0.1)[a]	20.2 (0.3)[b]	20.5 (0.2)[b]	$F_{2,21}=8.73$	0.002	14.6 (2.1)	14.2 (0.7)	12.1 (0.3)	$F_{2,21}=3.87$	0.144
Water content (g / core)	0.49 (0.07)	0.43 (0.06)	0.50 (0.06)	$F_{2,21}=0.43$	0.659	0.52 (0.04)[a]	0.70 (0.02)[b]	0.69 (0.05)[b]	$\chi^2=9.78$	0.008
Redox (Eh)	- 7.5 (55.36)	- 34.43 (43.18)	- 40.50 (57.21)	$F_{2,16}=0.11$	0.895	- 14.2 (29.4)	- 29.38 (35.86)	- 22.06 (43.81)	$F_{2,21}=0.13$	0.723
Chl a (µg / g sediment)	27.1 (6.9)	37.3 (7.0)	31.8 (9.2)	$F_{2,21}=0.43$	0.654	81.3 (19.3)	63.4 (16.4)	26.5 (11.3)	$F_{2,21}=3.05$	0.069
Zeaxanthin (µg/cm²)	0.67 (0.21)[a]	1.5 (0.60)[b]	1.26 (0.29)[b]	$\chi^2 = 2.62$	0.0009	4.56 (1.31)	5.39 (0.82)	5.24 (1.28)	$\chi^2 = 0.86$	0.651
Density (# / 18.1 cm²)	21.4 (8.2)[a]	75.9 (19.3)[b]	55.3 (16.1)[ab]	$\chi^2 = 5.93$	0.050	46.3 (15.7)	65.4 (9.3)	77.9 (22.5)	$F_{2,21}=0.91$	0.420
Species richness / 18.1 cm²	3.63 (0.75)	1.63 (1.05)	4.00 (0.89)	$F_{2,21}=0.31$	0.736	5.00 (1.15)	6.63 (0.68)	6.50 (0.82)	$F_{2,21}=0.99$	0.386
Biomass (mg / 18.1 cm²)	4.08 (1.44)	137.80 (124.67)	7.76 (2.38)	$\chi^2 = 2.59$	0.274	7.10 (2.39)	16.92 (4.08)	279.25 (262.88)	$\chi^2 = 4.63$	0.099
Diversity (Simpson's D)	0.42 (0.11)	0.29 (0.11)	0.28 (0.10)	$\chi^2 = 0.87$	0.648	0.64 (0.10)	0.66 (0.09)	0.46 (0.10)	$\chi^2 = 1.83$	0.400

Table 2.2. Comparison of responses to unshaded, shaded, and control treatments by the macrofaunal community (density, composition, and biomass) after 3 months (August) and 6 months (November) in a) *S. virginica* and b) *S. virginica* habitats. Mean density and biomass per core (18.1 cm^2) ($\pm$1 SE) are reported. Superscripted letters indicate *a posteriori* differences among treatments (P < 0.05).

a)

Spartina foliosa

Group	3 months					6 months				
	unshaded	shaded	control	χ^2_2 value	P value	unshaded	shaded	control	χ^2_2 value	P value
Crustacea										
density	0.8 (0.6)^a	7.4 (3.5)^b	4.8 (2.4)^b	5.75	0.023	0.6 (0.3)^a	7.3 (4.3)^{ab}	24.5 (12.6)^b	7.45	0.024
biomass	3.00 (2.96)	5.53 (1.70)	10.92 (5.78)	4.59	0.101	0.11 (0.09)^a	0.11 (0.09)^{ab}	2.16 (0.77)^b	7.04	0.030
% of total density	2.2 (1.7)	7.6 (3.3)	8.0 (4.2)	4.08	0.130	0.5 (0.2)^a	5.1 (2.0)^{ab}	13.7 (7.1)^b	6.67	0.036
Gastropoda										
density	0.1 (0.1)	0.5 (0.3)	0.5 (0.3)	1.31	0.519	0.0	0.0	0.0	n/a	n/a
biomass	0.01 (0.01)	0.03 (0.02)	0.16 (0.10)	1.06	0.590	0.0	0.0	0.0	n/a	n/a
% of total density	0.7 (0.7)	0.6 (0.3)	0.5 (0.4)	0.78	0.677	0.0	0.0	0.0	n/a	n/a
Insecta										
density	6.4 (1.8)	6.5 (1.5)	10.0 (4.3)	0.12	0.944	22.8 (8.1)^a	3.6 (1.3)^b	3.3 (1.0)^b	8.65	0.013
biomass	3.25(0.04)	11.61 (0.03)	4.05 (0.02)	2.70	0.259	132.80 (125.27)	3.43 (1.66)	5.79 (4.09)	2.43	0.296
% of total density	22.8 (6.0)	6.2 (1.1)	17.7 (6.3)	3.55	0.170	29.5 (9.6)^a	4.0 (1.2)^b	1.9 (0.6)^b	8.80	0.012
Oligochaeta										
density	17.9 (9.8)^a	84.9 (30.3)^b	35.0 (11.3)^b	10.27	0.006	82.3 (20.8)	101.4 (22.2)	122.4 (24.7)	0.95	0.623
biomass	0.34 (0.20)	1.64 (0.52)	1.10 (0.60)	5.59	0.061	3.33 (1.3)	2.30 (0.48)	3.31 (0.92)	0.67	0.717
% of total density	42.5 (12.2)	63.3 (7.2)	50.1 (8.4)	1.22	0.317	58.7 (9.3)	71.7 (7.4)	70.1 (10.6)	1.50	0.472
Polychaeta										
density	2.6 (1.5)^a	10.1 (2.6)^b	7.5 (2.6)^b	6.01	0.050	6.6 (3.4)	14.8 (7.2)	17.9 (5.0)	3.54	0.171
biomass	1.50 (0.82)	3.12 (1.16)	5.86 (3.69)	2.43	0.297	1003.01 (654)	3.36 (1.29)	9.36 (4.81)	3.26	0.196
% of total density	10.9 (5.6)	13.7 (4.8)	10.4 (2.1)	1.51	0.470	4.7 (2.2)	10.7 (5.2)	10.3 (2.8)	3.26	0.196
Other										
density	7.5 (4.2)	10.9 (2.8)	9.0 (3.3)	1.59	0.452	6.1 (2.9)	5.6 (2.3)	5.8 (2.0)	0.14	0.931
biomass	0.08 (0.0001)	0.01 (0.03)	0.07 (0.03)	1.64	0.440	0.06 (0.03)	0.06 (0.02)	0.05 (0.02)	0.34	0.846
% of total density	20.9 (10.4)	8.7 (2.1)	13.2 (4.8)	0.15	0.928	6.0 (3.0)	8.4 (5.2)	3.3 (1.1)	0.02	0.992

Table 2.2 (continued)

b)

Salicornia virginica

Group	3 months					6 months				
	unshaded	shaded	control	χ^2_2 value	P value	unshaded	shaded	control	χ^2_2 value	P value
Crustacea										
density	0.0 (-)[a]	1.9 (1.2)[b]	1.5 (0.6)[b]	5.75	0.023	1.3 (1.0)	1.3 (0.6)	1.8 (0.5)	3.13	0.209
biomass	0.0 (-)[a]	4.92 (3.63)[b]	3.23 (2.09)[b]	7.48	0.024	1.40 (0.94)	2.07 (1.20)	5.52 (2.28)	5.29	0.071
% of total density	0.0 (-)[a]	3.2 (1.5)[b]	18.3 (12.1)[b]	4.08	0.020	3.7 (2.8)	2.4 (1.0)	4.3 (2.4)	2.13	0.345
Gastropoda										
density	1.3 (0.9)	4.6 (3.3)	0.3 (0.2)	1.31	0.610	3.3 (1.8)	3.3 (2.0)	2.6 (0.9)	0.74	0.691
biomass	0.13 (0.08)	2.50 (1.73)	0.021 (0.01)	1.18	0.553	1.86 (1.01)	0.61 (0.32)	1.97 (0.98)	1.63	0.443
% of total density	5.8 (3.6)	9.0 (5.2)	0.4 (0.3)	0.78	0.589	7.8 (4.7)	6.8 (3.9)	5.8 (2.5)	0.43	0.807
Insecta										
density	4.8 (2.3)	2.6 (1.2)	3.9 (3.2)	0.12	0.331	15.4 (7.5)	22.4 (5.4)	4.8 (0.9)	4.40	0.111
biomass	3.30 (1.15)	1.40 (0.89)	1.53 (0.94)	3.14	0.209	2.19 (1.44)	7.12 (2.55)	16.29 (14.13)	3.44	0.179
% of total density	30.2 (11.7)	4.2 (2.3)	5.8 (3.7)	3.55	0.044	27.8 (8.0)	35.1 (6.3)	10.9 (4.1)	3.98	0.137
Oligochaeta										
density	14.9 (6.3)	61.6 (19.3)	46.6 (14.5)	10.27	0.101	24.5 (9.0)	30.9 (7.6)	59.4 (23.0)	1.46	0.482
biomass	0.45 (0.53)	1.84 (1.65)	1.40 (1.23)	4.01	0.135	0.89 (0.28)	0.89 (0.19)	1.66 (0.72)	0.14	0.934
% of total density	40.8 (12.1)[a]	77.7 (10.5)[b]	69.6 (12.5)[b]	1.22	0.041	44.1 (9.5)	43.7 (9.2)	64.5 (9.9)	1.68	0.432
Polychaeta										
density	0.4 (0.3)	1.0 (0.6)	0.8 (0.8)	6.01	0.380	0.5 (0.5)	3.4 (1.6)	2.4 (1.5)	2.74	0.254
biomass	0.58 (0.56)	2.03 (2.00)	1.10 (1.10)	1.92	0.383	0.72 (0.72)	6.21 (3.57)	253.71 (249.49)	2.29	0.318
% of total density	0.7 (0.5)	1.3 (0.7)	0.6 (0.6)	1.51	0.367	0.4 (0.4)	5.6 (2.4)	5.0 (4.3)	3.07	0.216
Other										
density	3.9 (3.6)	1.5 (0.8)	1.4 (0.7)	1.56	0.867	0.3 (0.2)	1.0 (0.5)	7.0 (6.4)	1.91	0.385
biomass	0.04 (0.04)	0.09 (0.08)	0.01 (0.005)	1.54	0.462	0.003 (0.003)	0.01 (0.005)	0.07 (0.06)	1.75	0.416
% of total density	10.0 (7.0)	1.8 (0.7)	5.1 (4.1)	0.15	0.940	0.9 (0.6)	1.7 (1.1)	9.4 (7.2)	1.70	0.427

Table 2.3. Mean δ^{13}C signatures of macrofauna (1 SE) with abundance changes indicated for unshaded treatment plots relative to control plots after 3 and 6 mos. in *S. virginica* habitat. When no SE is reported, n=1.

Species (Class or Order)	Unshaded δ^{13}C	Shaded δ^{13}C	Control δ^{13}C	Feeding group (citations below table)	Abundance changes (See Appendix A)
Enchytraeidae (Oligochaeta)	-19.53	-22.71 (0.045)	-23.38 (0.33)	detritivore[1]	decrease
Tubificoides browniae					
(Oligochaeta)	-21.89 (1.77)	-21.49 (0.34)	-23.75 (0.54)	detritivore[2]	decrease
Polydora nuchalis (Polychaeta)	-19.7	-20.23	-22.78	detritivore[3]	no change
Traskorchestia traskiana					
(Amphipoda)	-24.75	-21.39 (0.35)	-22.05 (0.15)	plant feeder[3]	decrease
Dolichopodidae larvae (Insecta)	-18.57 (0.29)	-21.66 (1.74)	-20.38 (0.81)	predatory[4]	increase
Staphylinidae adult (Insecta)	-21.73 (0.25)	n/a	-22.89 (0.74)	predatory[5]	no change
Ceratapogonidae larvae (Insecta)	-18.98 (0.73)	-20.25 (0.65)	-23.72 (0.85)	microalgal feeder[6]	increase
Muscidae larvae (Insecta)	-17.22	-19.77 (0.86)	-20.03 (3.35)	microalgal feeder[6]	increase
Cincindelidae adult (Insecta)	-18.04	-18.45 (0.62)	n/a	microalgal feeder[6]	no change
Staphylinidae larvae (Insecta)	-16.83 (0.22)	-21.10 (1.67)	-21.43 (1.25)	microalgal feeder[6]	no change
Stratiomyidae larvae (Insecta)	n/a	-25.45	-20.22 (0.94)	microalgal feeder[6]	no change
Ephydridae larvae (Insecta)	-18.95 (1.04)	-19.21 (0.82)	-18.40 (1.76)	microalgal feeder[6]	no change
Assiminea californica (Gastropoda)	-19.09 (1.66)	n/a	-19.73 (0.11)	microalgal feeder[6]	no change

[1] Dash and Cragg. 1972.
[2] Wavre and Brinkhurst. 1971
[3] Levin and Currin. 2005.
[4] Bickel and Dyte. 1989
[5] Holway, D. (pers. comm.)
[6] Moseman, et al. 2004.

Appendix 2.1: Comparison of responses to unshaded, shaded, and control treatments by the macrofaunal community (density) after 3 months (August) and 6 months (November) in a) *S. foliosa* and b) *S. virginica* habitats. Mean density of organisms per core (18.1 cm²) (±1 SE) are reported. Superscripted letters indicate *a posteriori* differences among treatments (P > 0.05).

a)

Spartina foliosa Species	3 months					6 months				
	Unshaded	Shaded	Control	χ^2_2	P value	Unshaded	Shaded	Control	χ^2_2	P value
Assiminea californica	0.13 (0.13)	0.50 (0.27)	0.50 (0.33)	1.31	0.519	0	0	0.13 (0.13)	2.00	0.368
Capitella spp. complex	0[a]	0[a]	1.38 (0.98)[b]	6.54	0.038	0.88 (0.44)	0.63 (0.26)	1,88 (1.74)	0.55	0.759
Capitellidae sp #2	0.13 (0.13)	0.75 (0.49)	0.50 (0.10)	2.15	0.342	n/a				
Ceratapogonidae larvae sp. 1	2.38 (1.34)	2.13 (0.93)	5.00 (3.84)	0.09	0.954	0.13 (0.13)	0	0.25 (0.16)	5.38	0.068
Coleoptera sp. 1	0	0.38 (0.18)	0.13 (0.13)	4.03	0.138	0.38 (0.18)[a]	0[b]	0[b]	6.57	0.037
Chironomid larvae sp 1	0	0	0			0	0	0.13 (0.13)	2.00	0.368
Corophium spp.	0.13 (0.13)	6.0 (3.53)	3.88 (2.38)	2.15	0.342	0.38 (0.18)	6.63 (4.37)	23.38 (12.76)	4.76	0.093
Dolicopodidae larvae sp 1	0.75 (0.53)	0.25 (0.16)	0.25 (0.16)	0.10	0.949	1.63 (0.68)[a]	0.88 (0.40)[ab]	0.25 (0.16)[b]	8.15	0.017
Enchytraidae sp 1	16.75 (9.84)[a]	70.5 (23.88)[b]	29.38 (10.40)[ab]	7.93	0.019	49.88 (13.99)	74.75 (21.80)	75.88 (24.35)	0.52	0.771
Ephydra larvae sp 1	0.13 (0.13)	1.13 (0.61)	0.75 (0.37)	3.32	0.190	0	1.25 (0.53)	0.63 (0.63)	7.75	0.021
Fabricia sabella	0.13 (0.13)	4.62 (1.74)	4.0 (2.81)	5.36	0.068	0	3.63 (3.21)	3.38 (3.38)	5.09	0.079
Ligia occidentalis	0	0	0.13 (0.13)	2.00	0.368	0.13 (0.13)	0	0.13 (0.13)	1.05	0.593
Mite 1	7.38 (4.12)	10.63 (2.70)	6.23 (3.10)	1.78	0.411	0	0	0.50 (0.50)	2.00	0.368
Mite 2	0.13 (0.13)	0.25 (0.16)	0.50 (0.27)	1.49	0.475	5.88 (0.13)	5.63 (0.16)	5.38 (0.27)	0.02	0.992
Muscidae larvae sp 1	1.88 (0.64)	2.25 (0.59)	2.38 (1.24)	0.63	0.731	22.75 (8.20)	1.75 (0.59)	1.25 (0.73)	4.63	0.099
Nemertea sp 1	0	0	0			0	0	0.13 (0.13)	3.86	0.145
Traskorchestia traskiana	0.63 (0.63)	1.38 (0.46)	0.75 (0.53)	3.11	0.211	0	0.38 (0.38)	0	6.02	0.049
platyhelminthes sp 1	0	0	0			0	0	0.63 (0.32)	4.18	0.124
poduridae sp 1	0	0	1.38 (1.38)	2.00	0.368	0	0	0		
Polydora cornuta	0.63 (0.63)	1.38 (0.94)	0	2.18	0.336	1.00 (0.65)	2.75 (2.75)	7.75 (3.17)	4.69	0.096
Paranais littoralis	0	0	0			31.13 (15.92)	26.50 (11.53)	42.25 (16.83)	0.62	0.732
Polydora nuchalis	0.13 (0.13)	2.75 (1.82)	1.38 (0.78)	2.00	0.368	4.63 (3.43)	5.25 (2.99)	0.5 (0.5)	1.60	0.449
Psychodidae sp 1	0.25 (0.25)	0.25 (0.25)	0	1.05	0.593	2.00 (0.53)[a]	0.88 (0.48)[ab]	0.13 (0.13)[b]	8.15	0.017
Spionidae sp 1	1.63 (0.98)	0.63 (0.42)	0.25 (0.16)	1.72	0.424	0	0.25 (0.25)	0	2.00	0.368
Staphylinidae larvae and adults sp 1	1.00 (0.50)	0	0.13 (0.13)	6.58	0.037	0	0	0		
Tubificidae sp 1	1.13 (0.99)[a]	14.38 (7.21)[b]	5.63 (1.95)[ab]	9.00	0.011	1.25 (0.49)	0.13 (0.13)	4.25 (4.11)	4.78	0.092

Appendix 2.1 (continued)

b)

Salicornia virginica Species	3 months					6 months				
	Unshaded	Shaded	Control	χ^2_2	P value	Unshaded	Shaded	Control	χ^2_2	P value
Assiminea californica	1.0 (0.87)	4.0 (3.34)	0.25 (0.16)	1.00	0.606	3.25 (1.76)	3.25 (2.02)	2.62 (0.94)	0.74	0.691
Barleeia sp.	0	0.25 (0.25)	0	2	0.368	0	0	0		
Capitella spp. complex	0	0	0			0	0	0.25 (0.25)	2.00	0.368
Ceratapogonidae larvae sp. 1	0	1.38 (1.10)	2.63 (2.63)	3.59	0.166	11.63 (6.78)	14.13 (5.14)	2.62 (0.84)	2.29	0.318
Cincindelidae adult sp. 1	0.5 (0.27)	0.25 (0.25)	0.13 (0.13)	1.81	0.405	0	0	0.25 (0.16)	4.18	0.124
Coleoptera sp. 1	0	0	0			0	0	0.13 (0.13)	2.00	0.368
Chironomid larvae sp 1	0	0	0			0	0.13 (0.13)	0	2.00	0.368
Dolicopodidae larvae sp 1	0	0	2.0 (1.33)	9.15	0.011	0.75 (0.49)[a]	2.88 (0.85)[b]	0.88 (0.30)[a]	6.77	0.034
Enchytraidae sp 1	14.88 (6.25)	61.63 (19.27)	46.63 (14.51)	4.59	0.100	24.25 (8.96)	29.00 (6.91)	59.13 (23.11)	1.34	0.151
Ephydra larvae sp 1	0	0.13 (0.13)	0.25 (0.25)	1.05	0.592	0.63 (0.42)	1.00 (0.42)	0	4.70	0.095
Ligia occidentalis	0	0	0.25 (0.25)	2.00	0.368	0	0	0		
Mite 1	0	0	0			0.25 (0.16)	0.75 (0.53)	6.50 (5.93)	1.56	0.458
Mite 2	0	2.13 (2.13)	0.13 (0.13)	1.05	0.592	0	0.13 (0.13)	0.50 (0.50)	1.05	0.592
Muscidae larvae sp 1	1.88 (1.04)	0.25 (0.16)	0.50 (0.19)	4.95	0.084	1.13 (0.52)	0.38 (0.26)	0.25 (0.16)	2.28	0.320
Nemertea sp 1	0	0.13 (0.13)	0.50 (0.50)	1.05	0.592	0.13 (0.13)	0	0	2.00	0.368
Neanthes succinea	0	0.13 (0.13)	0	2	0.368	0	1.00 (1.00)	1.50 (1.50)	1.05	0.592
Oniscid isopod sp 1	0	0.25 (0.25)	0.38 (0.26)	2.01	0.351	0[a]	0[a]	0.88 (0.50)[b]	6.55	0.037
Traskorchestia traskiana	0	1.63 (1.21)	1.00 (0.60)	5.57	0.062	1.25 (1.00)	1.25 (0.59)	0.88 (0.23)	1.57	0.456
platyhelminthes sp 1	3.88 (3.59)	2.00 (0.78)	0.88 (0.48)	1.71	0.426	0.88 (0.64)	3.63 (2.05)	0	3.78	0.151
Paranais littoralis	0	0	0			0.25 (0.16)	1.88 (1.61)	0.13 (0.13)	0.67	0.717
Polydora nuchalis	0.38 (0.26)	0.88 (0.61)	0.75 (0.75)	0.87	0.646	0.50 (0.50)	2.38 (1.50)	0.63 (0.63)	2.15	0.341
Psychodidae sp 1	0	0	0			0	0.25 (0.25)	0	2.00	0.368
Staphylinidae larvae and adults sp 1	0.13 (0.13)	0.25 (0.16)	0.25 (0.16)	0.48	0.785	0.50 (0.38)	0.63 (0.63)	0.25 (0.25)	0.45	0.799
Stratiomyidae larvae sp 1	0	0.25 (0.25)	0	2.00	0.368	0.88 (0.52)	2.63 (2.35)	0.25 (0.16)	0.53	0.767
Tubificidae sp 1	0	0	0			0	0	0.13 (0.13)	2.00	0.368

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CHAPTER III

INVASION OF TAMARISK (*TAMARIX* SPP.) IN A SOUTHERN CALIFORNIA
SALT MARSH

Abstract

Exotic plants have been demonstrated to be one of the greatest threats to wetlands, as they are capable of altering ecosystem-wide physical and biological properties. One of the most problematic invaders in the western United States has been salt cedar, *Tamarix* spp., and the impacts of this species in riparian and desert ecosystems have been well-documented. Here we document large populations of tamarisk in the intertidal salt marshes of Tijuana River National Estuarine Research Reserve, a habitat not often considered vulnerable to invasion by tamarisk. Initial research demonstrates that there are multiple species and hybrids of *Tamarix* invading the estuary and that the potential impact of tamarisk within this salt marsh is significant. This highlights the need for managers and scientists to be aware of the problems associated with tamarisk invasion of coastal marine habitats and to take early and aggressive action to combat any incipient invasion.

Introduction

Exotic organisms that physically or chemically modify ecosystems are among the most detrimental of invaders because they can strongly influence community structure and function (e.g., Vitousek et al. 1996, Mooney and Hobbs 2000, Talley and Levin 2001,

Crooks 2002). Early detection of incipient invasions and quickly coordinated responses are essential to effective management and/or eradication of invasive species before they become widely established (Federal Interagency Committee for the Management of Noxious and Exotic Weeds 2003). Thus, this letter documents an extensive invasion and modification of coastal salt marsh habitats by multiple species of trees and shrubs in the genus *Tamarix*.

Examples of ecosystem-altering plants can be found in wetlands across the United States (e.g., Zedler and Kercher 2004 and references therein, Neira et al. 2005). Despite these numerous wetland invaders in North America, until now most of the coastal salt marshes of southern California have been relatively free from the invasion of habitat-altering plants. The invasion of tamarisk or salt cedar (*Tamarix* spp.) into the Tijuana River National Estuarine Research Reserve (TR NERR) contrasts this trend, as the high intertidal, native pickleweed, *Sarcocornia pacifica* (=*Salicornia virginica*), marsh now supports dense stands of these salt-tolerant trees. This invasion converts the salt marsh from a succulent-dominated canopy of less than 1m to a landscape dominated by stands of woody trees that can grow to over 3 meters tall (Figure 3.1).

The genus, *Tamarix*, includes approximately 54 species several of which are known to hybridize. Nominated by The Nature Conservancy as one of America's twelve worst invaders (Stein and Flack 1996), tamarisks can be aggressive, woody invasive plants, and some species have become established over 1.5 million acres of floodplains, riparian areas, and freshwater wetlands in the western United States (Stenquist 2000). Tamarisks are native to Eurasia and Africa and are believed to have been first introduced into North America in the early 1800s by nurserymen (Di Tomaso 1998). Their westward spread

was facilitated by use as windbreaks, shade cover, erosion control or ornamental plants (Neill 1985). At least seven species of the genus have become established in the US (Baum 1978), and in riparian areas of the western United States, tamarisks, as a group, are the third most frequently occurring woody plant (Friedman et al. 2005).

Study site

The Tijuana River National Estuarine Research Reserve (TR NERR) is situated near Imperial Beach, in San Diego County, CA, on the US-Mexican border. The estuary is located at the mouth of the Tijuana River watershed, with over two-thirds of the 4420 km^2 watershed lying within Mexico (Zedler et al. 1992). Within the TR NERR, tamarisk is present throughout much of the reserve, including high pickleweed salt marshes, riparian habitats, and upland transition zones. Although tamarisk is known for its ability to tolerate relatively saline soils, it has not been typically viewed as an invader in areas of full marine salinity, such as coastal salt marshes, vegetated areas that are regularly inundated by at least the highest spring tides of each lunar month (Grossinger et al. 1998, California Exotic Pest Plant Council 1999).

Methods

Samples were collected from morphologically or geographically distinct plants and stored in vials with desiccant until analysis, and the fourth *Pep*C intron region of the genomic DNA was analyzed according to methods outlined in Gaskin and Schaal (2002, 2003). In addition, full cross sections of the trunk from each plant were obtained. Once back in the laboratory, these cross sections were sanded and polished with 400 grit sandpaper so that growth rings could be readily distinguished. The precise age of each plant (and thus the year of its invasion) was determined by cross-dating growth rings in

the sections using standard dendrochronological techniques (Stokes & Smiley 1996).

Results

Knowing the particular species of tamarisk that invaded Tijuana River NERR was important to understanding overall invasion dynamics as well as to potentially understanding tamarisk's ability to invade coastal salt marsh habitat. Initially, the tamarisk was identified morphologically as *Tamarix ramosissima*. However, genetic analysis revealed that there were, in fact, many species and hybrids within the *Tamarix* genus present in our study area. Out of 35 *Tamarix* spp. samples analyzed from the river valley, haplotypes from four different species were identified (Table 3.1).

Preliminary tree ring data indicates that 36% of all tamarisk examined (44 of 122 individuals) were established during the period of 1979-1984. Combining age data with historical data documenting extensive flooding in 1978, 1980 and 1983, we hypothesize that the tamarisk invasion within Tijuana River NERR most likely began in the early 1980's, perhaps benefited by flood conditions that decreased salinities and increased sediment deposition thus creating ideal germination spots along the river channel. Yet the true extent of the invasion and its potential for dramatic impact was fully appreciated only within the last five years. Preliminary data on the TR NERR habitat indicate dramatic structural changes to the salt marsh environment as a result of the presence of tamarisk. Tamarisk is acting as a physical support, facilitating *S. virginica* to reach heights far above its natural height. In addition, tamarisk alters physical conditions (such as temperature, humidity, and light regimes) under its canopy. Preliminary data about the sediment environment in tamarisk-invaded areas indicate that the invasion also influences the invertebrate and microalgal community compositions and biomass (Whitcraft et al.

unpublished), with additional ramifying effects throughout the food web (Talley et al. unpublished).

Discussion

Some hybridization and the presence of cryptic species in Tijuana River NERR would not have been surprising. However, the high number of different genotypes present within such a small sample set strongly suggests that a hybrid swarm of *Tamarix* spp. invaded TR NERR. Levels of introgression are unknowable from the single-locus DNA marker used initially, thus we are now genotyping samples using multi-locus AFLP (Amplified Fragment Length Polymorphism) markers and comparing these to the rest of the invasion. The genetic data are particularly worrisome, as hybrid plant lineages frequently demonstrate greater ecological amplitude than their parental species, invading ecological communities or habitat zones that have not been colonized by either parental species (Stace 1975, Daehler and Strong 1997, Neuffer & Hurka 1999). Hybridization is particularly common in populations that exist at the edges of their geographical or ecological range (Rieseberg 1997), as is presumably the case for tamarisk in the TR NERR.

The effects of tamarisk invasions have been well-documented for stream riparian areas. These include alterations of the chemical and physical conditions in its immediate environment as well as larger-scale effects on the entire invaded ecosystem (Ellis 1995, Di Tomaso 1998, Zavaleta 2000). Despite numerous, uninvestigated anecdotal reports, the invasion in Tijuana River NERR is the first studied example of a coastal salt marsh being invaded by tamarisk, and thus very little is known about the potential effects of tamarisk in this novel and particularly threatened habitat. Based on responses of riparian

communities, we predict that this invasion will dramatically affect the physical environment, which could translate into community-level effects for marsh biota (Stevens 2000, Crooks 2002). To combat this invasion in southern California, state- and federally-funded tamarisk eradication efforts have recently begun, providing a template for research and adaptive management (California Exotic Pest Plant Council 1999).

The invasion of tamarisk into the Tijuana River National Estuarine Research Reserve provides a clear indication that already dwindling coastal salt marshes are vulnerable to invasion by these plants. More broadly, the study of this invasion will assist us not only to quantify the possible effects of tamarisk invasions in salt marsh habitats but also help us to more broadly understand the structuring roles of invasive plants in wetlands. Studying the genetics aspect of this invasion contributes to theories on rapid evolutionary processes and invasion and paves the way for studies addressing physical, ecological, and genetic pathways of invasion. Friedman et al. (2005) noted that the debate regarding appropriate control of tamarisk has been frustrated by limited knowledge of the distribution and underlying environmental influences. These are particularly important data to collect regarding the tamarisk invasion into salt marsh habitats; knowing the consequences of the invasion into this novel system will provide managers and decision makers with invaluable information about the relative invasion potential of different species (and hybrids) of tamarisk, thus facilitating more informed management decisions.

a)

b)

Figure 3.1: Photographs showing contrast between a) the natural marsh landscape with short, succulent-dominated canopy (mainly *Salicornia virginica*) and b) an area invaded by invasive *Tamarix* spp., a woody plant that can grow to over 3m tall. Pictures were taken in Tijuana River National Estuarine Research Reserve, Imperial Beach, CA.

Table 3.1. Genetic species identification of 37 tamarisk samples collected from Tijuana River NERRS and associated river valley.

Species	# of plants of 39 sampled
T. aphylla	1
T. chinensis	1
T. chinensis x *T. gallica*	4
T. chinensis x *T. ramosissima*	6
T. gallica	2
T. ramosissima	16
T. ramosissima x *T. gallica*	5

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CHAPTER IV

"TERRESTRIALIZATION" OF COASTAL WETLAND ECOSYSTEMS BY A
RIPARIAN INVADER

Abstract

Invasions by introduced plants are currently one of the most serious threats to

biodiversity, and the impacts of various invaders have been documented throughout

multiple ecosystems. In addition to altering ecosystem structure, invasive plant species

may also be capable of changing the pace and/or direction of autogenic succession,

especially within ecotones such as wetlands. One of the most problematic invaders in the

western United States has been salt cedar, *Tamarix* spp.; the impacts of this species in

riparian and desert ecosystems have been well documented. Large stands of different

invasive genotypes of tamarisk now reside in the salt marshes in Tijuana River National

Estuarine Research Reserve (TRNERR). Salt marshes are a habitat not previously

considered vulnerable to invasion by tamarisk. We hypothesized that the tamarisk

invasion into TRNERR would "terrestrialize" the salt marsh habitat; in other words, the

invasion would speed natural succession towards a more terrestrial environment. Using

mensurative comparisons in a paired block design, we described the impact of tamarisk

invasion on abiotic and biotic properties of the sediment ecosystem in three zones along

an elevation and salinity gradient. In the low marsh, tamarisk-invaded areas exhibited

similar physical properties and microalgal community to the native succulent-dominated area with a slightly altered macrofaunal community composition. In the middle marsh zone, the physical environment was significantly drier, less humid with lower temperatures and increased light reduction. These physical changes were associated with increased microalgal biomass and increased abundance of mites and insects and a decreased density of marine oligochaetes and epifunal gastropods compared to native treatment plots. Within the high marsh, changes in physical and biological parameters between tamarisk-invaded and natural plots were again minimal. This research emphasizes the habitat-altering consequences of tamarisk's first foray into the marine realm while also revealing that each marsh habitat subject to tamarisk invasion will have to be managed with different eradication strategies.

Introduction

Terrestrialization is a common term used by riverine wetland ecologists to describe the change from a wetland to a terrestrial ecosystem due to the accumulation of sediment and organic matter or to the lowering of the water level (Henry and Amoros 1995). Often colonization by particular plant species can initiate or accelerate the terrestrialization process by increasing the production and accumulation of biomass and by increasing evapotranspiration rates (Tallis 1973, Amoros et al. 1987).

Salt marsh ecologists describe succession within salt marshes as the accumulation of alluvial sediments from the seaward edge that increases elevation and accelerates a transition towards a more terrestrial habitat (Adams 1990, 2002, van de Koppel et al. 2005). However, the term terrestrialization has not been applied previously to the salt marsh system. We argue that as a recognized mechanism of autogenic succession in

other systems, the concept of terrestrialization applies to the situation in salt marshes where colonization or invasion by plants modifies the environment and influences the performance of other species to create a more terrestrial environment (Davy 2000).

Exotic plants are one of the greatest threats to wetlands, as they are capable of altering ecosystem-wide physical and biological properties (Lonsdale 1999). Because coastal salt marshes develop at the boundary of the terrestrial, freshwater and marine habitats, they are susceptible to anthropogenic influences, such as invasion, from multiple ecosystems (van de Koppel et al. 2005, Levin et al. 2001). In these often low-diversity systems, shifts in diversity due to invasion are likely to alter ecosystem functioning or natural processes, such as succession (Levin et al. 2001).

Previous research has shown that invasion into salt marshes by typically terrestrial or freshwater, non-native plants can alter successional development of salt marshes. A hybrid form of *Sarcocornia* was able to colonize lower in elevation than either parent species and played an important role in structuring its intermediate elevation habitat (Figueroa et al. 2003). Until recently, *Phragmites* has been considered a freshwater and terrestrial invader, prevented from invading salt marshes by high soil salinities (Chambers et al. 1999, Silliman and Bertness 2004). Through clonal integration, *Phragmites* has proven quite able to invade areas of full salinity along east coast of the United States (Amesberry et al. 2000, Michinton and Bertness 2003). Its successful invasion in New England marshes was facilitated genetically as well as by increased nutrient loading and freshwater input (Silliman and Bertness 2004). The expansion of *Phragmites* represents a dramatic habitat alteration with severe reductions in insect, avian, and other animal assemblages (Chambers et al. 1999, Talley and Levin 2001). The

effect of *Phragmites* on trophic transfer is related to the amount of hydrologic disturbance, but in wetlands of restricted flow, alteration of trophic transfer pathways by *Phragmites* is linked to decreases in birds and insects (Chambers et al. 1999).

Tamarisk is an aggressive, woody invasive plant from Eurasia that is traditionally associated with salty, dry, or riparian habitats (Baum 1978, Brotherson 1987) and has become established on over 1.5 million acres in the western United States (Stenquist 2000). *Tamarix* spp. (tamarisk or saltcedar) has formed dense stands along brackish streams, within the high intertidal salt marsh, and within the upland transition zone of Tijuana River National Estuarine Research Reserve (TR NERR) (Whitcraft et al. in press). We hypothesize that the flood conditions in the 1980's that decreased salinities and increased sediment deposition created ideal germination spots along the river channel, thus facilitating an invasion of tamarisk within TR NERR (Whitcraft et al. in press). Extensive work has been conducted documenting the effects of tamarisk in freshwater riparian ecosystems where tamarisk has caused significant changes in flooding and erosion patterns, fire frequency, water utilization, and decreased wildlife value (Di Tomaso 1998, Lovich et al. 1994). The effect has been referred to as "overall drying out of the habitat" (Di Tomaso 1996). Although the effects of tamarisk invasion are well-documented in freshwater systems, the tamarisk invasion into marine systems is very recent, and the impacts of tamarisk invasion on salt marshes are unknown. Given tamarisk's known effects in riparian areas, we hypothesized that tamarisk invasion would affect physical resources and biotic communities, thus accelerating terrestrialization within the salt marsh.

The overall objectives of this study were to test how tamarisk introduction to coastal wetlands can influence the abiotic and sediment properties and the benthic floral and faunal communities and to test if changes would drive autogenic succession within a salt marsh system. We hypothesized that, relative to the corresponding natural marsh environment, the invaded system would resemble a more terrestrial system with drier, less organic rich sediment, increased temperature, decreased humidity, increased light reaching sediment surface, decreased algal growth, and altered infauna community structure (i.e., increased percent composition of insects, decreased percent oligochaetes and polychaetes). In addition, we evaluated the influence of tamarisk within three natural plant zones along a marine to terrestrial continuum (low, middle, and high marshes).

Study site

Studies were conducted in the Tijuana River National Estuarine Research Reserve (TR NERR), which is situated near Imperial Beach, in San Diego County, CA, on the US-Mexican border. The estuary is located at the mouth of the Tijuana River watershed, with two-thirds of the 4420 km^2 watershed lying within Mexico (Zedler et al. 1992). Within TR NERR, tamarisk is present throughout 60% of the reserve, including middle and upper pickleweed salt marshes, riparian habitats, and upland transition zones (UTZ) (Figure 4.1).

Materials and Methods

Paired sampling plots were established using a randomized complete block design with replicate plots in the salt marsh that included (a) a treatment plot encompassing the drip line (the imaginary line drawn to the soil from the edge of the tree canopy) of a single tamarisk tree (referred to as tamarisk plots) and (b) a control plot in native

vegetation of same area as its paired tamarisk-invaded plot (referred to as native plots) (Figure 4.2). The average plot area was 9.28 ± 1.87 m^2 with a range from 0.46 m^2 to 28.14 m^2. Sampling occurred in these paired vegetation areas in Fall 2003, Spring 2004, Fall 2004 and Spring 2005. To determine differences between tamarisk-invaded areas and native vegetation zones within each habitat, we surveyed abiotic and sediment properties as well as plant, microalgae, and macroinvertebrate community properties within each plot.

Blocks were initially classified into three habitat zones (low marsh, middle marsh, and high marsh) based on elevation and plant species present. An *a posteriori* analysis was conducted to reassess the assignment of blocks into the three major habitat types, and final determination was made using hierarchical divisive clustering analysis of sediment and physical parameters, percent plant cover, and algal data within the native plots within a given season (Kaufman and Rousseeuw 1990). Sediment variables used in the cluster analysis were porewater temperature, water content, and organic matter content. Algal data used in the cluster analysis included benthic chlorophyll *a*, while percent cover variables included total percent cover of each species, greatest plant height, number of species present, and percent bare area. This yielded 4 paired plots in the low marsh, 10 paired plots in the middle marsh, and 9 paired plots in the high marsh.

Abiotic and sediment properties: Within each treatment plot, temperature ($\pm$ 0.1°C) and redox potential at 2 cm depth were measured using a portable Ingold Mettler-Toledo digital thermometer and a portable Mettler Toledo mV-meter, respectively. These 4 mV redox readings were corrected to the standard hydrogen electrode value by adding 207 mV (Giere et al. 1988). Temperature at the sediment surface was also measured

hourly using StowAway Tidbit Temp Loggers (Onset Computer Corporation, Pocasset, MA). Water content of the top 0.5 cm was determined by weight loss after drying a known volume of sediment (Buchanan 1984). Humidity at the sediment surface was measured using Fisher Scientific digital relative humidity meter. Light intensity readings were also made hourly using StowAway LI light intensity loggers (Onset Computer Corporation, Pocasset, MA). One sediment core (4.8 cm diameter x 6 cm) was collected within each treatment plot for analysis of particle size and organic matter content (Neira et al. 2005).

Plant and algae parameters: Bare area and plant cover estimates for each species were made in three permanent randomly placed $0.25m^2$ quadrats within the tamarisk and native plots, and the height of the tallest marsh (i.e. not tamarisk) species was measured. Also in each larger vegetation area, one core was taken haphazardly for chlorophyll *a* ($0.95cm^2$ x 5mm) to provide a proxy for microalgal biomass. Once back in the laboratory, chlorophyll *a* was extracted with 90% acetone, and the concentration was determined spectrophotometrically (Plante-Cuny 1973).

Macrofauna sampling: Macrofaunal cores were taken in each vegetation area using a cylindrical push core (4.8 cm diameter, 18.1 cm^2) inserted to a depth of 2 cm. Most of the macrofauna (78 – 89%) in southern California marshes is found in the top 2 cm of sediment (Levin et al. 1998). Cores were preserved (unsieved) in 8% buffered formalin with Rose Bengal. For macrofaunal quantification, the core sediments were washed through a 0.3 mm mesh. The animals retained were sorted under a dissecting microscope at 12x magnification, identified to the lowest possible taxonomic level, counted, and stored in 70% ethanol. In addition, all epifauna within a subsection (0.25

m^2) of each treatment plot were identified visually and enumerated.

Statistical Analysis: All univariate tests were conducted with JMP 5.1 statistical software (SAS Institute, NC, USA). Data were tested for normality and square root or $\log_{10}$-transformed as needed prior to analysis. If no transformation yielded normal data, nonparametric Wilcoxon tests were utilized. Comparisons of abiotic, sediment, and algal properties, macrofauna percent composition, and macrofauna species-level density, abundance, richness, diversity and biomass data among vegetation types (tamarisk versus native) were conducted with paired t-tests within habitat zone followed by *a posteriori* Tukey's HSD tests. In figures, one standard error about the mean is presented for all data unless otherwise noted.

Multivariate non-metric multi-dimensional scaling (nMDS) analyses were carried out on macrofaunal count data (4th root transformed) using Primer 5 (Plymouth Marine Laboratory, Clarke 1993, Clark and Warwick 1994). Analyses are based on Bray-Curtis similarity indices (Clarke 1993). Pairwise comparisons of overall community similarity were made using Analysis of Similarity (ANOSIM) and SIMPER. Second-stage nMDS and an additional ANOSIM test were used to determine if invertebrate communities from tamarisk-invaded plots had a significantly different trajectory of change through time than those from native vegetation plots (Clarke et al. 2006).

Results

Habitat designations: We have used the terms, low, middle and high marsh, as relative names to clearly refer to different elevations within the estuary. The low marsh habitat was inundated daily and dominated by *Sarcocornia pacifica* (*Salicornia virginica* in the literature). The middle marsh habitat was defined to be an area inundated during

positive tides of each cycle (usually classified as high marsh habitat), and its plant community was dominated by *S. pacifica* and *Frankenia grandifolia*. The high marsh could also be termed an upland transition zone (UTZ) and was irregularly inundated at only the highest tides of each cycle. Its plant community was also dominated by *S. pacifica* with significantly higher percentages of *Jaumea cornosa* than the other habitat zones ($\chi^2 = 6.78$, P = 0.009).

Abiotic and sediment properties: Because patterns seen in the incident light and sediment surface temperature were consistent throughout all seasons and years (Table 4.1), the data from multiple seasons are discussed together. In the middle marsh, sediment beneath tamarisk demonstrated consistently lower incident light and lower porewater temperatures during the day than under native vegetation over the duration of the experiment as measured both by continuous data loggers (light: t = 3.13, P = 0.002, n = 360) (temperature: t = 7.62, P < 0.0001, n = 109) (Figure 4.3 a,b) and by a hand-held thermometer (Table 4.1). At night, continuous loggers recorded higher temperature under the tamarisk plots than under the natural vegetation, suggesting tamarisk might provide an insulating influence (t = 13.47, P < 0.0001, n = 70). Within the high marsh in three seasons, tamarisk-invaded plots had a decreased temperature within the sediments (at a depth of 1cm) than native plots (P < 0.05) (Table 4.1). Redox potential measurements were extremely variable among blocks, seasons, and plant species and did not demonstrate any effects related to tamarisk or habitat. Of all the other physical parameters, only water content showed a pattern among seasons and years with decreased porewater content in the natural vegetation areas in the middle marsh in Fall 2004 (Wilcoxon, Fall 2003, Spring 2005 > Fall 2003, $\chi^2_2 = 6.47$, P = 0.039) (Table 4.1).

Within the low marsh environment, sediment characteristics (grain size, organic matter content, temperature, water content) did not differ between tamarisk-invaded and native areas (Table 4.1). In the middle marsh habitat, significant differences in physical characteristics existed among the habitats. In most seasons where data were available, tamarisk-invaded areas had drier conditions with lower percent soil organic matter content (Fall 2003: native, 17.73 ± 4.34 %, tamarisk, 10.50 ± 1.36 %, $t_6 = 2.50$, P = 0.047), decreased humidity (Spring 2005: native, 33.50 ± 9.32 %, tamarisk, 29.6 ± 8.37 %, $t_8 = 2.23$, P = 0.056), and decreased porewater content (Fall 2003: native, 0.37 ± 0.03 g / core, tamarisk, 0.28 ± 0.02 g/core, $t_8 = 1.53$, P = 0.051). There was an increased percent organic matter in the tamarisk-invaded plots relative to the natives in Spring 2005 only (native, 10.94 ± 2.48 %, tamarisk, 14.32 ± 2.22 %, $t_6 = 3.01$, P = 0.024) (Table 4.1).

Plant community: The plant community response to tamarisk invasion did not differ between years and seasons so all results are summarized together (Table 4.1). In general, species richness and species composition were similar in native versus tamarisk-invaded plots within each habitat. However, the amount of bare space under tamarisk trees in all habitats was significantly greater than under native vegetation in all seasons (P < 0.05, Table 4.1). Because the native plants in tamarisk plots were often supported by the structure of the tamarisk branches and trunk, the height of the tallest marsh species, usually *S. pacifica* or *F. grandifolia*, was also significantly greater under tamarisk trees than in native plots in all habitats (P < 0.05, Table 4.1, Figure 4.4).

Microalgal community: Chlorophyll *a* values varied by block within season but did not differ among seasons (P > 0.05) (Table 4.1). Tamarisk treatment plots had higher chlorophyll *a* concentrations than native vegetation treatment plots in Fall 2003 and

Spring 2005 in the middle marsh habitat (all units µg/g sediment; Fall: native = 14.87 ±

4.93, tamarisk = 28.07 ± 6.92, t_{10} = 2.58, P = 0.027; Spring: native =16.43 ± 6.34,

tamarisk = 30.98 ± 8.06, t_3 = 9.91, P = 0.010) (Table 4.1). In the low and high marshes,

chlorophyll *a* concentration did not differ between tamarisk-invaded areas and native

areas (Table 4.1).

Macrofauna: The response of the macrofauna in the upper 0-2 cm differed among

habitats and seasons so all results are discussed separately with details of season and

habitat type given in Table 4.2. No significant changes existed among community

parameters within the low marsh (Table 4.2). In Fall 2003, tamarisk-invaded areas in the

middle marsh exhibited a reduction in species richness (t_4 = 3.16, P=0.030) and decreased

density of organisms (t_4 = 2.39, P = 0.050) relative to the native vegetation areas (Table

4.1). Other seasons exhibited a similar pattern, but with lowered densities and increased

variability, many of these differences disappeared. Density and richness changes in

tamarisk-invaded areas involved a significant percentage loss of marine enchytraid

oligochaetes and an increase in terrestrial insect larvae (Figure 4.5, Tables 4.2 a,b). This

percent increase of insect larvae in tamarisk-invaded areas was primarily driven by a

density increase in Coleoptera larvae sp. 1 in two seasons (Fall 2003: native = 4.40 ± 2.87

larvae, tam = 13.60 ± 4.23 larvae, t_6 = 3.84, P = 0.019; Spring 2004: native = 0.00 larvae,

tamarisk = 18.80 ± 5.86 larvae, t_6 = 3.21, P = 0.033). In Spring 2004 and 2005 in the

high marsh habitat, tamarisk-invaded areas exhibited a significant percentage increase in

crustaceas, primarily *Littorophiloscia richardsonae* (an oniscid isopod) (Spring 2004:

native = 0.00 isopods, tamarisk = 53.07 ± 21.17 isopods, t_4 = 2.51, P = 0.051; Spring

2005: native = 16.67 ± 16.67 isopods, tamarisk = 56.67 ± 21.86 isopods, t_6 = 6.93, P =

0.020) (Table 4.2).

We observed positive relationships between water content and the density and species richness of total macrofauna in Fall 2003 as well as between algal biomass (chlorophyll *a*) and density of insects in Fall 2003 and Spring 2005 when vegetation areas and habitats were pooled. Increases in algal biomass were positively correlated with increased insect density (Figure 4.6).

Univariate statistics often don't show change on the assemblage level, thus we have also utilized multivariate statistics that better capture community change (Clarke et al. 2006). In Fall 2004, the low marsh tamarisk-communities showed no difference than the native vegetation plots (ANOSIM, P = 0.200). In Fall 2003 in the high marsh, the macrofaunal communities of the tamarisk-invaded plots were significantly different than the native vegetation plots (high marsh: ANOSIM, P = 0.008) while the middle marsh communities were similar (middle marsh: ANOSIM, P = 0.865). These differences in the high marsh environment were driven by a decreased density of *Littorophiloscia richardsonae* (an oniscid isopod) and an increased density of Coleoptera larvae sp. 1 in tamarisk-invaded plots (SIMPER). In the middle marsh in Spring 2004, the macrofaunal community in the tamarisk-invaded plots was significantly different from the community in native vegetation plots (middle marsh: ANOSIM, P = 0.002). Although the high marsh community appeared to follow the trend, it was not significant (high marsh: ANOSIM, P = 0.100). The altered composition in the middle marsh was caused by similar species as seen in the high marsh in the previous seasons, an increased density of mites and Coleoptera larvae in the tamarisk-invaded plots (SIMPER) as in more terrestrial environments. These composition changes were also reflected in species

density changes as the mite sp. 2 increased in the tamarisk plots (tamarisk: 0, native: 6.00

$+$ 3.34, χ^2_1 = 3.94, P = 0.011). In Fall 2004 and Spring 2005, there were no macrofaunal

community differences between tamarisk-invaded plots and native vegetation plots

(ANOSIM, P > 0.05). Using nMDS, the communities do cluster by vegetation type

(tamarisk versus native) in the high marsh in Fall 2003, within middle and high habitats

in Spring 2004, in the low and middle marshes in Fall 2004, and in the high marsh in

Spring 2005 (Figure 4.6).

Overall, the most common epifaunal species was the native, grazing snail,

Melampus olivaceus. In tamarisk-invaded plots in the low and middle marsh, the density

of *M. olivaceus* was significantly reduced as compared to native plots (low marsh: 11.88

$\pm$ 3.84 *M. olivaceus* / 0.25 m^2 vs. 1.88 $\pm$ 0.69 *M. olivaceus* / 0.25 m^2, t = 2.40, P = 0.048;

middle marsh: 2.55 $\pm$ 1.46 *M. olivaceus* / 0.25 m^2 vs. 9.44 $\pm$ 3.54 *M. olivaceus* / 0.25 m^2, t

= 2.85, P = 0.008) while in the high marsh, *M. olivaceus* occurred infrequently in both

tamarisk-invaded and native plots (0 vs. 1.76 $\pm$ 1.34 *M. olivaceus* / 0.25 m^2, t = 1.31, P =

0.199).

Discussion

Tamarisk effects on sediment and fauna: Tamarisk influence on abiotic

conditions, algal and infaunal communities varied among marsh zones. Little tamarisk

influence was observed in the low and highest marsh zones. In the middle marsh habitat,

tamarisk-invaded areas had drier, more terrestrial conditions with decreased soil organic

matter content, decreased humidity, decreased porewater content, and increased

chlorophyll *a* values relative to the native vegetation areas (Figure 4.8).

Changes in algal biomass in middle marsh tamarisk-invaded areas probably influenced the community structure of macroinvertebrate consumers (Figure 4.6) because algae are a high quality food resource with lower CHN ratios than tamarisk litter (Whitcraft et al. in prep, Kennedy and Hobbie 2004, Anderson and Sedell 1979). The increased algal biomass in tamarisk-invaded areas in the middle marsh, as indicated by chlorophyll *a* concentration, could be caused by several factors: (1) increased shade causing an increased chlorophyll *a* to carbon ratio (Wetzel 2001), (2) increased bare area, removing the competition for open space that occurs under the native vegetation, or (3) decreased grazing due to a decline in density of microalgal grazers like the gastropod, *Melampus olivaceus*.

In the middle marsh environment, the epifaunal community composition was significantly altered by the loss of marsh species, such as the pulmonate gastropod, *M. olivaceus*. These animals potentially contribute to the decomposition and detrital cycling of the system (Proffitt et al. 1993, Whitcraft et al. in press) and could then be essential to the maintenance of coastal food webs. Thus, their loss could have cascading impacts on the food web in tamarisk-invaded areas. Regardless of the causes of the change, an increased algal mat could translate into community-level effects in the form of an increased food supply or increase in microalgal grazers, such as seen in Fall 2003 with increased density of insect larvae in tamarisk-invaded areas. In the low and high marshes, the fact that no differences existed among tamarisk and native plots again seemed indicative of inundation regimes. In the high marsh, algal biomass was low due to dry conditions throughout the zone while in the low marsh, algal biomass was consistently high.

The infaunal communities are more variable among seasons and plots than the physical parameters (Figure 4.5). In Fall 2003 and Spring 2004 in the middle marsh, we observed significant community composition differences between tamarisk-invaded and native vegetation plots that involved the loss of burrowing marine oligochaetes and an increase in surface-dwelling species, such as Coleoptera and mites. The loss of oligochaetes could be related to grater susceptibility of these species to changes in abiotic parameters, food supply, flow, or variation in predation pressure (Neira et al. 2005). Manipulative experiments should be conducted to tease out the mechanisms behind this faunal loss. Variability among the sampling seasons and years (Tables 4.1 & 4.2) could be explained by a wetter year preceding Fall 2004 and Spring 2005 than preceding Fall 2003 and Spring 2004 (Figure 4.9). The increased amount of rain would have created wetter conditions under tamarisk plots, potentially reducing invaded versus native community differences.

Influence of salinity and tidal height: Differences in physical parameters, microalgal biomasses, and invertebrate communities among the three habitats indicate that the effects of tamarisk invasion are very elevation-specific. In the low marsh, inundated at least once daily, few differences existed between invaded and native plots, leading us to hypothesize that the effects of tamarisk are ameliorated by constant salt water inundation. In the middle marsh environment, there are significant changes in physical parameters that follow our *apriori* hypotheses that tamarisk-invaded areas would have more terrestrial environmental and sediment conditions (decreased humidity, lower sediment porewater content, and decreased sediment organic matter content) (Table 4.1). Finally, in the high marsh, few differences, with the exception of reduced temperature

(most likely due to decreased light) existed between tamarisk-invaded and native plots (Figures 4.3 & 4.8). Impacts of invasive plants have been previously demonstrated to vary along salinity gradients, especially in the case of *Phragmites* where the strongest effects, particularly on invertebrate community composition, were evident in the least saline settings (Talley and Levin 2001). In addition to tidal elevation, contributing factors may include variation among microhabitats, time since invasion, and genetic differences among the trees.

Comparisons with freshwater tamarisk invasions: Research on tamarisk in freshwater systems has documented more xeric conditions (Lovich et al. 1994, Lovich and de Gouvenain 1998), lowered water tables due to increased water use (Van Hylckama, 1970, Everitt, 1980, Sala, Smith & Devitt 1996), increased soil salinities (Duncan 1994), decreased abundance and health of native vegetation (Everitt, 1980, Busch & Smith, 1995), increased algal production (Kennedy and Hobbie 2004), altered plant community composition (Carmen and Brotherson 1982, Griffen et al. 1989), changes in algal production (Kennie and Hobbie 2004), and lowered density, diversity and species richness of animal communities (Kerpez and Smith 1987) in tamarisk areas relative to native vegetation areas. The tamarisk invasion into a marine system appears to have similar consequences: drier physical conditions similar to those of a decreased water table area, increased microalgal biomass, and altered infaunal communities. However, since the soils are already saline in a marine environment, increased salt deposition is not a significant effect in the salt marsh system. We hypothesize that the role of salinity is most important as it relates to tidal inundation, affecting the magnitude of tamarisk effects. In addition, the native plant community associated with tamarisk in a

marine environment did not shift in composition (except for addition of tamarisk) although tamarisk-invaded plots do have increased percent bare space relative to native plant communities (Table 4.1). Instead of lowered plant fitness as seen in freshwater systems, there may be some fitness advantage to native plants through pre-emptive access to light that is conferred to the plants that are able to use structure of tamarisk to grow taller than those in the native vegetation areas (Figure 4.4 a,b) (Falster and Westoby 2003). Research on tamarisk invasion into the salt marsh environment demonstrates changes in the same ecosystem parameters as those affected in freshwater systems. However, perhaps due to a more striking difference between native vegetation (short, succulent) and tamarisk (woody shrub or tree) in the salt marsh as opposed to riparian systems where both are shrubs or trees (Figure 4.10), the abiotic parameter alterations as well as the impacts on the microinvertebrate community appear to be of a greater magnitude than in freshwater systems.

Patterns among salt marsh invaders: There are few consistent, general trends evident in comparisons of physical conditions and macrobenthos inhabiting invasive versus native marsh vegetation, even when considered only one genus (e.g. tamarisk, this study or *Spartina*, Neira et al. 2005). Just as the benthic response to tamarisk invasion in TR NERR varied by marsh zone, the benthic response reported among invaders varies with location and with the dominant plant in the native habitat (Talley and Levin 2001, Neira et al. 2005).

However, comparisons with invasions of *Spartina* and *Phragmites* into salt marsh habitats have important parallels to the tamarisk invasion into TR NERR habitats. In a *Salicornia* marsh in San Francisco, CA, Neira et al. (2005) observed higher species

richness and increased densities of tubificid species, insect larvae, and gastropods within the *Spartina*-invaded than native *Salicornia* habitat. In a tidal flat in the same area, the same study found lower total density and species richness in the *Spartina* hybrid invaded areas than in the tidal flat, due to a loss of surface feeders (Neira et al. 2005, Levin et al. 2006). These habitat-specific effects emphasized that both elevation and the dominant native species surrounding the invasion influence the magnitude and type of effects that an invader will have on the benthic communities. The salt marsh areas invaded by *Phragmites* had decreased organic matter content, decreased macrofaunal density, and altered macroinvertebrate community composition with a loss of burrowing oligochaetes and midges and an increase in poduridae (Talley and Levin 2001). This loss of marine oligochaetes and increase in more terrestrial fauna like insects parallels the patterns of loss (decrease in enchytriadae oligochaetes and increase in Coleoptera) seen in the TR NERR tamarisk invasion. Terrestrialization of the benthic environment by an invasive plant appears to be a pattern that repeats when plants typically found in higher tidal elevations (either upland or marine) become capable of colonizing areas lower in elevation (such as mudflats or salt marshes).

Consequences of tamarisk invasion and management implications: The conclusion that tamarisk-invaded areas have altered vegetation structure, sediment properties, and invertebrate communities is not a surprise. In fact, wetlands and the high marsh have been predicted to be particularly vulnerable to invasions (Posey et al. 1993, Adam 2002), and invasive wetland plants have repeatedly been demonstrated to dramatically modify their surroundings (e.g. Posey 1988, Zedler and Kercher 2004 and references therein, Chambers et al. 1999, Grosholz et al. in press). Our research

contributes to understanding of tamarisk invasions by describing a community process of "terrestrialization" that changes depending on tidal elevation (Figure 4.7). In the case of tamarisk, the most vulnerable zone to tamarisk invasion appears to be the middle marsh, where conditions are less extreme. In the high and the low marshes, the tamarisk-invaded areas had more similar physical environment in the native vegetation zone than in the middle marsh. In the low marsh, frequent tidal inundation appeared to decrease tamarisk's ability to cause drier conditions; in the high marsh, where abiotic conditions are naturally quite dry, tamarisk did not cause drier conditions and might have even provided less harsh environment for infauna by reducing light intensity (Figure 4.3).

Experiments have demonstrated that the light reduction function provided by the vascular plant canopy is crucial to maintaining the natural biotic community of southern California salt marsh sediments in a zone where physical stressors dominate, such as the middle marsh (Whitcraft and Levin, in press). Our research demonstrates that one of tamarisk's greatest abiotic alterations is to reduce the amount of light reaching the sediment surface, thus we predict that harsher physical properties in the middle marsh are driving changes in the biotic communities. Further manipulative experiments should be conducted to determine the exact mechanisms of tamarisk's ability to alter its surroundings, particularly in the middle marsh

Within Tijuana Estuary, tamarisk is now identified as an important salt marsh invader with significant impacts on the ecosystem that are very context-specific with abiotic setting determining the strength of the interactions. This has important implications for managers, particularly for focusing effort and selection of eradication techniques. Based on our results, we predict that if tamarisk trees are removed from low

and high marshes, physical conditions (water content, temperature, humidity) would easily return to conditions characteristic of the surrounding natural marsh because the alterations were not significant. However, eradication in the low and high marsh might still be advisable due to other potential tamarisk effects not discussed in this study, such as higher order trophic effects and roosting sites for predatory birds. Post-eradiation areas in the middle marsh might need additional treatment (i.e. mechanical, chemical) to promote the return of native fauna and flora. While experimental manipulation is necessary to understand the exact mechanisms and processes that control marsh development, our research highlights the roles of tamarisk in altering physical conditions for associated algae and macroinvertebrates and thus hastening succession to a terrestrial regime in the middle marsh environment.

<p style="text-align:center">Acknowledgements</p>

Figure 4.1: Overview of tamarisk invasion into Tijuana River National Estuarine Research Reserve (TRNERR). Estimated densities of tamarisk are outlined with hatching over aerial photograph of the reserve. Figure created by J. Boland and K. Cody.

a) tamarisk treatment plot   b) control plot: native vegetation

Figure 4.2: Treatments for mensurative comparison of parameters associated with tamarisk invasion: (a) tamarisk plot and (b) control plot in native vegetation.
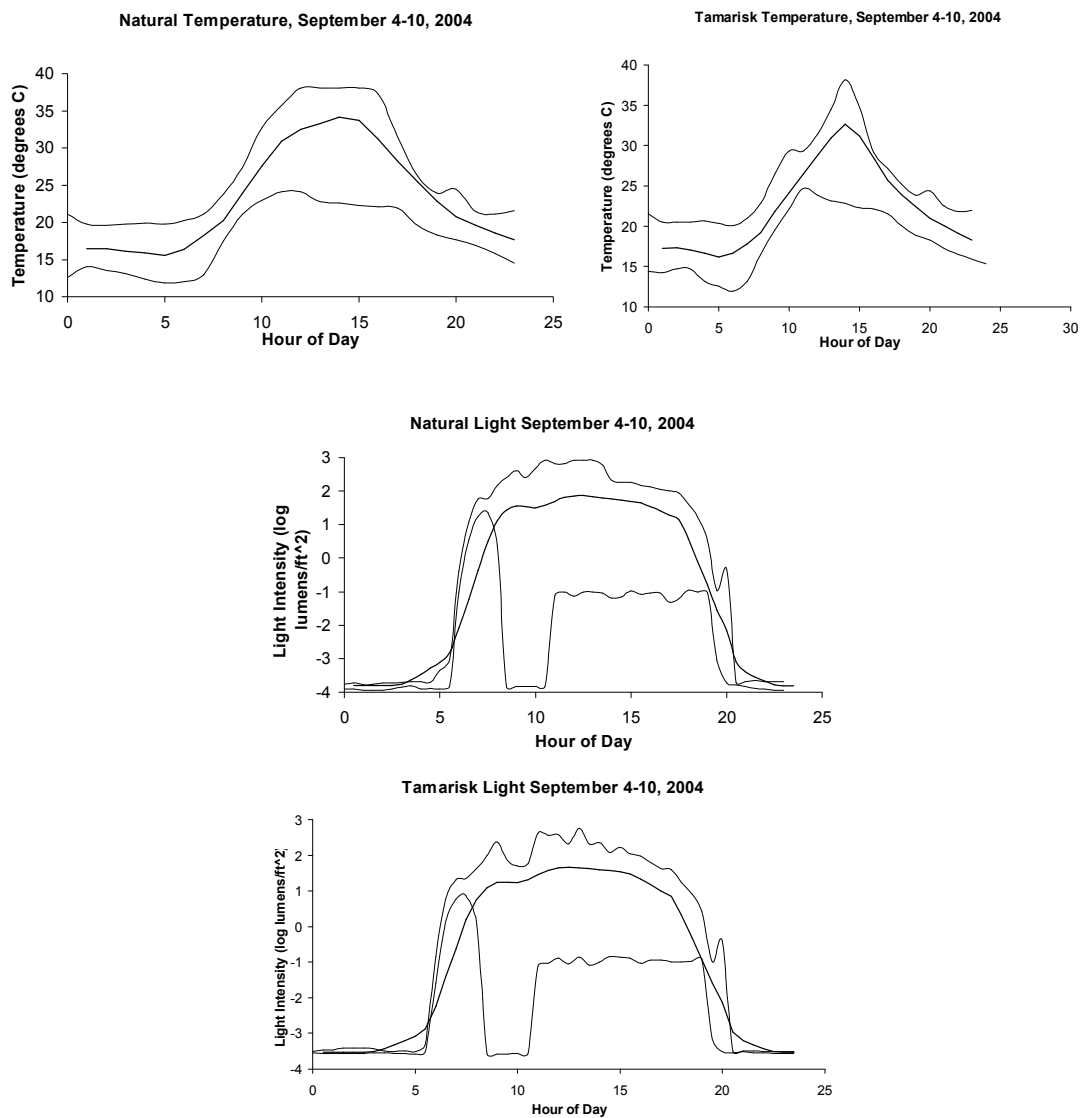
Figure 4.3: Graphs showing average, minimum and maximum native vegetation plot values versus tamarisk-invaded plot values for both temperature (ºC) and light (log lumen/ft^2) over a 5-6 day period in September 2004 in the middle and high marsh habitats. The entire x-axis represents a 24-hour period, divided into 4 hour intervals, and the values graphed on the y-axis are an average of values for the 6 days described.

(a)

(b)
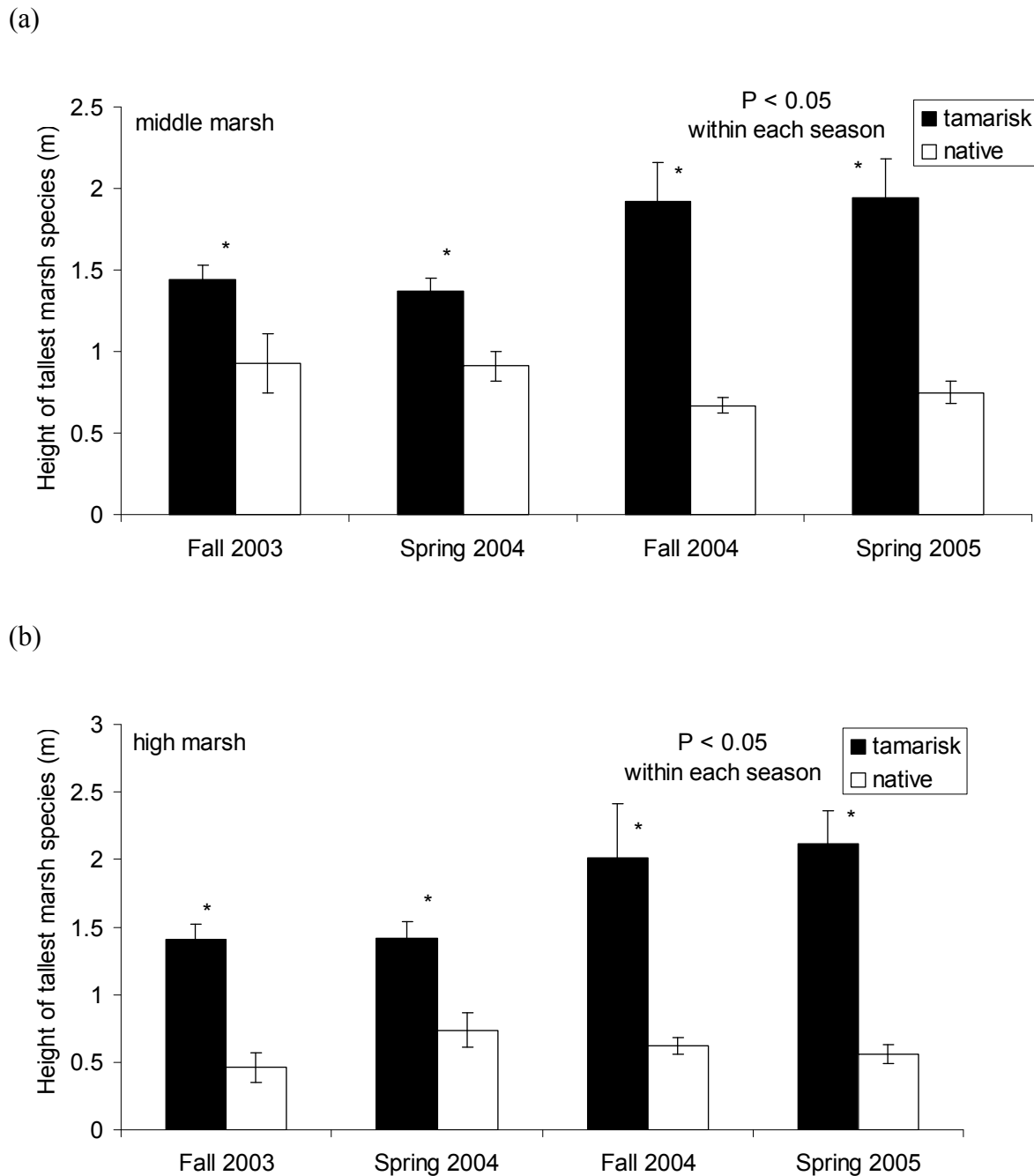
Figure 4.4: Graphs showing height of tallest marsh species in native vegetation plots versus tamarisk-invaded plots in (a) middle marsh and (b) high marsh habitats. Significant differences ($P < 0.05$) within season between plots are indicated with an asterisk**.**
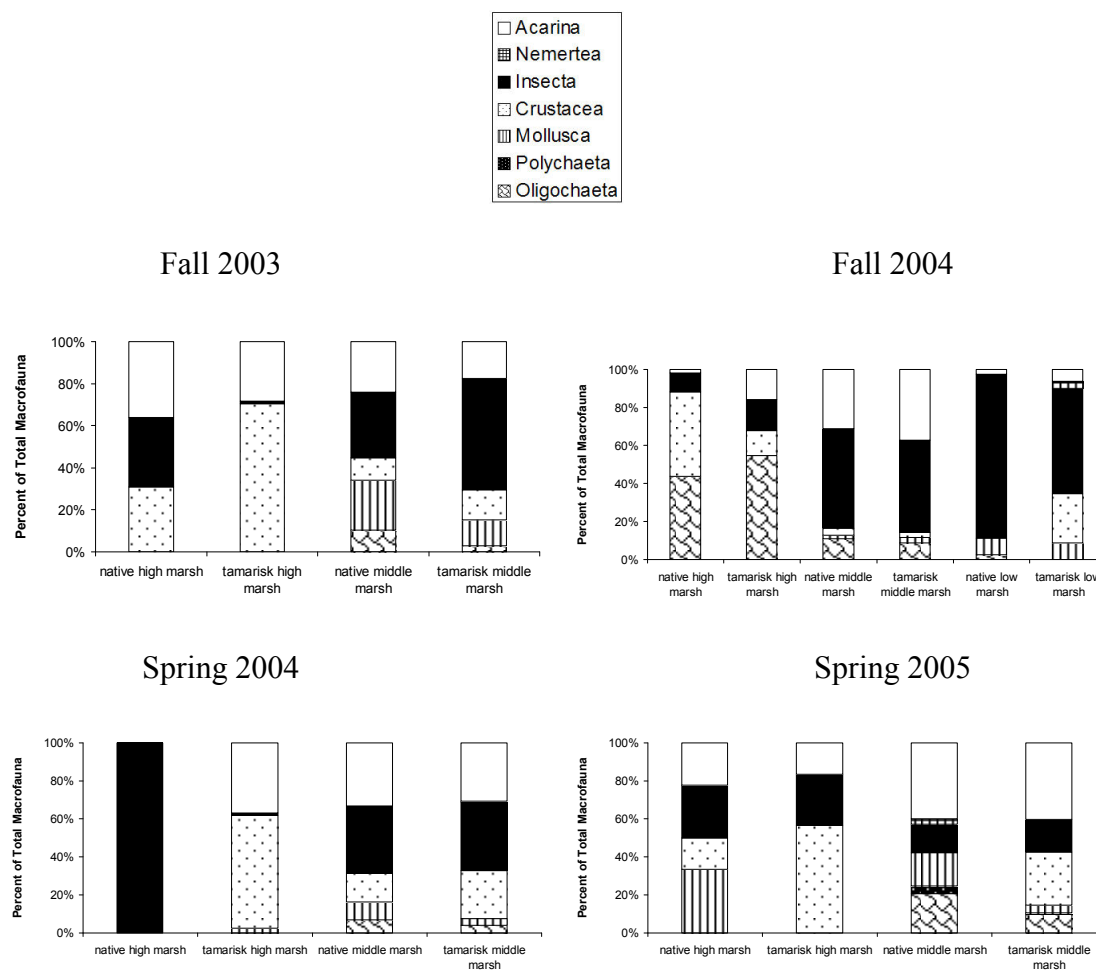
Figure 4.5: Macrofaunal community composition (based on counts) in tamarisk-invaded and native plots in three habitats and four seasons (Fall 2003, Spring 2004, Fall 2004, Spring 2005)

a) Fall 2003
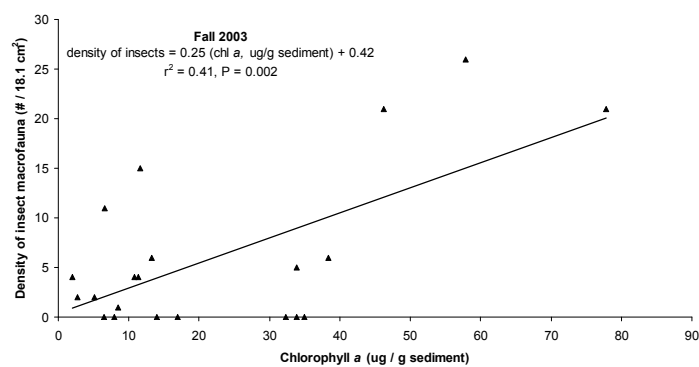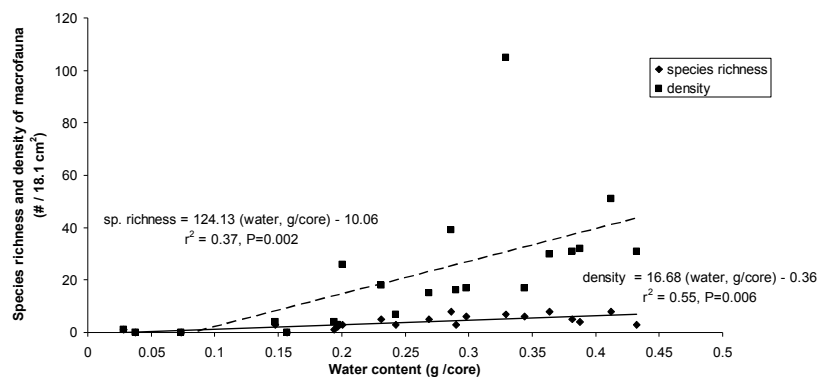
b) Spring 2005
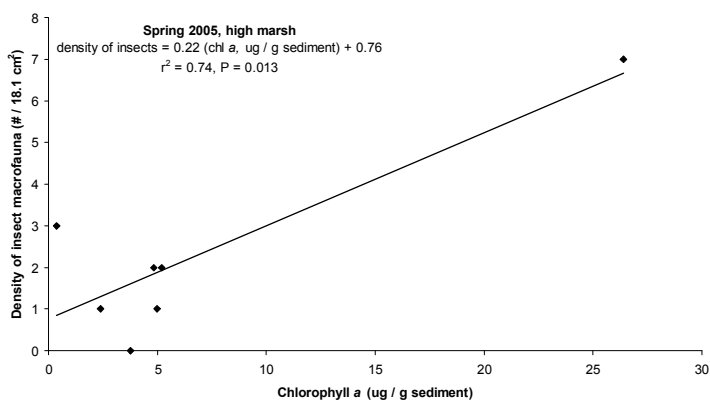
Figure 4.6: Regressions showing relationships between (a) sediment water content and species richness and density of macrofauna in Fall 2003 and (b) chlorophyll *a* and density of insect macrofauna in Fall 2003 and Spring 2005.
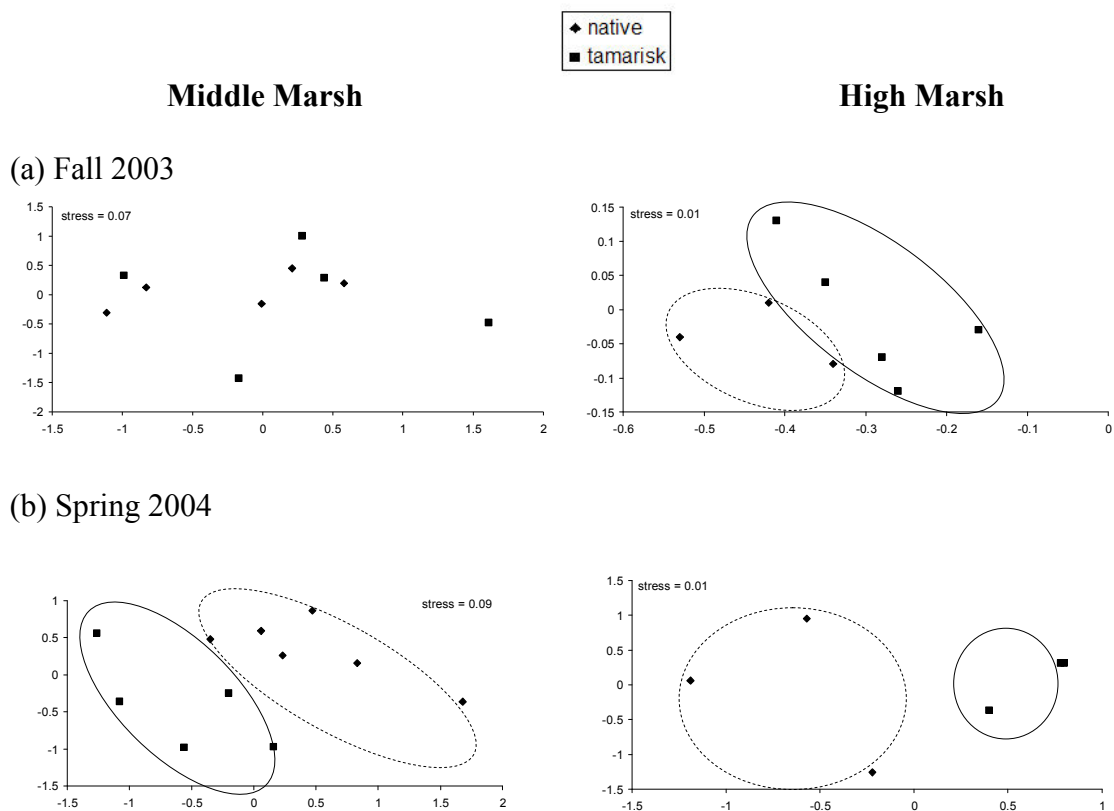
Figure 4.7: First-stage nMDS plots indicating separation of macroinvertebrate communities between native vegetation and tamarisk-invaded plots in middle and high marsh habitats in four seasons (a) Fall 2003, (b) Spring 2004, (c) Fall 2004, and (d) Spring 2005. Circles are drawn on graphs to illustrate groupings of points and do not indicate significance.

(c) Fall 2004
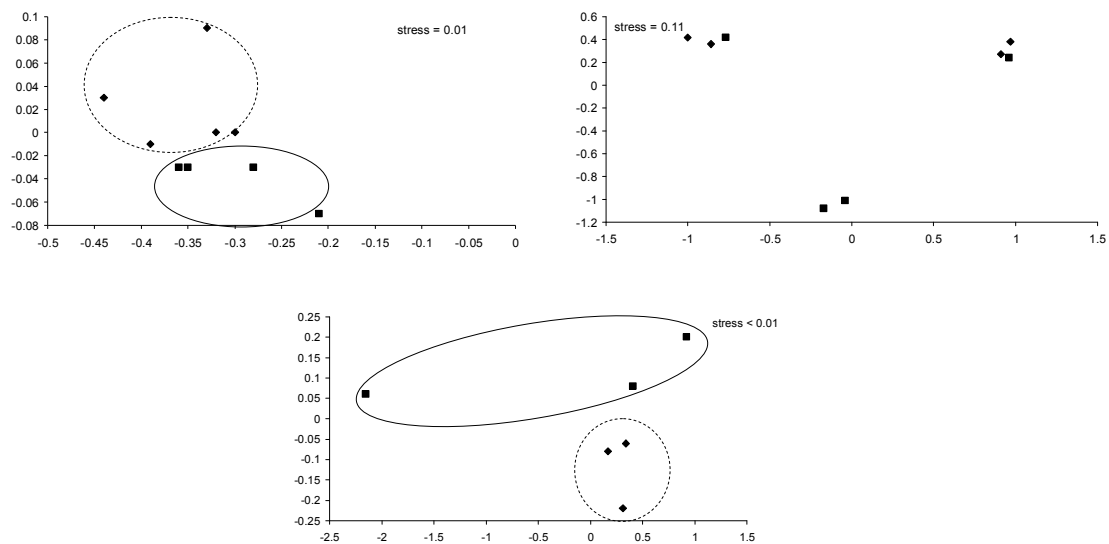
(d) Spring 2005
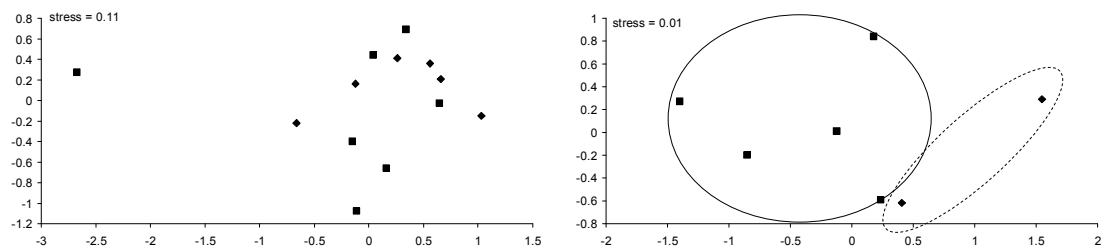
Figure 4.7 (continued)
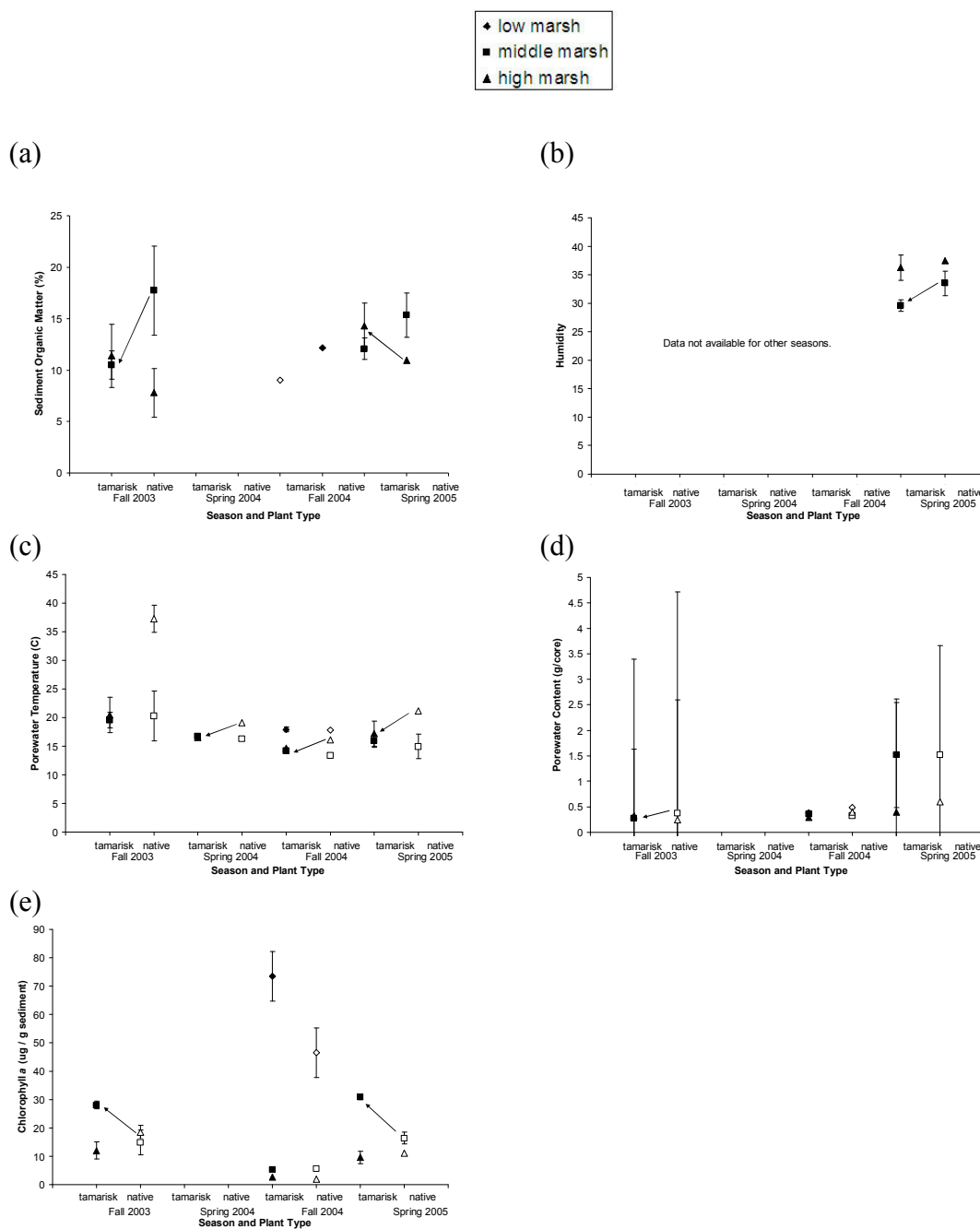
Figure 4.8: Physical and algal parameters (a-e: sediment organic matter, humidity, porewater temperature, sediment water content) by habitat, season, and plant type. An arrow indicates the direction of significant changes (P < 0.05) between native vegetation and tamarisk-invaded areas, Shifts in the indicated direction are indicative of "terrestrialization" as defined by our *apriori* hypotheses (see text).

$\chi^2_9 = 17.53$, P = 0.041
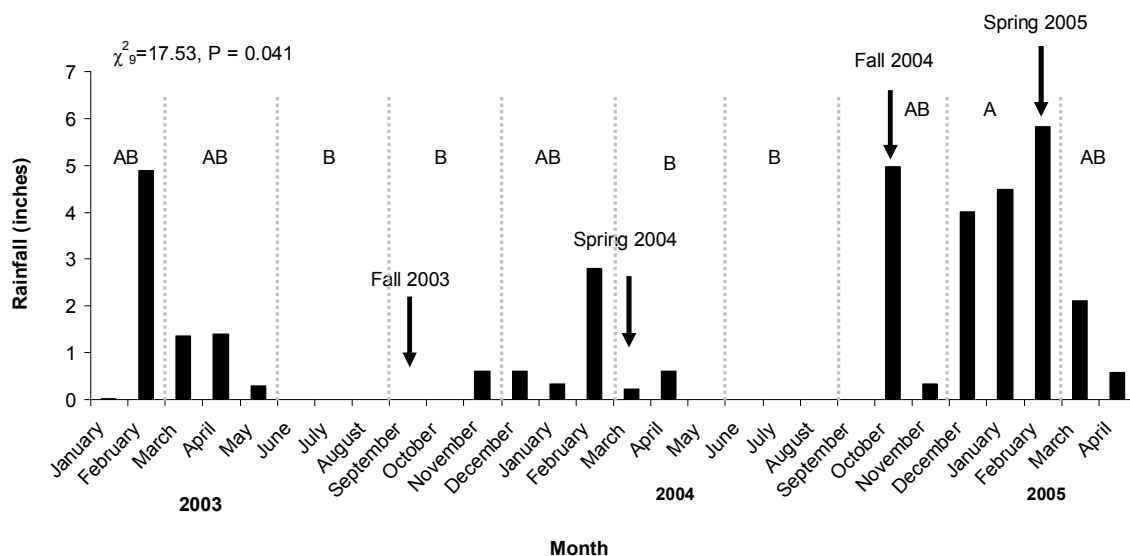
Figure 4.9: Amount of rainfall in inches as calculated from monthly averages (National Weather Service public data, (http://www.weather.gov/climate/) with sampling times for this research marked with arrows. Gray lines indicate divisions among seasons with December, January, and February as winter, March, April, and May as spring, June, July, and August as summer, and September, October, and November as fall. Significant differences, Tukey HSD, (P < 0.05) among seasons are indicated with letters.

Figure 4.10: Photograph showing contrast between a) the natural marsh landscape with short, succulent-dominated canopy (mainly *Salicornia virginica*) and the architecture and height of invasive *Tamarix* spp., a woody plant that can grow to over 3m tall. Picture was taken in Tijuana River National Estuarine Research Reserve, Imperial Beach, CA**.**

Table 4.1: Comparison of responses in tamarisk-invaded versus native plots by sediment properties, abiotic physical parameters, and the algal and infaunal community. Mean (1 SE) noted. Superscripted letters indicate *a posteriori* differences (P < 0.05).

Low marsh

Property	Fall 2003				Spring 2004				Fall 2004				Spring 2005			
	native	tamarisk	t value	P value	native	tamarisk	t value	P value	native	tamarisk	t value	P value	native	tamarisk	t value	P value
Grain size (% mud)	No data				No data				99.78 (0.14)	89.73 (4.92)	$t_3=2.01$	0.138		no data		
Organic matter (%)									12.16 (1.45)	9.04 (1.01)	$t_3=1.55$	0.218		no data		
Humidity										no data				no data		
Temperature (° C)									17.78 (0.06)	17.95 (0.44)	$t_3=0.43$	0.693				
Water content (g / core)									0.49 (0.36)	0.39 (0.15)	$t_2=0.40$	0.727	1.15 (0.11)	1.52 (0.20)	$t_3=1.51$	0.229
Redox (Eh)										no data						
Percent bare area									46.51 (8.76)	73.45 (8.69)	$t_3=-2.31$	0.104	41.50 (13.22)	41.01 (21.35)	$t_3=0.29$	0.787
Average height marsh (m)														no data		
Chl a (µg / g sediment)									74.33 (21.22)	22.33 (9.21)	$t_2=1.73$	0.225		no data		
Density (# / 18.1 cm²)									3.67 (2.08)	3.67 (2.08)	$t_2=0$	1.000				
Species richness / 18.1 cm²														no data		
Diversity (Simpson's D)									0.22 (0.12)	0.45 (0.15)	$t_2=1.05$	0.405		no data		

Middle marsh

Property	Fall 2003				Spring 2004				Fall 2004				Spring 2005			
	native	tamarisk	t value	P value	native	tamarisk	t value	P value	native	tamarisk	t value	P value	native	tamarisk	t value	P value
Grain size (% mud)	88.27 (5.16)[a]	66.92 (8.40)[b]	$t_7=2.39$	0.054	99.78	100	n/a	n/a		no data				no data		
Organic matter (%)	17.73 (4.34)[a]	10.50 (1.36)[b]	$t_6=2.50$	0.047		no data				no data			15.34 (2.14)	12.08 (1.03)	$t_4=1.18$	0.304
Humidity		no data				no data				no data			33.50 (9.32)[a]	29.6 (8.37)[b]	$t_5=2.23$	0.056
Temperature (° C)	20.28 (0.97)	19.52 (0.18)	$t_5=-0.90$	0.411	16.27 (0.62)	16.71 (0.61)	$t_9=1.76$	0.112	13.32 (0.44)	14.16 (1.80)	$t_9=2.18$	0.072	14.94 (0.73)	15.89 (0.91)	$t_7=0.99$	0.356
Water content (g / core)	0.374 (0.029)[a]	0.275 (0.023)[b]	$t_6=1.53$	0.051		no data			0.328 (0.055)	0.355 (0.052)	$t_5=0.54$	0.613	1.52 (0.08)	1.52 (0.07)	$t_2=1.51$	0.229
Redox (Eh)	83.63 (9.14)	99.63 (14.21)	$t_{10}=1.61$	0.137		no data				no data				no data		
Percent bare area	1.00 (0.53)[a]	15.67 (4.33)[b]	$t_{14}=3.35$	0.005	1.50 (1.06)[a]	21.00 (4.77)[b]	$t_1=3.83$	0.004	0.71 (0.38)[a]	16.79 (3.73)[b]	$t_{13}=4.33$	0.0008	3.00 (2.13)[a]	31.50 (5.38)[b]	$t_9=4.50$	0.002
Average height marsh (m)	0.93 (0.18)[a]	1.44 (0.09)[b]	$t_{13}=2.20$	0.046	0.91 (0.09)[a]	1.37 (0.08)[b]	$t_1=3.62$	0.006	0.67 (0.05)[a]	1.92 (0.24)[b]	$t_{13}=5.78$	<0.0001	0.75 (0.07)[a]	1.94 (0.24)[b]	$t_9=4.51$	0.002
Chl a (µg / g sediment)	14.87 (4.93)[a]	28.07 (6.92)[b]	$t_{10}=2.58$	0.027		no data			5.69 (3.03)	5.23 (1.20)	$t_5=0.23$	0.831	16.43 (6.34)[a]	30.98 (8.06)[b]	$t_9=9.91$	0.010
Density (# / 18.1 cm²)	27.5 (5.45)	35.5 (14.7)	$t_4=0.93$	0.404	30.6 (8.91)	31.8 (14.3)	$t_4=0.54$	0.619	22.6 (5.0)	26.8 (5.6)	$t_4=0.11$	0.917	21.8 (12.3)	12.2 (4.6)	$t_4=0.85$	0.442
Species richness / 18.1 cm²	6.2 (0.7)[a]	5.2 (0.8)[b]	$t_5=3.16$	0.030	5.4 (1.3)	4.8 (1.0)	$t_4=0.43$	0.689	4.8 (0.5)	4.4 (0.5)	$t_4=0.61$	0.573	8.6 (4.8)	6.2 (1.5)	$t_4=1.51$	0.206
Diversity (Simpson's D)	0.61 (0.05)[a]	0.46 (0.07)[b]	$t_5=2.39$	0.050	0.57 (0.08)	0.42 (0.10)	$t_4=1.19$	0.299	0.72 (0.07)	0.44 (0.16)	$t_3=1.68$	0.192	0.72 (0.04)	0.57 (0.15)	$t_4=0.96$	0.392

High marsh

Property	Fall 2003				Spring 2004				Fall 2004				Spring 2005			
	native	tamarisk	t value	P value	native	tamarisk	t value	P value	native	tamarisk	t value	P value	native	tamarisk	t value	P value
Grain size (% mud)	42.97 (14.63)	51.70 (11.83)	$t_5=0.68$	0.532	99.79 (0.21)	97.46 (2.31)	$t_1=1.11$	0.466		no data				no data		
Organic matter (%)	7.79 (2.36)	11.39 (3.08)	$t_4=1.70$	0.164		no data				no data			10.94 (2.48)[a]	14.32 (2.22)[b]	$t_3=3.01$	0.024
Humidity		no data				no data				no data			37.50 (5.90)	36.25 (5.57)	$t_3=1.20$	0.265
Temperature (° C)	37.28 (14.65)	20.45 (0.90)	$t_3=-1.21$	0.313	19.10 (1.23)[a]	16.57 (10.56)[b]	$t_6=3.16$	0.019	16.13 (1.15)[a]	14.66 (0.73)[b]	$t_5=-1.65$	0.004	21.16 (2.29)[a]	17.18 (0.74)[b]	$t_3=2.39$	0.044
Water content (g / core)	0.240 (0.055)	0.322 (0.055)	$t_5=1.53$	0.165		no data			0.294 (0.072)	0.395 (0.089)	$t_5=2.25$	0.072	0.598 (0.123)	0.396 (0.054)	$t_5=0.98$	0.507
Redox (Eh)	69.25 (9.71)	92.63 (10.10)	$t_7=1.80$	0.116		no data				no data				no data		
Percent bare area	1.67 (1.18)[a]	7.78 (2.65)[b]	$t_4=2.35$	0.047	1.11 (0.74)[a]	12.22 (2.37)[b]	$t_1=5.12$	0.0009	6.10 (3.98)	7.00 (4.16)	$t_9=0.14$	0.893	7.00 (3.39)	28.00 (5.83)	$t_4=2.75$	0.052
Average height marsh (m)	0.46 (0.11)[a]	1.41 (0.11)[b]	$t_6=6.78$	0.0001	0.74 (0.13)[a]	1.42 (0.12)[b]	$t_1=3.49$	0.008	0.67 (0.05)[a]	2.01 (0.40)[b]	$t_9=3.76$	0.004	0.56 (0.07)[a]	2.12 (0.24)[b]	$t_9=3.76$	0.004
Chl a (µg / g sediment)	18.48 (5.64)	12.09 (1.91)	$t_7=1.29$	0.239		no data			1.92 (0.51)	2.70 (0.60)	$t_6=-1.03$	0.344	11.08 (4.91)	9.62 (4.15)	$t_6=0.19$	0.854
Density (# / 18.1 cm²)	7.8 (6.1)	9.5 (7.2)	$t_4=0.38$	0.722	20.6 (10.5)	22.6 (7.9)	$t_4=1.43$	0.227	6.4 (4.9)	16.6 (7.3)	$t_4=0.12$	0.911	8.6 (4.8)	6.2 (1.5)	$t_4=0.41$	0.704
Species richness / 18.1 cm²	1.8 (0.8)	1.5 (0.6)	$t_4=0.78$	0.474	2.8 (1.0)	3.4 (0.9)	$t_4=0.27$	0.800	1.4 (0.5)	1.6 (0.7)	$t_4=0.42$	0.697	2.6 (0.9)	2.0 (0.4)	$t_4=0.58$	0.591
Diversity (Simpson's D)	0.20 (0.13)	0.21 (0.11)	$t_2=0.09$	0.936	0.33 (0.33)	0.10 (0.10)	$t_2=0.45$	0.698	0.28 (0.16)	0.31 (0.21)	$t_2=0.14$	0.898	0.33 (0.33)	0.36 (0.15)	$t_2=0.14$	0.865

Table 4.2. Comparison of the macrofaunal community (density, composition) in native vegetation and tamarisk-invaded areas at four sampling times (a) Fall 2003 and Fall 2004 and (b) Spring 2004 and Spring 2005. Mean density per core (18.1 cm^2) and mean percent composition ($\pm$ 1 SE) are reported. Superscripted letters indicate *a posteriori* differences among treatments (P < 0.05).

a)

Group	Fall 2003 High marsh natural	tamarisk	t_6	P value	Fall 2003 Middle marsh natural	tamarisk	t_6	P value	Fall 2004 High marsh natural	tamarisk	t_6	P value	Fall 2004 Middle marsh natural	tamarisk	t_6	P value	Fall 2004 Low marsh natural	tamarisk	t_3	P value
Crustacea																				
density	6.00 (6.00)	5.00 (3.11)	0.14	0.896	1.71 (0.78)	2.43 (1.19)	1.00	0.356	9.00 (6.14)	3.25 (1.70)	0.99	0.395	1.43 (0.72)	0.57 (0.20)	1.44	0.200	0.00 (-)	2.33 (2.33)	1.00	0.423
% of total density	23.00 (23.00)	53.00 (20.97)	1.90	0.153	30.71 (9.23)	14.00 (7.95)	1.00	0.355	44.23 (26.00)	13.13 (8.59)	1.43	0.249	3.01 (1.53)	2.36 (1.24)	0.40	0.705	0.00 (-)	25.93 (25.93)	1.00	0.423
Gastropoda																				
density	0.00 (-)	0.00 (-)	-	2.000	8.43 (3.34)	9.00 (6.87)	0.07	0.944	0.00 (-)	0.00 (-)	-	2.000	1.95 (0.83)	3.74 (1.19)	1.45	0.197	8.33 (7.84)	2.67 (1.76)	0.61	0.604
% of total density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	12.57 (7.10)	1.38	0.217	0.00 (-)	0.00 (-)	-	2.000	0.86 (0.34)	1.00 (0.31)	0.55	0.604	8.94 (8.44)	8.70 (4.49)	0.02	0.987
Insecta																				
density	1.00 (1.00)	0.25 (0.25)	1.00	0.391	6.86 (2.63)	11.14 (3.65)	1.93	0.102	0.75 (0.48)	3.50 (2.87)	1.10	0.351	14.57 (5.89)	15.43 (10.77)	0.09	0.934	62.00 (17.35)	15.67 (8.95)	1.98	0.186
% of total density	25.00 (25.00)	0.75 (0.75)	1.00	0.391	21.43 (4.35)[a]	55.57 (12.51)[b]	2.59	**0.042**	10.10 (6.15)	16.01 (13.81)	0.43	0.700	43.74 (10.26)	41.85 (15.04)	0.15	0.886	86.18 (8.76)	55.46 (27.93)	1.57	0.257
Oligochaeta																				
density	0.00 (-)	0.00 (-)	-	2.000	2.28 (0.64)	2.14 (1.67)	0.08	0.940	1.00 (0.71)	14.00 (10.72)	1.29	0.287	3.28 (1.30)	2.42 (1.00)	0.52	0.623	2.33 (1.86)	0.00 (-)	1.26	0.336
% of total density	0.00 (-)	0.00 (-)	-	2.000	11.00 (3.42)[a]	1.43 (0.89)[b]	2.71	**0.035**	43.75 (25.77)	54.83 (24.56)	2.16	0.120	15.42 (5.62)	12.11 (6.58)	0.96	0.374	2.40 (1.89)	0.00 (-)	1.27	0.332
Polychaeta																				
density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000
% of total density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000
Nemertea																				
density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.7 (0.7)	1.00	0.423
% of total density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	3.7 (3.7)	1.00	0.423
Other																				
density	0.75 (0.48)	4.25 (3.92)	0.83	0.465	5.29 (2.11)	6.71 (3.86)	0.33	0.755	0.25 (0.25)	4.75 (4.42)	0.10	0.393	10.29 (3.07)	8.15 (2.42)	1.51	0.182	1.66 (1.20)	1.33 (0.88)	0.23	0.840
% of total density	27.00 (24.41)	21.25 (12.87)	0.23	0.829	21.00 (7.09)	17.57 (11.71)	0.31	0.770	1.92 (1.92)	16.03 (15.35)	0.87	0.446	35.88 (5.79)	39.94 (11.88)	0.36	0.731	2.48 (1.28)	6.20 (3.27)	1.87	0.202

Table 4.2 (continued)

b)

	Spring 2004								Spring 2005							
	High marsh				Middle marsh				High marsh				Middle marsh			
Group	natural	tamarisk	t_4	P value	natural	tamarisk	t_5	P value	natural	tamarisk	t_6	P value	natural	tamarisk	t_6	P value
Crustacea																
density	0.00 (-)	6.68 (3.34)	1.80	0.170	1.57 (0.95)	5.86 (0.90)	1.53	0.176	0.67 (0.33)	4.30 (1.86)	2.62	0.120	0.00 (-)	0.00 (-)	-	2.000
% of total density	0.00 (-)[a]	53.07 (21.17)[b]	2.51	0.051	14.85 (12.28)	25.51 (15.54)	0.56	0.605	16.67 (16.67)[a]	56.67 (21.86)[b]	6.93	0.020	0.00 (-)	0.00 (-)	-	2.000
Gastropoda																
density	0.00 (-)	0.5 (0.5)	1.00	0.391	1.71 (0.81)	1.57 (0.90)	0.11	0.919	0.33 (0.33)	0.00 (-)	1.00	0.423	2.00 (1.22)	1.75 (1.18)	0.15	0.889
% of total density	0.00 (-)	0.88 (0.88)	1.00	0.363	9.48 (3.77)	3.26 (2.12)	1.33	0.254	33.33 (33.33)	0.00 (-)	1.00	0.423	17.61 (10.99)	6.39 (4.23)	0.95	0.412
Insecta																
density	1.25 (0.63)	0.25 (0.25)	1.41	0.252	10.86 (4.04)	14.86 (6.26)	0.59	0.578	0.00 (-)	1.67 (0.88)	1.00	0.423	1.75 (0.63)	3.00 (1.58)	0.87	0.448
% of total density	8.33 (8.33)	0.44 (0.44)	0.94	0.392	35.89 (16.28)	36.00 (16.63)	0.01	0.992	27.78 (14.70)	26.67 (17.64)	0.05	0.968	14.96 (5.31)	21.50 (13.09)	0.63	0.571
Oligochaeta																
density	0.00 (-)	0.00 (-)	-	2.000	2.42 (0.97)	1.57 (0.69)	0.63	0.550	0.00 (-)	0.00 (-)	-	2.000	2.00 (1.08)	4.00 (2.31)	0.88	0.444
% of total density	0.00 (-)	0.00 (-)	-	2.000	6.76 (3.66)	4.13 (1.74)	0.63	0.563	0.00 (-)	0.00 (-)	-	2.000	20.52 (12.26)	14.84 (8.58)	0.48	0.660
Polychaeta																
density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.50 (0.50)	0.25 (0.25)	1.00	0.391
% of total density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.00 (-)	-	2.000	4.17 (4.17)	0.89 (0.89)	1.00	0.391
Nemertea																
density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.29 (0.18)	1.55	0.172	0.00 (-)	0.00 (-)	-	2.000	0.25 (0.25)	0.00 (-)	1.00	0.391
% of total density	0.00 (-)	0.00 (-)	-	2.000	0.00 (-)	0.42 (0.42)	1.00	0.374	0.00 (-)	0.00 (-)	-	2.000	2.78 (2.78)	0.00 (-)	1.00	0.391
Other																
density	0.25 (0.25)	7.00 (7.00)	0.95	0.411	7.71 (2.23)	5.86 (3.36)	0.67	0.525	0.67 (0.67)	1.67 (1.67)	0.48	0.678	4.50 (1.32)	6.75 (2.95)	0.63	0.573
% of total density	8.33 (8.33)	12.28 (12.28)	0.24	0.817	33.00 (10.62)	30.68 (16.83)	0.20	0.853	22.22 (22.22)	16.67 (16.67)	0.16	0.547	39.96 (10.14)	56.39 (16.00)	0.68	0.547

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CHAPTER V

UTILIZATION OF INVASIVE TAMARISK BY SALT MARSH CONSUMERS

Abstract

Upland plant invasion of coastal wetlands is increasing over time. Recent examples include *Phragmites australis* (Chambers et al. 2003), *Arundo donax* (Herrera and Dudley 2003), *Limonium sinuatum* (Simpson and Rebman 2001) and now *Tamarix* spp. (this study). Invasive plant alteration of salt marsh litter dynamics represents one of the fundamental impacts of a novel species on an ecosystem. Beyond basic ecology, understanding invader effects on litter cycling can aid management efforts by prioritizing responses based on invader trophic effects on detritus-based food webs, which are particularly important in salt marshes. We utilized litter dynamics study techniques and stable isotope enrichment experiments to evaluate the trophic consequences of invasion by tamarisk (*Tamarix* spp.) on detrital food chains in the Tijuana River National Estuarine Research Reserve (TR NERR) salt marsh. Our results demonstrate that tamarisk is readily available to benthic macroinvertebrates as a labile detrital food source; numerous macroinvertebrate taxonomic and trophic groups both in and on the sediment utilized ^{15}N derived from labeled tamarisk detritus. The information generated through the use of natural abundance and isotopic enrichment stable isotope analyses enables scientists and managers to trace invader plant detritus input to the food web, an especially

valuable tool when small organisms are involved. This research contributes to the general knowledge of how exotics alter ecosystem function and can help direct local control and large-scale eradication effects.

Introduction

Invasion by vascular plants in coastal wetlands is increasing globally, with dramatic ecosystem-level consequences that include local extinctions of native species, genetic modifications, species displacements and habitat degradation (Chapin et al. 1997, Grosholz 2002). Although slow to be described at first, trophic modifications by invasive plants in wetlands are often severe and are important mechanisms underlying overall ecosystem change (Vitousek et al. 1996, Wardle et al. 1994, Neira et al. 2005, Levin et al. 2006). Examples of ecosystem-altering plants can be found in wetlands across the United States and include *Phragmites australis* (common reed) on the East Coast (Talley and Levin 2001, Rooth et al. 2003, Chambers et al. 2003), *Spartina* spp. (4 species of cordgrass) in San Francisco Bay (Ayres et al. 2003, Neira et al. 2005, Levin et al. 2006), and *Zostera japonica* (Japanese eelgrass) in the Pacific Northwest (Posey 1988). Knowing the extent and relative scale of trophic effects of an invasion will allow managers to predict which invaders will be the "worst" for trophic alteration through detrital pathways, can help to evaluate the efficacy of eradication, and can guide recovery strategies for restoring trophic webs.

The trophic consequences of plant invasions often occur at the base of the food web through alteration influencing the abundance, composition, and diversity of sediment microbial and animal communities (Wardle et al. 2004, Levin and Talley 2000). This type of plant influence on belowground communities occurs through structural, physical,

and chemical mechanisms (Neira et al. 2006). Invasive plant species can modify the quantity and quality of detritus in invaded habitats. Detritus is a dominant feature of most vegetated ecosystems, and a significant portion of primary production is cycled through detrital pathways (Moore et al. 2004). Yet, the importance of the detrital pathways as the driving force behind observed plant influence is often omitted from the study of plant invasion consequences (Kennedy and Hobbie 2004, Levin et al. 2006).

One example of an ecosystem-altering vascular plant is *Tamarix*, salt cedar or tamarisk, a group containing 54 species and several hybrids. Considered by many as one of the worst invaders in the United States (Morisette et al. 2006, Stein and Flack 1996), tamarisk trees are aggressive, woody plants that have become established over 1.5 million acres of floodplains, riparian areas, and freshwater wetlands in the western United States (Zavaleta 2000). Native to Eurasia, tamarisk was introduced into North America for horticulture, erosion control and shade in the early 1800s (Di Tomaso 1998). Since its introduction, at least seven species have become established in the US (Baum 1978). In riparian areas of the western United States, tamarisk is now the third most frequently occurring woody plant (Friedman et al. 2005).

Despite widespread invasion of some coastal wetlands by plants, until now most of the salt marshes of southern California have been relatively free from the invasion by habitat-altering plants. An important exception is invasion of tamarisk or salt cedar (*Tamarix* spp.) into the Tijuana River National Estuarine Research Reserve (TR NERR) where the intertidal, pickleweed (*Sarcocornia pacifica*) marsh now supports thick stands of these salt-tolerant trees (Whitcraft et al., in press). The trees invading the low salt marsh habitat are primarily a hybrid, *T. ramossisma* x *T. gallica*. This tamarisk invasion

converts the salt marsh from a succulent-dominated canopy of less than 1m height to a landscape dominated by stands of woody trees that can grow to over 3 meters tall (C. Whitcraft, pers. obs.). Information about the effects of tamarisk invasion comes primarily from low salinity systems. Because animal communities differ and effects in salt marsh systems could vary, salt marsh-specific studies are crucial to effective management in these newly invaded systems.

In riparian areas, tamarisk litter decomposes more quickly compared to native cottonwood litter, an alteration in the litter dynamics associated with a decrease in macroinvertebrate richness and abundance and an alteration in macroinvertebrate community structure (Bailey et al. 2001). Eradication of the salt cedar in freshwater systems resulted in a restoration of native macroinvertebrates due to an increased availability of algae (Kennedy et al. 2005). In the salt marsh ecosystem, we predict that the community change from pickleweed (*Sarcocornia pacifica*) to tamarisk (*Tamarix* spp.) will also dramatically affect the litter dynamics of the system, potentially translating into community-level food web effects through the alteration of detrital pathways (Stevens 2000, Crooks 2002). Any effects noted from the utilization of tamarisk as fresh detrital material in the food web should be incorporated into potential eradication plans.

The overall objective of this research is to examine the effect of tamarisk invasion on the salt marsh detrital pathway. We utilized litter dynamics techniques and stable isotope natural abundance and enrichment experiments to address several general questions: a) Is tamarisk available to benthic macroinvertebrates as a detrital food source? b) Which species and trophic groups consume tamarisk detritus? c) Does tamarisk detritus utilization by infauna differ by depth in the sediment and/or between adjacent

invaded and native habitats? and d) How does tamarisk alter litter cycling and how might this influence direct management and eradication plans for tamarisk?

Materials and Methods

Invasion site description: Tijuana River National Estuarine Research Reserve (TR NERR) is situated near Imperial Beach, in San Diego County, CA, on the US-Mexican border. The estuary is located at the mouth of the Tijuana River watershed, with two-thirds of the 4420 km^2 watershed lying within Mexico (Zedler et al. 1992). This work was conducted in the intertidal salt marsh, immediately adjacent to the main channel of the Tijuana River in the USA.

Litter dynamics: To quantify vertically falling tamarisk input to the system, we secured one basket (0.25m^2) under the drip line of 10 tamarisk trees (1 basket per tree) (Kennedy and Hobbie 2004). To quantify lateral transport of detritus away from the tree, tubs (26 cm diameter) were buried even with the sediment surface at a distance of 2 m from the drip line of the same 10 tamarisk trees (1 tub per tree). To quantify standing stock of ground detritus, all accumulated ground litter was collected from quadrats (0.25m^2) under the same tamarisk tree and in adjacent native habitat (1 quadrat per tree) once during July 2005. All litter collections were done 4 days later, sorted to species (where possible), dried overnight at 65 ºC and weighed.

To measure tamarisk and native plant decomposition rates, four grams of air-dried tamarisk or native *Sarcocornia pacifica* were placed in litterbags (20 x 20 cm, mesh 1mm) constructed of window screening. Five tamarisk litterbags and one *S. pacifica* litterbag were placed under 6 of the 10 tamarisk trees mentioned above on July 25, 2005 and fastened to the sediment surface with stakes. After 25, 75, and 107 days for tamarisk

and 25 days for *S. pacifica*, litterbags were collected and placed in individual plastic bags for transport to the laboratory. In the laboratory, the litter from each bag was rinsed with Milli Q® water, air-dried, weighed, dried overnight at (65 ºC) and reweighed. Decay constants were calculated for each litterbag at each of the plots assuming a simple negative exponential decay (k) (Olson 1963): $\ln M_t/M_0 = -kt$ where M_t is the litter mass at time t and M_0 is the initial litter mass.

Palatability: C:N ratios of plants have been utilized as an important measure of leaf palatability (Pennings et al. 1998). To measure C and N content, leaf material from tamarisk and several native plants (*S. pacifica, Juncus acutus*, *Jaumea cornosa*) was collected from the study site, rinsed with Milli-Q$^®$ water, placed in pre-combusted vials or tin boats, dried at 65 ^{o}C, and kept in a dessicator until analysis. In addition, particulate organic matter (POM), sediment organic matter (SOM), and benthic microalgae were collected and processed as discussed below. A subset of these samples was analyzed for C:N content by D. Harris (Stable Isotope Facility, UC Davis) using an elemental analyzer (PDZ Europa ANCA-GS, Northwich, UK).

Natural abundance stable isotope analysis: To determine natural abundance isotopic signatures (δ^{13}C, δ^{15}N) of food web components, samples of particulate organic matter (POM), sediment organic matter (SOM), microalgae, macroalgae, plants, and macrofauna were collected in September 2004 in the tamarisk and *S. pacifica* habitats. Collection and processing methods were similar to those described in Moseman et al. (2004) and Levin et al. (2006). POM was obtained by filtering 2 L of local tidal creek water onto Whatman GFF filters. SOM was sampled by collecting surface sediment (upper 2 cm), drying and homogenizing sediments. Microalgae were collected using

density centrifugation with ludox (colloidal silica), providing a pure algal sample (devoid of sediment) (Blanchard et al. 1988). Macrofaunal invertebrates were sieved on a 0.3 mm mesh, sorted live, and identified to species. All animals were kept alive in seawater and allowed to evacuate guts for up to 24 hours. Animal material was then washed in Milli-Q$^®$ water, placed in pre-combusted vials or tin boats, dried at 65 ^{o}C, and kept in a desiccator until analysis. Larger organisms were removed from the shell or carapace, dried at 65°C and then ground with a mortar and pestle. All samples were treated with Pt Cl$_2$ to remove inorganic carbon.

Isotopic composition of animal and algal samples was also analyzed. Stable isotope abundance is expressed in parts per thousand in a ratio of heavy to light isotope content (^{15}N:^{14}N or ^{13}C:^{12}C). Working standards, sucrose and ammonium sulfate, were δ^{13}C =-23.83‰ vs. Vienna Pee Dee Belemnite Standard or δ ^{15}N = +1.33‰ vs. air N$_2$. Typical sample precision is better than 0.1‰.

Isotope labeling and enrichment experiments: In order to trace an invasive plant through the food web using stable isotopes, it is necessary for the invader to have an isotopic signature distinct from the native food sources. If different potential food sources have overlapping signatures, alternative approaches must be utilized to distinguish the invader. One effective alternative is isotopic labeling of the invasive plant with ^{15}N to track the labeled material into consumer tissues. In this study, we apply the ^{15}N enrichment approach due to the overlap of tamarisk isotope natural abundance values (δ^{13}C, δ^{15}N) with an important native food (benthic microalgae) (See Results).

Four small *Tamarix ramosissima* x *Tamarix gallica* hybrid trees (in TR NERR) were labeled with ^{15}N by enclosing plants *in situ* in 4 plastic pots with the bottoms cut out

during June 2004. Sediments surrounding the tamarisk plants were injected daily with 250 ml of 6 mmol/L ammonium sulfate (98 atom % $^{15}NH_4$) per pot for a 3-day period (method modified from White and Howes 1994 and Levin et al. 2006). Plants were harvested 12 weeks after injections (September 2004) and deployed one day later as detritus. In the field, we established 4 plots in native habitat and 4 plots in tamarisk-invaded habitat immediately adjacent to the native plots.

The ^{15}N-labeled tamarisk leaves, roots, and stems were chopped into pieces approximately 5 mm in length. Nylon litter bags (2.6 x 1.2 cm, 5 mm mesh) were filled with 7g of either leaf, root, or stem material and were deployed at a depth of 1-2 cm below the sediment surface in each quadrat. We buried 3 replicate bags of detritus (1 bag of leaves, 1 bag of roots, and 1 bag of stems) in each habitat, holding them in place with wooden dowels. We collected the bags 14 and 90 days later, washed the bags, sieved the overlying sediment, and sorted the associated macroinvertebrates under a dissecting microscope. In addition, to test for N-leaching and uptake by bacteria and algae, ^{15}N-labeled tamarisk leaves were deployed in Nitex® mesh (61 μm) bags (1 per habitat). We collected the bags 90 days later, washed the bags, sieved the overlying sediment, and sorted the associated macroinvertebrates under a dissecting microscope.

^{15}N-labeled tamarisk leaves were also cut into 5 mm pieces and placed in the field as loose, surface detritus. This loose plant material was spread uniformly on the surface in 5 circular 90 cm^2 plots per quadrat, pressed 1 mm into sediment with forceps, and marked at the center with red wire so that the exact location could be sampled later (as in Levin et al. 2006). These surface detritus areas were sampled by scooping the surface

sediment up from within the marked circular plots at 0, and 1, 4, 14, 90, and 270 days after deployment.

Immediately after deployment of litter bags and detritus on the sediment surface (time 0), we collected samples of infauna (> 0.3 mm) , macroalgae, microalgae, particulate organic material (POM), and sediment organic material (SOM) to determine 0 time point (T0) values for $\delta^{13}C$ and $\delta^{15}N$ isotope signatures. This provided background values and checked for labeling artifacts. Microalgae were subsequently collected 1, 4, 14, 90, and 270 days after deployment for stable isotope analysis. Samples from the isotope enrichment experiments were treated as described above for the natural abundance stable isotope samples.

Statistical Analysis: All univariate tests were conducted with JMP 5.1 statistical software (SAS Institute, NC, USA). Data were tested for normality, and square root or log_{10} transformed as needed prior to analysis. If no transformation yielded normal data, nonparametric Wilcoxon tests were utilized. For stable isotope analyses, species mean isotopic signatures were used as replicates for tracer uptake comparisons of subsurface vs. surface, of tamarisk vs. natural habitats, among feeding groups, among food preference groupss, and among species in one-way ANOVAs and Wilcoxon nonparametric tests with *a posteriori* Tukey's HSD tests. In figures and text, one standard error about the mean is presented for all data unless otherwise noted.

Mixing models were applied to estimate the fraction of tamarisk and other food sources in the infaunal diets. We applied a single isotope, two-source mixing model for $\delta^{15}N$ in which labeled tamarisk detritus was treated as one food source and unlabeled

(background) native food sources (i.e. microalgae, POM and SOM) were treated as a second food source, using the following formula:

$$\% \text{ tamarisk-derived N} = [(\delta^{15}N_{infauna} - \delta^{15}N_{background}) / (\delta^{15}N_{labeled\ tam.} - \delta^{15}N_{background})] * 100$$

Using this approach, we calculated the percentage of N in infaunal tissues that was derived from the labeled tamarisk detritus. A trophic level shift of 1‰ for $\delta^{13}C$ (Fry and Sherr 1984) and 2.2‰ for $\delta^{15}N$ was applied (McCutchen et al. 2003).

Results

Litter dynamics and palatability: A significant amount of tamarisk detritus fell from trees (average = 1.09 g [day^{-1} 0.25 m^{-2}]) yet the standing stock of tamarisk material on the sediment surface was low (average = 0.2 g [0.25 m^{-2}]), and only a small amount was exported to surrounding marsh (vertical input greater than standing stock and export, χ^2 = 12.59, P = 0.002). Decomposition experiments revealed a decomposition rate for tamarisk of 22% dry weight per month (decay constant of 0.012 $\pm$ 0.005 from a single-rate decay model). This is more than 2.5 times higher than the decomposition rate for *S. pacifica* of 8% dry weight per month (decay constant of 0.002 $\pm$ 0.001 from a single-rate decay model). *T. ramosissima* x *T. gallica* detritus had a significantly lower C:N ratio (13.74 $\pm$ 1.13) than *Juncus acutus* (36.86 $\pm$ 3.42) and equivalent C:N ratios to other native food sources (*Jaumea cornosa*: 30.45 $\pm$ 11.70 and *Sarcocornia pacifica*: 19.43 $\pm$ 1.29, SOM: 14.33 $\pm$ 1.13, POC: 6.79 $\pm$ 0.24, microalgae: 10.03 $\pm$ 0.69) (ANOVA, $F_{7,18}$ = 11.53, P < 0.001) (Figure 5.1).

Natural abundance stable isotope analysis: $\delta^{13}C$ and $\delta^{15}N$ analyses of food sources and consumers in tamarisk-invaded, mid-marsh habitat demonstrated isotopic differences

as a function of habitat (natural versus tamarisk). The natural marsh microalgae and SOM exhibited lighter $\delta^{13}C$ and heavier $\delta^{15}N$ than the microalgae from tamarisk habitat (Figure 5.2a, Appendix 5.1).

In addition, two of the potential food sources (tamarisk and microalgae) had overlapping signatures within the tamarisk habitat, leading to our use of an isotopic enrichment experiment (Figure 5.2b). *Salicornia pacifica* and *Juamea cornosa* had overlapping signatures that were distinct from the *Juncus sp*. signature; all three were distinguishable from tamarisk and microalgae (Figure 5.2b).

Isotope enrichment experiment: At the start of the enrichment experiment, labeled tamarisk detritus had a mean $\delta^{15}N$ signature of 394‰, 225‰, and 234‰ (equivalent to 10,214%, 5790%, and 6025% enrichment compared to ambient levels) for leaves, stems and roots, respectively.   Several macroinvertebrate species acquired substantial quantities of ^{15}N equally from leaves, stems, and roots; there were no significant differences in the mean isotopic signatures of species feeding on different plant parts (animals in leaf treatment = 35.77‰ $\pm$ 9.86, animals in stem treatment = 32.8‰ $\pm$ 13.08, animals in root treatment = 58.25‰ $\pm$ 21.36, Wilcoxon, χ^2_2 = 2.34, P = 0.333). The maximum $\delta^{15}N$ value (34‰) was observed at 14 days and indicated up to 554% enrichment from background tamarisk values. This elevated ^{15}N was observed in microalgae within 24 hours, potentially reflecting leaching from the labeled tamarisk detritus, but the signals were an order of magnitude lower than that of the labeled detritus. In addition, a comparison of $\delta^{15}N$ signatures of invertebrates from leaching bag treatments with $\delta^{15}N$ signatures of invertebrates from normal litter bag treatments revealed that uptake of ^{15}N by animals exposed to N leached through 61 μm mesh were

significantly less than uptake of ^{15}N by animals exposed to N in either surface or subsurface treatments with much lower δ^{15}N values (Wilcoxon across all species, $\chi^2_2 =$ 17.18, P<0.0001, by species, P < 0.05) (Appendix 5.1).

Member species of several major taxa (Acarina, Insecta, Mollusca, Crustacea, Oligochaeta, Polychaeta, and Turbellaria) in tamarisk-invaded and natural habitats incorporated significant amounts of δ^{15}N label after 4 days, such that at least 0.5% of their N was estimated from a two-source mixing model to have been derived from labeled tamarisk detritus (Table 5.1). Averaged across species, utilization percentage did not differ among animals in tamarisk-invaded and natural marsh habitats (ANOVA, $F_{1,80} =$ 1.43, P = 0.235). For most taxa, utilization of tamarisk-derived N peaked at 14 days and declined after 90 and 270 days (ANOVA, T14 different than rest of time periods, $F_{4,77} =$ 5.07, P = 0.0011). Major taxonomic groups did not differ in percent utilization (ANOVA, $F_{6,75} = 0.50$, P = 0.801). Psychodidae insects and *Grandidierella japonica* (Crustacea) incorporated the most ^{15}N label after 14 and 90 days, respectively, such that >50% of their N was estimated to have been derived from labeled tamarisk detritus (Table 5.1). The majority of other species had intermediate levels of uptake: Staphylinidae (both adults and larvae) and Stratiomyidae (Insecta), Gammaridae and Oniscidae (Crustacea), *Polydora nuchalis* (Polychaeta), Enchytraidae (Oligochaeta), *Assiminea californica* and *Melampus olivaceus* (Gastropoda) had ^{15}N values that indicated that between 5-20 % of their N was derived from labeled tamarisk detritus. Coleoptera larvae, Chironomidae larvae, Cincinilidae adults, Dolichopodidae larvae sp. 1, *Ephydra* sp. 1, and Hydrophyillid sp.1 (all Insecta) derived <5% of their N from labeled tamarisk detritus. Finally, *Cerithidea californica* (Gastropoda), Hydrophillidae sp. 1

(Insecta), *Transorchestra traskiana* (Crustacea) exhibited minor uptake of ^{15}N-label (0.1 – 1%) (Table 5.1).

Uptake in surface versus subsurface animals: Surface utilization of tamarisk-derived N was greater than sub-surface utilization in both tamarisk and natural habitats at day 14 (Wilcoxon across all species, $\chi^2_1 = 13.37$, P = 0.003). There was no effect of utilization depth (Wilcoxon) except in *Assiminea californica* which had higher sub-surface utilization than surface utilization at 14 days ($\chi^2_1 = 6.00$, P = 0.014). Utilization of tamarisk-derived N was similar in animals in both natural and tamarisk-invaded habitats at all time points so data from both habitats were combined for taxonomic, habitat, and time period comparisons.

Taxonomic comparisons: A comparison of the tamarisk utilization (change in δ^{15}N signatures from background signatures) revealed taxon differences at the surface only after 270 days. After 270 days in the surface treatment, mites had higher uptake than crustaceans, insects, and gastropods, and insects and crustacean had higher uptake than gastropods (Figure 5.3). Unlike surface treatments, after 14 days all taxonomic groups in the subsurface treatment differed in tamarisk utilization with insects being significantly greater than oligochaetes and gastropods, which utilized more tamarisk-derived N than crustaceans (Figure 5.3). Use patterns were similar at 90 days in the subsurface treatment (oligochaetes and insects showed more utilization than crustaceans) (Figure 5.3).

Feeding groups: Macroinvertebrates were divided into feeding groups based on natural abundance isotope data generated for this project and on literature designations to make comparisons of tamarisk utilization among food preference type (detritivores,

microalgal feeders, and mixed-diet feeders) (Table 5.2). Uptake of tamarisk-derived ^{15}N differed by food preference type with greater uptake in detritivores than in microalgal and mixed-diet feeders after 4 days and greater uptake by mixed-diet feeders than detritivores and microalgal feeders after 270 days (Figure 5.4).

Species-level comparisons at each time period indicated several species exhibited increased N uptake relative to the rest of the species. The greatest tamarisk-derived ingestion, as indicated by elevation of δ^{15}N signatures above background ($\Delta\delta^{15}$N) at 14 days (surface and subsurface) and 90 days (surface only) was by species normally considered to be mixed diet feeders (Psychodidae sp. 1) or detritivores (*Grandidierella japonica*) (Figures 5.5 & 5.6). ^{15}N-labeled tamarisk contributed greater than 50% of the N in these animals at different time points (Table 5.1). Lesser uptake of ^{15}N label was observed in many other taxa, including microalgal consumers (Figures 5.5 & 5.6, Table 5.1).

Discussion

Is tamarisk available as a food source? Vertically falling tamarisk detritus reaches the sediment surface in the marsh, yet the low amount of tamarisk on the sediment and in the export traps indicates that tamarisk is being consumed by detritivores, decomposed, or carried out of the system. Assuming a positive relationship between leaf decay rates and invertebrate feeding preferences (Webster and Benfield 1986, Kennedy and Hobbie 2004), we used difference in decay rates among litter types to make inferences about the relative quality of litter types as a food source for infaunal consumers. Tamarisk's significantly higher decomposition rate and equivalent C:N ratio to native *S. pacifica* supports our hypothesis that tamarisk is a more labile and readily

available food than the dominant native plants in the salt marsh and thus has the potential alter the food web and influence consumers.

Which species consume tamarisk? Does utilization vary with depth or habitat? Because there were no significant differences in change in $\delta^{15}N$ among species when offered ^{15}N-enriched different tamarisk parts, only the data from leaf detritus are discussed below. We hypothesized labeled ^{15}N from tamarisk could end up in consumer tissue through (a) direct consumption, (b) leaching of N and uptake by algae or (c) remineralization by bacteria and subsequent ingestion by bacterivores or grazers. But leaching treatments collected at 90 days after experiment initiation suggest that this utilization pathway is minor compared to direct detritus consumption. The isotope enrichment data reflect consumption of tamarisk-derived N by species from many taxa and feeding groups, equally in both invaded and non-invaded habitat patches (Table 5.1).

Although most species were able to derive N from tamarisk detritus (Figure 5.7), Psychodidae and *Grandidierella japonica* incorporated significantly more than did other species. *Grandidierella japonica* is an exotic corophiid amphipod first reported in the United States in San Francisco Bay, CA in 1966 (Chapman and Dorman 1975) and was first identified in the Tijuana Estuary in 1994 although it may have been present prior to this date (Williams and Zedler 2001). Rapidly reproducing, opportunistic species, like *G. japonica*, are capable of taking advantage of expanded resources, such as an input of tamarisk detritus (Zajac and Whitlatch 1982, Greenstein and Tiefenthaler 1997, West et al. 2003).

Species with greatest tamarisk ingestion were detritivores, while microalgal feeders (primarily insects) had lower tamarisk consumption (Figure 5.5). In some cases,

mixed diet feeders, such as Acarina and Pscychodidae sp. 1, also indicated high levels of tamarisk ingestion, suggesting a possible shift to tamarisk use in higher trophic levels (Figure 5.6). Some tamarisk N uptake in microalgal feeders, such as insect larvae and gastropods, may have been due to increased microalgal colonization on the surface of tamarisk detritus and subsequent grazing (Figure 5.7).

What are the overall food web effects? We have demonstrated that tamarisk is affecting the sediment food web in multiple ways through alterations of the quantity or quality of food and through changes to the growth of a food source (benthic microalgal and SOM changes due to shading). First, measured input of tamarisk litter provides ample food for mixed diet feeders and detritivores, such as Psychodidae and *Grandidierella japonica*, to consume (Figure 5.6), and we predict that long-term tamarisk presence could shift the infaunal community towards specialized detritivores or towards opportunistic species, including exotics like *G. japonica*. The observed isotopic differences in SOM and microalgae between tamarisk-invaded and natural habitats (lighter $\delta^{13}C$ and heavier $\delta^{15}N$ in natural habitats) have several possible explanations (Figure 5.2a). The algal and SOM signatures could reflect the signatures of organic matter exuded by vascular plants; *S. pacifica*, more dominant in the natural environment, has lighter $\delta^{13}C$ than tamarisk, the more dominant plant in tamarisk-invaded environment. In addition, the isotopic signature differences could be due to C-limitation and fractionation associated with increased shading in natural areas (Whitcraft et al. in prep), or to greater contribution of cyanobacteria in natural areas. Because cyanobacteria tend to be more dominant in shady, wetter environments, this could be an example of how structural alterations can change the growth of a food source (Whitcraft and Levin in

press). Although this suggests that some changes in tamarisk-invaded habitats are bottom-up processes, other factors, including top-down control, grazer access to food sources, flow regime modifications, and indirect changes in food supply, may also structure this benthic ecosystem.

How do these results influence direct management and eradication plans for tamarisk? This research, demonstrating the incorporation of tamarisk into the food web through input of labile detritus, has important implications for understanding how trophic shifts can occur as discussed above, for appreciating crucial differences among invaders, and for increasing our knowledge of how best to manage invasions. The demonstrated food web effects of tamarisk raise interesting parallels with other invasive plant species and may help develop additional hypotheses as to why some wetland plants are more successful or invasive than others. *Phragmites australis* (reed canary grass) in the northeast United States, perhaps the best-studied invader in North American coastal wetland habitats, has multiple effects on higher trophic-levels. For example, fewer juvenile fish (*Fundulus heteroclitus*) occurred on the marsh surface in *Phragmites*-invaded habitat than in native *Spartina*-dominated areas (Able et al 2003, Osgood et al. 2003), perhaps driven by altered invertebrate availability (Raichel et al. 2003). Blue crabs (*Callinectes sapidus*) preferentially consumed *Spartina* over *Phragmites*, and Currin et al (2003) suggested that mummichogs incorporate *Phragmites* detritus in amounts proportional to the abundance of *Phragmites* in the marsh.

A second example, a hybrid of *Spartina alterniflora* x *foliosa* (cordgrass) in San Francisco Bay, also has dramatic effects on the trophic structure of salt marsh habitats. This invasion shifted the dominant primary producers from algae (on open mudflats) to

taller, dense stands of hybrid *Spartina* (in invaded patches). The increased plant detrital production led to decreased carbon and nutrient cycling (Grosholz et al. submitted) as well as an invertebrate community shift to one dominated by detritivores capable of consuming the detritus (Levin et al. 2006).

Essential to effective management is development of metrics to assess the success of invasive eradication or removal. Knowledge of which macrofauna species are consuming tamarisk detritus allows scientists to use macrofauna groups as indicator species, potentially serving as a metric of recovery after eradication, and understanding that detritus becomes a portion (sometimes large) of invertebrate diets emphasizes the point that early eradication is essential for restoring the trophic structure with minimal disruption, including the possible trophic support of exotic cosumers. Vigilant monitoring for incipient invasions and rapid, coordinated responses are essential to effective management and eradication of invasive species.

Our research also demonstrates that isotope enrichment of wetland plants is a powerful method to track the fate of introduced plants within food webs and thus potentially assess the impacts of an invader or the recovery of a system. Natural abundance stable isotope methods have proved valuable for tracking food sources through food webs provided that the organic matter sources have distinct signatures (Fry and Sherr 1984, Petersen et al. 1985, Currin et al.1995, Kwak and Zedler 1997, Levin et al. 2006). However, in situations where important food source signatures overlap as occurs in the TRNERR mid-marsh, isotopic enrichment experiments allow researchers to identify key consumers of the enriched species, and to identify trophic succession (shifts in feeding groups) as a possible cause of potential community changes (Levin et al. 2006,

this study). This approach can also be used to evaluate trophic recovery following management action.

Conclusions

Genera such as tamarisk (*Tamarix*), reed canary grass (*Phragmites*), and cordgrass (*Spartina*) act as ecosystem engineers (Bruno and Bertness 2001), greatly altering the structure of an invaded site and potentially shifting hydrological conditions and animal communities. Integrating detrital pathways into the study of these and other plant invasions may prove to be crucial in predicting and mitigating against the effect of wetland plant invaders both in the salt marsh and other invaded ecosystems. In the case of tamarisk, our enrichment experiments demonstrate that several native consumers can modify their diets to include N derived from invasive tamarisk. As suggested by Zavaleta et al. (2001), removal of well-established exotic species can result in undesirable changes to native ecosystem elements, for example loss of taxa, like Psychodidae that are now dependent on tamarisk-derived nitrogen.

The spread of tamarisk through the southwestern United States has substantially altered those freshwater ecosystems, causing significant changes in flooding and erosion patterns, fire frequency, and both plant and animal diversity (Di Tomaso 1998). Yet, effects of tamarisk as a detrital food source in these systems have not been thoroughly evaluated. Results of this salt marsh study, if relevant to freshwater wetlands, imply that the consequences of tamarisk invasion in these systems could go beyond the observed declines in wildlife use value and affect the entire food web from the bottom up.

Acknowledgements

Figure 5.1. C:N ratios of unlabeled invasive tamarisk and natural food sources in the Tijuana River NERR salt marsh. Letters indicate *a posteriori* differences among treatments (P < 0.05).
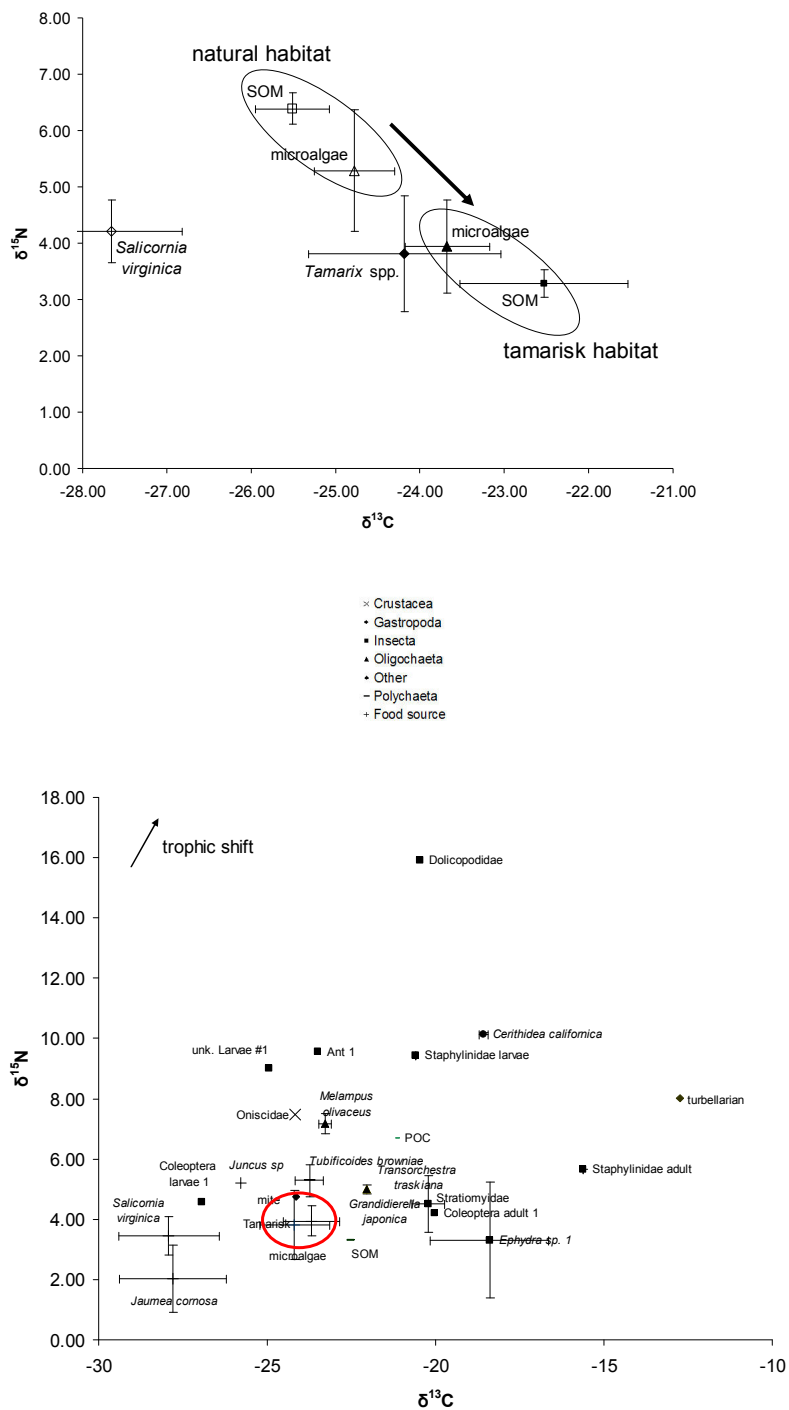
Figure 5.2. Dual isotope plots of natural abundance δ^{13}C and δ^{15}N signatures (mean $\pm$ 1 se) (a) among primary food sources in both tamarisk-invaded and natural habitats and (b) of major primary producers and infaunal consumers in tamarisk-invaded sediments. The arrow (b) represents the trophic level shift. The overlap between microalgae and tamarisk detritus is evident in tamarisk-invader habitat, as shown with circle.

Figure 5.3. Mean (+ 1 se) Δ $\delta^{15}N$ signatures ($\delta^{15}N_{experiment}$ - $\delta^{15}N_{background}$) of infaunal invertebrate taxa following periods of exposure to ^{15}N-labeled tamarisk detritus at the sediment surface and at subsurface depth of 1cm in litterbags. The absence of error bars indicates very small error terms or n=1. Letters indicate *a posteriori* differences among treatments (P < 0.05).

Subsurface, Habitats Combined
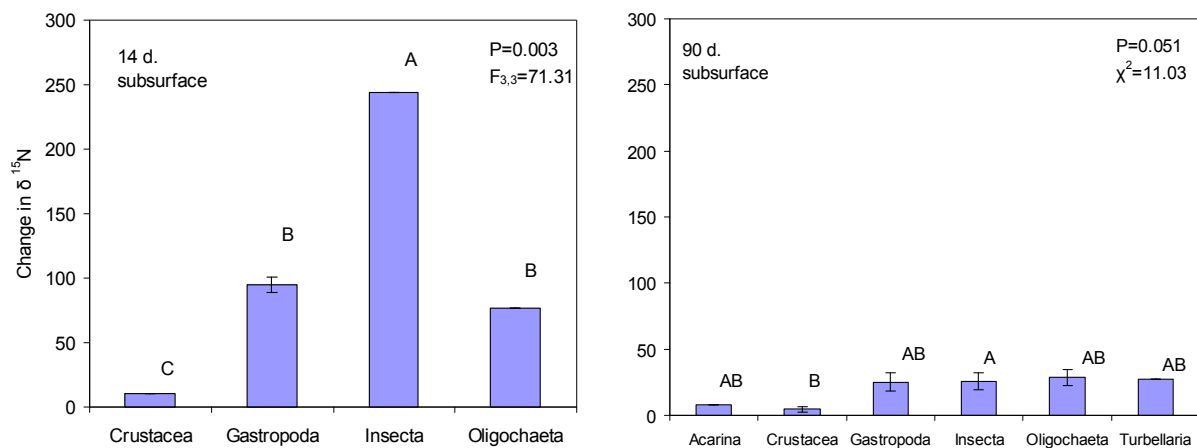
Figure 5.3 (continued)
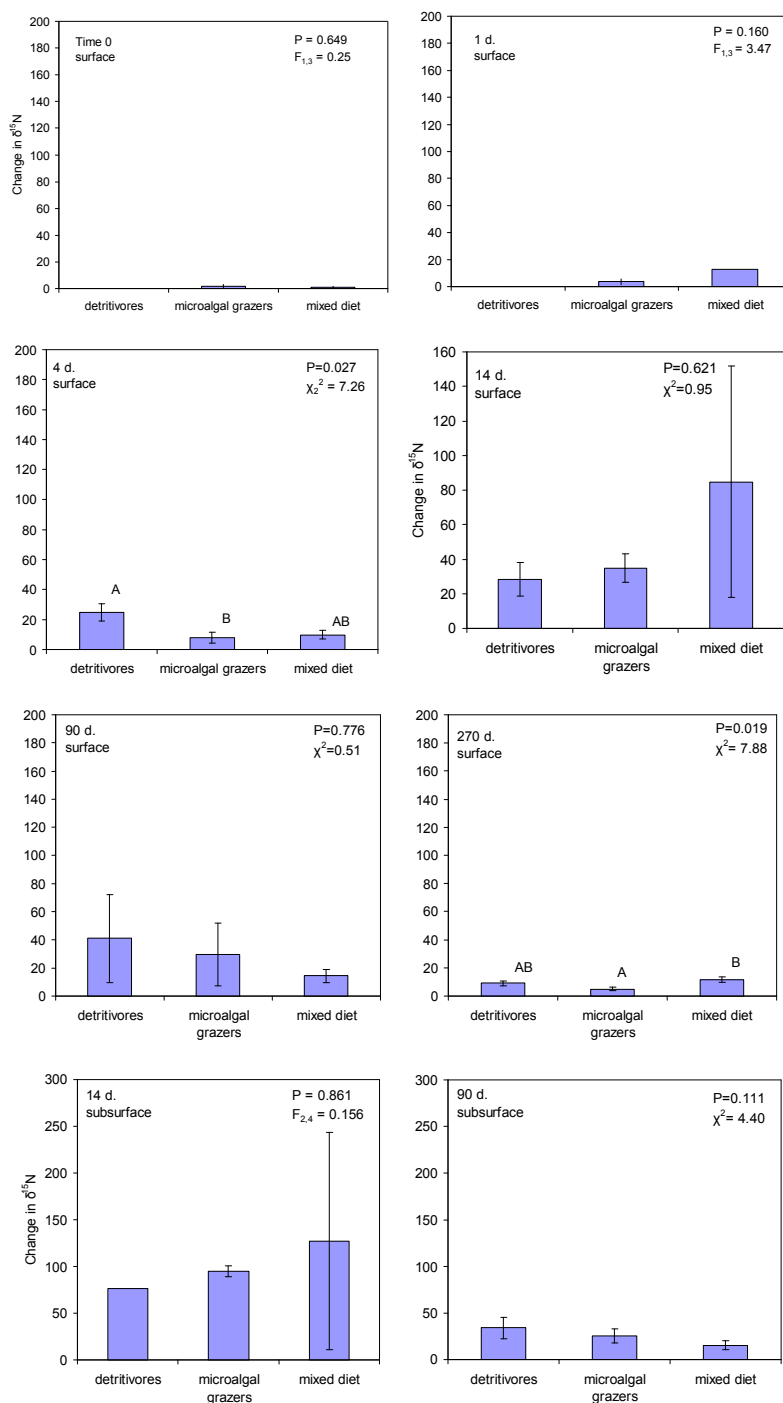
Figure 5.4. Mean ($\pm$ 1 se) $\Delta\ \delta^{15}$N signatures (δ^{15}N$_{experiment}$ - δ^{15}N$_{background}$) of infaunal invertebrate feeding groups following periods of exposure to ^{15}N-labeled tamarisk detritus at the sediment surface and at subsurface depth of 1cm in litterbags. The absence of error bars indicates very small error terms or n=1. Letters indicate *a posteriori* differences among treatments (P < 0.05).
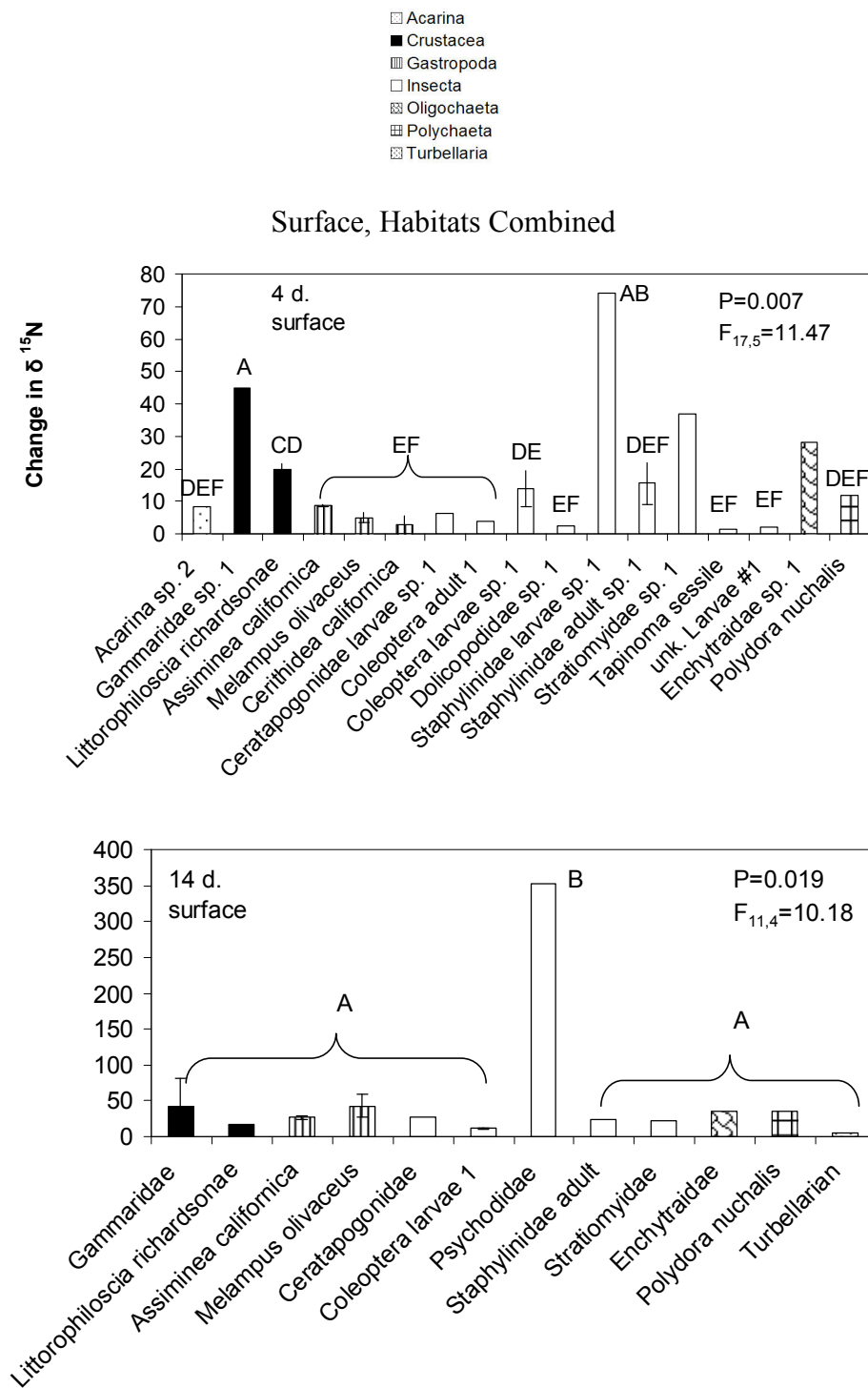
Figure 5.5. Mean ($\pm$ 1 se) change in $\delta^{15}N$ signatures from background $\delta^{15}N$ signatures of infaunal invertebrate species and families following periods of exposure to ^{15}N-labeled tamarisk detritus at the sediment surface and at subsurface depth of 1cm in litterbags. The absence of error bars indicates very small error terms or n=1. The p value reflects results of ANOVAs comparing uptake among species.

Figure 5.5 (continued)

Figure 5.5 (continued)

Figure 5.6. Hypothesized food web based on ^{15}N tamarisk detritus utilization (percent of tamarisk-derived 15N in individual species).

Table 5.1: Percent of N in invertebrate diets that was derived from δ^{15}N labeled-tamarisk detritus at 1, 4, 14, 90 and 270 days after deployment of surface-deployed labeled material. Missing values indicate that that species was not collected at that time point. Percentages are calculated from a single isotope, two-source mixing model for δ^{15}N in which labeled tamarisk detritus was treated as one food source and unlabeled (background) native food sources (i.e. microalgae, POM and SOM) were treated as a second food source.

NATURAL MARSH

Species	T1	T4	T14	T90	T270
Gastropoda					
Assiminea californica	2.55	2.18	17.54	1.39	1.63
Cerithidea californica	0.42	0.49			
Melampus olivaceus	0.76	1.83	22.82		1.08
Insecta					
Ceratapogonidae larvae			6.56	7.08	1.62
Coleoptera larvae		4.01	2.06	3.45	
Chironomidae larvae					2.29
Cincinilidae adult					1.99
Dolicopodidae larvae		3.08		4.69	
Ephydra sp. 1					1.38
Hydrophilid sp. 1				0.87	
Psychodidae			64.12	0.27	
Staphylinidae adult				7.84	
Staphylinidae larvae		17.71			
Crustacea					
Gammaridae			20.28		
Oniscidae		4.86		3.67	2.49
Polychaeta					
Polydora nuchalis		2.98	9.12		
Oligochaeta					
Tubificoides browniae				1.35	
Enchytraidae		7.08	17.32		
Other					
Acaria sp. 1				0.93	3.29

TAMARISK-INVADED MARSH

Species	T1	T4	T14	T90	T270
Gastropoda					
Assiminea californica		2.31	23.17	2.39	1.18
Cerithidea californica		0.85			
Melampus olivaceus	1.04	0.9	21.03		0.32
Insecta					
Ceratapogonidae larvae		1.13		1.12	1.93
Coleoptera adult		0.38			
Coleoptera larvae		1.63	2.22	2.78	
Dolicopodidae larvae				1.19	
Ephydra sp. 1					1.38
Orthoptera					
Poduridae				12.84	
Staphylinidae adult		3.54	6.27	2.17	
Staphylinidae larvae				18.81	1.75
Stratiomyidae		8.9	4.94	2.35	1.57
Tapinoma sessile		1.18			
unk fly adult #1					4.3
unk. larvae #1		1.14			
Crustacea					
Gammaridae		11.09	0.61		3.48
Grandidierella japonica				50.17	
Oniscidae	3.51	5.8	4.22		1.77
Transorchestia traskiana				0.05	0.51
Other					
Turbellarian sp 1			1.57		
Acaria sp. 2		1.72		1.61	6.28

Table 5.2: Feeding behavior designations for the macroinvertebrates found in isotope samples. These designations are based on natural abundance signatures and/or published literature.

Species	Taxonomic Grouping	Feeding behavior
mite sp. 1	Acaria	mixed diet[1]
mite sp. 2	Acaria	mixed diet[1]
mite sp. 3	Acaria	mixed diet[1]
Gammaridae	Crustacea	detritivore[2]
Grandidierella japonica	Crustacea	detritivore[2]
Oniscidae sp. 1	Crustacea	mixed diet[3]
Transorchestia traskiana	Crustacea	detritivore[2]
Assiminea californica	Gastropoda	microalgal grazer[2]
Cerithidea californica	Gastropoda	microalgal grazer[2]
Melampus olivaceus	Gastropoda	microalgal grazer[2]
Ceratapogonidae larvae	Insecta	mixed diet[4]
Chironomid larvae	Insecta	microalgal grazer[4]
Cincinlidae adult sp. 1	Insecta	detritivore[4]
Coleoptera larvae	Insecta	detritivore[4]
Coleoptera sp. 1	Insecta	detritivore[4]
Dolicopodidae larvae	Insecta	mixed diet[5]
Ephydra sp. 1 pupae	Insecta	mixed diet
Hydrophilid sp. 1	Insecta	microalgal grazer[4]
Muscidae larvae	Insecta	mixed diet[4]
Poduridae sp. 1	Insecta	mixed diet[4]
Psychodidae larvae	Insecta	mixed diet[6]
Staphylinidae adult	Insecta	mixed diet[7]
Staphylinidae larvae	Insecta	microalgal grazer[4]
Stratiomyidae larvae	Insecta	detritivore[4]
Tapinoma sessile	Insecta	mixed diet[8]
unk. larvae #1	Insecta	microalgal grazer[4]
unknown adult fly	Insecta	mixed diet[4]
Enchytraidae	Oligochaeta	detritivore[9]
Tubificoides browniae	Oligochaeta	detritivore[10]
Polydora nuchalis	Polychaeta	detritivore[2]
Turbellarian	Turbellaria	mixed diet

[1] Di Sabatino et al. 2000
[2] Levin and Currin 2005
[3] Carefoot 1973
[4] Moseman et al. 2004
[5] Bickel and Dyte 1989
[6] Schlein and Muller 1995
[7] D. Holway (pers. com.)
[8] S. Menke (pers. com.)
[9] Dash and Cragg 1972
[10] Wavre and Brinkhurst 1971

Appendix 5.1. Mean δ^{15}N and δ^{13}C signatures of macrofauna (±1 SE) by sampling time point (days after initiation of experiment). No individuals of that species were collected when cell is left blank. When no SE is reported, n=1.

Background and T0				^{15}N				^{13}C	
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
Oniscidae sp. 1	Crustacea		9.87				-24.17		
Assiminea californica	Gastropoda	9.68				-22.08			
Cerithidea californica	Gastropoda	9.54 (0.24)	10.13 (0.14)			-20.64 (0.27)	-18.58 (0.07)		
Melampus olivaceus	Gastropoda	7.18 (0.19)		not collected at this time point		-23.29 (0.33)		not collected at this time point	
Coleoptera larvae sp. 1	Insecta	33.46 (25.05)				-26.22 (0.45)			
Dolicopodidae	Insecta	15.91				-20.46			
Staphylinidae adult	Insecta		9.45				-15.60		
Staphylinidae larvae	Insecta		5.65				-20.61		
microalgae	Algae	5.29 (1.09)				-24.78 (0.48)			
POC	Other	6.68 (0.08)	6.68 (0.08)			-21.20 (0.21)	-21.23 (0.21)		
SOM	Other	6.39 (0.28)	3.29 (0.24)			-25.51 (0.45)	-22.51 (0.99)		
Jaumea cornosa	Plantae	2.82	2.02 (1.58)			-25.67	-27.80 (1.11)		
Juncus sp	Plantae	4.24	5.2			-22.65	-25.81		
Salicornia virginica	Plantae	4.22 (2.58)	3.45 (1.49)			-27.66 (0.84)	-27.90 (0.63)		
Tamarix spp.	Plantae		3.82 (1.03)				-24.22 (1.15)		

T1				^{15}N				^{13}C	
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
Oniscidae sp. 1	Crustacea		20.18 (2.22)				-24.24 (0.36)		
Assiminea californica	Gastropoda	16.45		not collected at this time point		-13.87		not collected at this time point	
Cerithidea californica	Gastropoda	8.15 (0.91)				-20.37 (1.19)			
Melampus olivaceus	Gastropoda	9.46 (0.49)	9.69 (1.24)			-23.50 (0.27)	-22.70 (0.35)		

T4				^{15}N				^{13}C	
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
mite 2	Acaria		13.20				-13.42		
Gammaridae sp. 1	Crustacea		49.72				-24.88		
Oniscidae sp. 1	Crustacea	25.43	29.11 (2.36)			-24.96	-23.94		
Assiminea californica	Gastropoda	15.00	15.50			-15.15	-9.19		
Cerithidea californica	Gastropoda	8.33 (0.25)	9.36 (0.87)			-23.55 (3.01)	-20.66 (1.99)		
Melampus olivaceus	Gastropoda	13.74 (0.71)	10.70 (1.37)			-21.78 (0.51)	-21.74 (1.69)		
Ant 1	Insecta		11.08 (0.33)				-25.52 (0.03)		
Ceratopogonidae larvae	Insecta		10.88				-10.86		
Coleoptera adult 1	Insecta		7.97	not collected at this time point			-16.78	not collected at this time point	
Coleoptera larvae sp. 1	Insecta	22.11	12.83			-24.66	-21.44		
Dolicopodidae	Insecta	18.50				-20.18			
Staphylinidae adult	Insecta		20.30 (7.72)				-4.07 (5.12)		
Staphylinidae larvae	Insecta	75.54	43.24			3.62	-10.16		
Stratiomyidae	Insecta		41.20				-20.85		
unk. Larvae #1	Insecta		10.95				-26.84		
winged ant	Insecta		11.67				-24.20		
Enchytraidae	Oligochaeta	34.09				-22.12			
Polydora nuchalis	Polychaeta	18.11							

T14				^{15}N				^{13}C	
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
Gammaridae	Crustacea	85.55	8.86			-23.97	-21.92		
Oniscidae sp. 1	Crustacea		24.85 (3.85)		18.18 (6.27)		-22.89 (0.26)		-25.36 (1.15)
Assiminea californica	Gastropoda	30.49	35.99 (5.09)	97.06 (14.18)	117.10 (13.20)	-17.42	-13.03 (2.13)	-17.77 (0.46)	-16.45 (1.35)
Melampus olivaceus	Gastropoda	33.65	66.21	101.63 (10.57)	90.05 (15.27)	-20.83	-21.40	-21.91 (0.29)	-21.39 (0.49)
Ceratapogonidae	Insecta	32.06				-14.58			
Coleoptera larvae sp. 1	Insecta	14.52	15.14			-22.36	-27.55		
Psychodidae	Insecta	352.05		253.58 (52.33)		-24.20		-23.38 (0.18)	
Staphylinidae adult	Insecta		30.94 (15.52)				-14.62 (4.77)		
Stratiomyidae	Insecta		25.74				-14.24		
Enchytraidae	Oligochaeta	40.81		82.30 (2.88)		-24.93		-23.92 (0.33)	
Polydora nuchalis	Polychaeta	42.06 (4.28)				-20.39 (0.06)			
Turbellaria sp. 1	Turbellaria		12.60 (0.93)				-23.48 (0.44)		

T90				^{15}N				^{13}C	
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
red mite	Acaria	10.11	12.78		13.02	-24.33	-20.19		-22.21
Grandifolia japonica	Crustacea		202.07		18.50		-20.78		-23.73
Oniscidae sp. 1	Crustacea	20.81		9.45 (0.34)	10.19 (2.19)	-23.46		-23.67 (0.33)	-25.40 (0.82)
Oniscidae sp. 2	Crustacea			6.85 (1.84)				-24.87 (0.80)	
Transorchestra traskiana	Crustacea		6.71	8.40 (0.12)	11.74		-23.15	-24.34 (0.20)	-23.78
Assiminea californica	Gastropoda	11.91 (2.77)	15.80 (4.44)	14.29 (1.24)	25.91 (4.57)	-18.98 (5.17)	-22.03 (1.67)	-19.79 (0.38)	-19.66 (0.26)
Melampus olivaceus	Gastropoda			42.47 (11.14)	45.61 (22.76)			-21.56 (0.81)	-20.57 (0.73)
Ceratapogonidae	Insecta	34.10 (16.74)	10.85 (1.49)	24.17 (5.91)	66.26 (45.31)	-22.89 (0.17)	-22.48 (1.00)	-23.75 (0.34)	-22.70 (0.67)
Coleoptera larvae sp. 1	Insecta	19.94	17.35	23.93 (13.12)	138.79	-24.39	-18.49	-27.25 (0.44)	-24.97
Dolicopodidae	Insecta	24.76	11.15	9.90	11.12	-23.37	-20.49	-22.32	-25.07
Hydrophilid	Insecta	9.90		9.13		-22.32		-13.81	
Muscidae	Insecta			24.73				-24.23	
Poduridae	Insecta	18.50	56.55 (41.19)	17.85 (2.27)	23.76 (8.16)		-23.39 (1.63)	-24.64 (0.29)	-24.22 (0.32)
Psychodidae	Insecta	7.55		38.16 (9.01)		-23.31		-23.00 (0.34)	
Saldidae	Insecta				9.16				-24.04
Staphylinidae adult	Insecta	37.05	14.96 (1.58)	23.25 (9.24)	81.05 (48.62)	-26.81	-23.33 (0.79)	-24.55 (0.49)	-23.55 (0.28)
Staphylinidae larvae	Insecta		79.85		11.7 (1.08)				-24.30 (2.17)
Stratiomyidae	Insecta		15.65		71.46 (54.32)		-23.89		-21.25
Tubificicoides browniae	Oligochaeta	11.74		23.56 (3.61)	25.82 (3.60)			-23.36 (0.15)	-23.80 (0.12)
Tubificidae sp. 1	Oligochaeta			37.49 (22.70)	48.93	-23.78		-20.12 (2.55)	-23.42
Turbellaria sp. 1	Turbellaria								

T270				^{15}N				^{13}C	
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
orange mite	Acaria	19.3	30.97			-20.45	-24.99		
Gammaridae sp. 1	Crustacea		20.06				-23.09		
Oniscidae sp. 1	Crustacea	16.19	13.41 (3.35)	13.02 (1.18)		-22.66	-24.27	-23.65 (0.23)	
Transorchestra traskiana	Crustacea		8.49	13.69			-22.63	-23.85	
Assiminea californica	Gastropoda	12.86 (0.01)	11.12 (0.62)	14.86 (3.84)	17.61 (2.00)	-17.81 (1.14)	-19.27 (0.69)	-17.60 (0.17)	-16.36 (0.39)
Melampus olivaceus	Gastropoda	10.73	7.73 (1.09)			-24.68	-20.40 (0.62)		
Ceratapogonidae	Insecta	12.81 (0.08)	14.01 (0.43)	40.8		-24.00 (0.44)	-22.45 (0.67)	-23.41	
Chironomidae	Insecta	15.42				-24.12			
Cincinilidae	Insecta	14.26				-26.36			
Ephydra sp. 1	Insecta	11.86	11.89 (1.18)			-18.18	-18.88 (0.57)		
Muscidae	Insecta			10.28				-25.92	
Staphylinidae larvae	Insecta		13.33	17.14			-24.11	-24.48	
Stratiomyidae	Insecta		12.63	13.13			-24.47	-26.84	
unk fly	Insecta		23.25 (8.05)	13.57	37.19		-23.19	-23.67	-23.98

Appendix 5.2. Mean δ^{15}N and δ^{13}C signatures of macrofauna in leaching treatments ($\pm$1 SE) by sampling time point (days after initiation of experiment). No individuals of that species were collected when cell is left blank. When no SE is reported, n=1.

T90 - Leaching treatment		^{15}N				^{13}C			
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
red mite	Acaria				5.58				-26.00
Oniscidae sp. 1	Crustacea				7.50 (1.90)				-23.93 (0.80)
Assiminea californica	Gastropoda			10.59	6.80 (0.80)			-18.66	-20.20 (0.82)
Melampus olivaceus	Gastropoda			10.66				-24.51	
Ceratapogonidae	Insecta	not collected			19.22	not collected			-23.04
Poduridae	Insecta			10.63	3.94			-25.61	-25.49
Saldidae	Insecta				3.53				-21.63
Staphylinidae larvae	Insecta				11.61				-23.62
Stratiomyidae	Insecta				110.97				-22.37

T270 - Leaching treatment		^{15}N				^{13}C			
Species	Group	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface	Natural	Tamarisk	Natural subsurface	Tamarisk subsurface
Oniscidae sp. 1	Crustacea			10.23	9.74 (0.22)			-23.3731	-24.11 (0.20)
Transorchestra traskiana	Crustacea			7.55	7.43 (0.05)			-20.1269	-20.81 (0.35)
Assiminea californica	Gastropoda			9.03				-18.5981	
Melampus olivaceus	Gastropoda				7.53 (0.26)				-20.62 (0.44)
Ceratapogonidae	Insecta	not collected		14.21		not collected		-23.9593	
Cincinlidae	Insecta				12.80			-23.0061	-23.0061
Coleoptera larvae sp. 1	Insecta				13.88				-22.6133
Dolicopodidae	Insecta			22.64				-22.8014	
Stratiomyidae	Insecta			9.68				-21.9356	
Enchytraidae	Oligochaeta			21.16				-23.9578	

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CHAPTER VI

TROPHIC ROLES OF AN EPHEMERAL SEAGRASS, *RUPPIA MARITIMA*, IN A
SOUTHERN CALIFORNIA LAGOON

Abstract

When southern California lagoons close for extended periods, the widgeon grass

Ruppia maritima L. thrives in the resulting lower-salinity, higher-temperature water.

Because plant cover is a main source of spatial heterogeneity in Pacific coast wetlands,

such changes in plant communities can influence the abundance, diversity, and food web

structure of benthic invertebrates. Using mensurative comparisons in two vegetation

zones (one dominated by *Ruppia maritima* and one bare mudflat), we examined *R.*

maritima effects on abiotic environmental and biotic factors. In the subtidal *R. maritima*

zone, soils exhibited lower salinities, higher microalgal biomass, and altered macrofaunal

community composition with higher species richness, increased abundance, and a larger

proportion of crustaceans compared to intertidal areas. Differences in macroinvertebrate

communities between the two habitats are interpreted in association with animal feeding

preferences and ability of consumers to utilize *R. maritima*. *Ruppia maritima*

consumption by invertebrates was studied using natural abundance isotope signatures and

^{15}N isotope enrichment experiments. Results suggest that *R. maritima* consumption

occurs mainly among detritivores, such as amphipods, and mixed diet feeders, such as

naidid oligochaetes, and that community structure may be influenced by the availability

of *R*.

maritima detritus. Understanding the benthic community alterations due to changes in plant cover will increase knowledge of complex wetland interactions and aid in management decisions about southern California lagoon ecosystems.

Introduction

In arid climates, the coastal landscapes are dotted with a series of lagoons. In southern California (between the US Mexican Border and Point Conception), these lagoons provide critical support for wetland-dependant species, including several endangered bird and plant species, as well as birds migrating along the Pacific Flyway (Thayer et al. 1982, Zedler 1982, 1991). Although most of the lagoons are naturally occurring features, they have been highly modified in terms of the intensity and frequency of ocean flushing and with respect to inputs of freshwater, nutrients and sediments (Zedler 1996a). Due to the Mediterranean climate of southern California, these lagoons episodically receive freshwater input from rain events. They also receive significant inputs of energy, nutrients and organisms from the marine environment. While large embayments typically remain permanently open, smaller lagoons experience periodic closures. These result from natural or anthropogenic activities that cause increased sediment deposition from the upland watershed (Conners et al. 1991, Callaway 2001) or from division of wetland habitats by roads and railroads (West et al. 2001). Some of the lagoon mouths close for extended periods (many months), with ensuing changes in water level, oxygen, pH, salinity, temperature (West et al. 2001), microbial populations (Gersberg et al. 1995), and algal growth (Nozais et al. 2001, Froneman 2004). These changes can also be associated with alterations to the animal communities within the lagoons.

When lagoons are closed for extended periods or during specific reproductive seasons, key species with life cycles dependent on a connection with the ocean may disappear. On the reverse side, some plants rely on the conditions produced when lagoons close. One such plant species is *Ruppia maritima* L (widgeon grass), an opportunistic species that thrives in warm (Johnson et al. 2003) and less saline water (Kantrud 1991, Koch and Dawes 1991) partially due to its ability to osmoregulate (Kantrud 1991). Low salinity, warm conditions are typical of a lagoon that has been closed for extended periods. In open lagoons of southern California with higher salinity and decreased temperatures, *R. maritima* frequently disappears (Williams et al. 2003). Thus, *R. maritima* exists in marginal seagrass habitats or as a secondary species where other seagrasses, such as *Zostera marina*, dominate (Lazar and Dawes 1991, Johnson et al. 2003). Changes to the status of submerged vegetation, in this case loss of or reduction in percent cover of widgeon grass, can have major consequences for the entire lagoon ecosystem (Scheffer et al. 1993, Van Donk and Otte 1996, Perrow et al. 1997).

A significant portion of research on *R. maritima* species has been conducted in freshwater lagoons where *Ruppia* spp. are important in the diet of waterfowl, fish and invertebrates (Rodriguez-Perez and Green 2005, Garcia et al. 2005, Casagranda et al. 2006). Yet, little effort has been focused on describing the role of *R. maritima* in brackish and marine ecosystems, where it is an ephemeral species. One southern California study indicated that widegeon grass maintained a high biomass in summer and was a labile food source for the macroinvertebrate community (Johnson 2000). Literature descriptions from southern California habitats portray *R. maritima* as a marginal species that only exists when environmental conditions are unfavorable for

more dominant species, like *Zostera marina* (Johnson et al. 2003).   However, temporarily open/closed lagoons offer environments where *R. maritima* is the dominant subtidal species and where we predict that, similar to its role in freshwater systems where it not ephemeral, *R. maritima* will be a labile food source and have an important influence on the trophic structure of southern Californian lagoons. We also predict that the species most able to utilize *R. maritima* will be species capable of responding to temporally patchy food inputs.

Using benthic assessment tools, we characterized the plant, algal and invertebrate communities of two lagoon habitats (intertidal and subtidal *R. maritima* zones), whose occurance will shift with lagoon state. We then utilized stable isotope natural abundance and enrichment experiments to evaluate the importance of *Ruppia maritima* in structuring the benthic food web as a detrital food source. Specifically, we hypothesized that the distribution of macroinvertebrates within the *R. maritima* habitat is a function of their nutritional dependence on *R. maritima* and its associated epiphytes. Understanding the coupling between *R. maritima* and the invertebrate trophic structure will help evaluate potential management options for southern California lagoon ecosystems.

Materials and Methods

Site description: San Dieguito Lagoon (SDL), located in northwest San Diego, contains approximately 260 acres of wetland habitat that forms the lower part of the San Dieguito River Valley (http://ceres.ca.gov/wetlands). Historically, the hydrology of this lagoon has been strongly influenced by several major events, including the construction of Lake Hodges Dam in 1919 and the filling in of wetlands during construction of Del Mar Fairgrounds in 1935. As a result of these changes, the lagoon mouth began to close

more frequently due to a reduction in the tidal prism and less frequent scour during river flooding (reviewed in SCE 2001). Temporal variability in the condition of the inlet has resulted in long-term unstable ecological conditions throughout the lagoon. This pattern continues today as San Dieguito opens and closes regularly based on rainfall amounts and flood scour (Elwany & Flick 1998).

Sampling design and dates: Field data for vegetation and sediment samples for infaunal analyses were collected in San Dieguito Lagoon at 3 locations on four dates (October 5 and October 21, 2002, March 14 and September 14, 2003). October 5, 2002 and September 14, 2003 followed periods of extended inlet closure (241 and 129 days respectively) while October 21, 2002 and March 14, 2003 followed periods of intermittent opening and closing with the longest period of closure at 72 days. At each of the 3 sites, we established a transect running parallel to the channel and sampled 3 replicate plots along that transect for a total of 36 plots sampled. These samples were used as background to understand the variability of invertebrate communities within the lagoon and with changing inlet status. In addition, within the eastern end of the lagoon in April 2005 and 2006, six blocks were established in patches of *R. maritima* (at least 90 percent cover), and six blocks were established in intertidal unvegetated mudflat areas immediately adjacent to *Sarcocornia pacifica* marsh. Hereafter, these will be referred to as *R. maritima* and intertidal plots, respectively. Vegetation and infaunal sampling (n=6) as well as natural abundance isotope sample collection and isotope enrichment experiments were collected in April 2005 and April 2006 at these locations.

Abiotic and sediment properties: Within each plot at all time points, soil salinity of the top 0.5 cm ($\pm$ 1 psu) was measured weekly by squeezing porewater from the

sediment surface through a Whatman No. 1 qualitative grade filter onto a hand-held salinity refractometer. Temperature ($\pm$ 0.1ºC) at 2 cm depth was measured weekly using a portable Ingold Mettler-Toledo digital thermometer.

Plant and microalgal sampling: Plant cover estimates for each species were made within 0.25 m^2 quadrats on all sampling dates. In April 2006 in each treatment plot, separate cores (0.95 cm^2 x 5 mm) were taken for chlorophyll *a* as a proxy for microalgal biomass. Back in the laboratory, chlorophyll *a* was extracted with 90% acetone, and the concentration was determined spectrophotometrically (Plante-Cuny 1973).

Macrofauna sampling: At all sampling points, macrofaunal cores were taken in each plot using a cylindrical push core (4.8 cm diameter, 18.1 cm^2) inserted to a depth of 2 cm as 78 – 89% of the macrofauna in southern California marshes is found in the top 2 cm of sediment (Levin et al. 1998). We selected a 4.8-cm diameter core to target macrofauna typically in the 1-2 mm size range (Levin et al. 1998). We recognize that this is likely to exclude megafauna, such as large clams or crabs. Cores were preserved (unsieved) in 8% buffered formalin with Rose Bengal. For macrofaunal quantification, the core sediments were washed through a 0.3 mm mesh. The animals retained were sorted under a dissecting microscope at 12x magnification, identified to the lowest possible taxonomic level, counted, and stored in 70% ethanol. Most insects collected were larvae, and identifications of these were at the family level only. For other organisms, identifications were to species level, although putative names were used in some cases.

Natural abundance stable isotope analysis: To determine trophic utilization of *R. maritima* by consumers based on stable isotope methods, samples of suspended

particulate organic matter (POM), sediment organic matter (SOM), microalgae,
macroalgae, plants, and macrofauna were collected in April 2005 in the intertidal and
subtidal *R. maritima* habitats. Collection and processing methods were similar to those
described in Moseman et al. (2004), Levin et al. (2006), and Whitcraft and Levin (in
press). POM was obtained by filtering 2 L of lagoon water onto Whatman GFF filters.
SOM was sampled by collecting surface sediment (upper 2 cm), drying and
homogenizing sediments. Benthic microalgae were collected using density centrifugation
with ludox (colloidal silica), providing a pure algal sample devoid of sediment
(Blanchard et al. 1988). Macrofaunal invertebrates were sieved on a 0.3 mm mesh,
sorted live, and identified to species. All animals were kept alive in seawater and
allowed to evacuate guts for up to 24 hours. Animal material was then washed in Milli-
$Q^®$ water, placed in pre-combusted vials or tin boats, dried at 65 ^{o}C, and kept in a
desiccator until analysis. Larger organisms were removed from the shell or carapace,
dried at 65°C and then ground with a mortar and pestle. All samples were treated with Pt
Cl_2 to remove inorganic carbon.

Isotopic composition of animal and algal samples was analyzed using a PDZ
Europa 20-20 mass spectrometer connected to an elemental analyzer (PDZ Europa
ANCA-GS, Northwich, UK). Stable isotope abundance is expressed in parts per
thousand in a ratio of heavy to light isotope content (^{15}N:^{14}N or ^{13}C:^{12}C). Working
standards, sucrose and ammonium sulfate, were δ^{13}C =-23.83‰ vs. Vienna Pee Dee
Belemnite Standard or δ^{15}N = +1.33‰ vs. air N_2.   Typical sample precision is better
than 0.1‰.

Isotope labeling and enrichment experiments: One effective method to identify plant consumers is isotopic labeling of the plant with ^{15}N to track the labeled material into consumer tissues. In April 2006, *R. maritima* was labeled by collecting plants with roots and surrounding sediments from San Dieguito Lagoon and reestablishing them in the laboratory in aquaria (0.5m x 0.25m x 0.3m). These aquaria were maintained with physical conditions that mimicked ambient field conditions from the collection day with salinity of 15, temperature of 20 ºC, and light for 12 hours / day. Once in the laboratory, the sediment porewaters were injected daily with 250 ml of 6 mmol/L ammonium sulfate (98 atom % ^{15}NH$_4$) for a 3-day period (method modified from White and Howes 1994 and Levin et al. 2006). Plants were harvested 2 weeks after injections (April 2006) and deployed in the field one day later as detritus. In the field, we established a complete-random block design, consisting of 4 blocks with paired treatments in adjacent intertidal and subtidal *R. maritima* habitats for a total of 8 quadrats. We conducted experiments in intertidal habitat because although *R. maritima* was not present as live plants, it was extremely naturally abundant as detritus.

The ^{15}N-labeled *R. maritima* plants and roots were cut into pieces approximately 5 mm in length. Nylon litter bags (2.6 x 1.2 cm, 5 mm mesh) were filled with 5g of detrital material and were deployed on the sediment surface in each quadrat where they were held in place with metal stakes. We collected one replicate bag 4 and 14 days later, washed the bags, sieved any accumulated sediment, and sorted the associated macroinvertebrates under a dissecting microscope. In addition, to test for N-leaching and uptake by bacteria and algae, ^{15}N-labeled *R. maritima* was also deployed in Nitex® mesh (61 µm) bags (1 per habitat). We collected the bags 4 days later, washed the bags, sieved

the accumulated sediment, and sorted the associated macroinvertebrates under a dissecting microscope.

Immediately after deployment of litter bags (time 0), we collected samples of infauna (> 0.3 mm), macroalgae, microalgae, particulate organic material (POM), and sediment organic material (SOM) to determine initial time point (T0) values for δ^{13}C and δ^{15}N isotope signatures. This provided background values and checked for labeling artifacts. Microalgae were subsequently collected 1, 4, and 14 days after deployment for stable isotope analysis. Samples from the isotope enrichment experiments were treated as described above for the natural abundance stable isotope samples.

Statistical Analysis: All univariate tests were conducted with JMP 5.1 statistical software (SAS Institute, NC, USA). Data were tested for normality, and square root or $\log_{10}$ transformed as needed prior to analysis. If no transformation yielded normal data, nonparametric Wilcoxon tests were utilized. Relationships among abiotic and biotic factors were analyzed for significance using Spearman's Rho. For macrofaunal community analysis, multivariate analyses were conducted on macrofaunal count data (square root transformed) using Primer 5 (Plymouth Marine Laboratory, Clarke 1993, Clark and Warwick 1994). Analyses are based on Bray-Curtis similarity indices (Clarke 1993). Pairwise comparisons of overall community similarity were made using Analysis of Similarity (ANOSIM).

For stable isotope analyses, species mean isotopic signatures were used as replicates for tracer uptake comparisons of intertidal verus subtidal *R. maritima* habitats, among food preference groups, and among species in Wilcoxon nonparametric tests with *a posteriori* Tukey's HSD tests. In figures and text, one standard error about the mean is

presented for all data unless otherwise noted. Mixing models were applied to estimate

the fraction of *R. maritima* and other food sources in the infaunal diets. We applied a

concentration dependent, three-source, two-isotope mixing model to the natural

abundance data (Phillips and Koch 2002). The three food sources were (1) *R. maritima*,

(2) microalgae, and (3) POC/SOM. Models involving macroalgae (*Ulva* sp.) did not

resolve and thus are not included. Concentrations of C and N were determined for each

food source by CHN analysis. In addition, for data generated from the isotope

enrichment experiment, we applied a single isotope, two-source mixing model for $\delta^{15}N$ in

which labeled *R. maritima* detritus was treated as one food source and unlabeled

(background) native food sources (microalgae, POM and SOM) with similar signatures

were grouped and treated as a second food source, using the following formula:

% *R. maritima*-derived N = $[(\delta^{15}N_{infauna} - \delta^{15}N_{background}) / (\delta^{15}N_{labeled\ Ruppia} - \delta^{15}N_{background})]$

$$*100$$

Using this approach, we calculated the percentage of N in infaunal tissues that was

derived from the labeled *R. maritima* detritus. A trophic level shift of 1‰ for $\delta^{13}C$ (Fry

and Sherr 1984) and 2.2‰ for $\delta^{15}N$ was applied in mixing models (McCutchen et al.

2003).

Results

Abiotic and sediment properties: Porewater salinity and porewater temperature

measurements were extremely variable among sampling dates, showing changes related

to both season and inlet status (by season - salinity: $\chi^2_2 = 47.70$, P < 0.0001; temperature:

$\chi^2_2 = 26.87$, P < 0.0001) (Figure 6.1 a,b). In April 2006, the intertidal had higher

porewater salinity values than the *R. maritima* habitat while the intertidal and *R. maritima*

habitats showed no differences in porewater temperature (salinity: $t_7 = 7.51$, P = 0.0001; temperature: $t_7 = 1.36$, P = 0.217).

Plant community response: Tidal flat transects were dominated by the seagrass *R. maritima maritima* on October 5, 2002 after 249 days of closure but were largely covered by *Ulva* sp. in October 21, 2003 (open for 17 days), March 14, 2003 (intermittently open), and September 14, 2003 (closed 129 days) (Figure 6.1c). Comparisons among seasons revealed significant differences in *R. maritima* and *Ulva* cover (P < 0.05) (Figure 6.1c).

Microalgal community response: In April 2006, the intertidal plots had greater chlorophyll *a* and phaeopigment concentrations than the subtidal *R. maritima* plots (Wilcoxon, *R. maritima* = 2.60 ± 0.53 µg / g sediment, intertidal = 8.55 ± 2.81 µg/g sediment chl *a*: $\chi^2_8 = 5.80$, P = 0.050) (Wilcoxon, phaeopigment: *R. maritima* = 41.25 ± 14.65 µg / g sediment, intertidal = 454.63 ± 123.46 µg/g sediment, $\chi^2_8 = 13.07$, P = 0.002).

Macrofaunal community response: Macrofauna in the upper 0-2 cm exhibited varied responses among sampling dates with details of season given in Tables 6.1 a,b. The infaunal community in March 2003 exhibited an increased density of organisms (Wilcoxon, $\chi^2 = 20.82$, P < 0.0001) and altered community composition as compared to the other seasons (ANOSIM, P = 0.001), driven by changes in every major taxonomic group (Table 6.1a). The infaunal community in September 14, 2003 (closed for 129 days) had lower species richness than the other seasons (Wilcoxon, $\chi^2 = 15.77$, P = 0.001) (Table 6.1a). We observed no significant relationships between *R. maritima* cover and macrofaunal density, or diversity.

Relative to the intertidal plots, *R. maritima* plots exhibited increased species richness (Wilcoxon, intertidal = 3.33 $\pm$ 1.14 species / 18.1 cm^2, *R. maritima* = 7.67 $\pm$ 0.33 species / 18.1 cm^2, t_5 = 3.88, P=0.012), increased density of organisms (Wilcoxon, intertidal = 18.00 $\pm$ 9.16 # / 18.1 cm^2, *R. maritima* = 315.00 $\pm$ 78.52 # / 18.1 cm^2, t_5 = 3.62, P=0.015), and altered macrofaunal community composition based on count and biomass data (ANOSIM, intertidal $\neq$ *R. maritima* zone, P < 0.002) (Figure 6.2a). Density and richness changes in *R. maritima* plots involved a significantly higher number of naidid oligochaetes (*Paranais littoralis*), polychaetes (*Streblospio benedicti, Polydora nuchalis*), amphipods (*Monocorophium insidiosum*) and turbellarians compared to intertidal plots (Figures 6.2 a,b, Table 6.2b, Appendix 6.1).

Macroinvertebrates were divided into feeding groups based on natural abundance isotope data generated for this project and on literature designations to make comparisons of *R. maritima* influence on macroinvertebrate feeding behaviors (detritivore, microalgal feeder, mixed diet) (Table 6.2). Using these designations, *R. maritima* habitats had significantly greater densities of detritivores and mixed diet feeders than intertidal habitats (Figure 6.2c).

Natural abundance stable isotope analysis: δ^{13}C and δ^{15}N analyses of food sources and consumers in intertidal and *R. maritima* habitats demonstrated few isotopic differences as a function of habitat, so habitats are combined for analyses and mixing models. Details of habitat and season are contained in Appendices 2 and 3. Dual isotope plots illustrated mean natural abundance δ^{13}C and δ^{15}N signatures of key primary producers and consumers in sediments (Figure 6.3). Use of a three-source mixing model suggests that *R. maritima* formed > 20% of the diet of the *Capitella* species complex,

Polydora nuchalis, *Paranais litoralis*, and *Streblospio benedicti*. The predator, Turbellaria sp. 1, consumes prey species with at least 20% *R. maritima* in their diet (Table 6.2). *Ruppia maritima* formed none of the diet of Stratiomyidae sp. 1 larvae while microalgae (primarily diatoms) formed 75% of the diet and POC formed 35% (Table 6.2). *Ruppia maritima* was 9% of the diet of *Monocorophium insidiosum* and the remainder of the diet was the combined sources of SOM/POM (or their consumers) form >75% of their diet (Table 6.2). These analyses suggest but do not reveal definitively, which taxa consume *R. maritima*. Thus, an isotopic tracer approach was adopted to answer these questions.

Isotope enrichment experiment: At the start of the enrichment experiment, ^{15}N-labeled *R. maritima* detritus had a mean δ^{15}N signature of 52,221‰ (equivalent > 16% atom and > 10^6 % enrichment). The maximum δ ^{15}N value in a consumer (1762‰) was observed in *Polydora nuchalis* 4 days after detritus placement and indicated up to 1500% enrichment from background values. Species of several major taxa (Acarina, Insecta, Mollusca, Crustacea, Oligochaeta, Polychaeta, and Turbellaria) in both habitats incorporated minor amounts of δ^{15}N label after 4 and 14 days, such that less than 0.5 % of their N was derived from labeled *R. maritima* detritus, as estimated from a two-source mixing model (Table 6.3). Averaged across species, utilization percentage did not differ among animals in low marsh and *R. maritima* habitats (^{15}N - T4: *R. maritima* habitat = 24.68 $\pm$ 3.05, intertidal = 24.74 $\pm$ 4.93, χ^2 = 0.09, P = 0.766; T14: *R. maritima* habitat= 16.12 $\pm$ 1.91, intertidal = 14.03 $\pm$ 1.79, χ^2 = 0.07, P = 0.788). For most taxa, utilization of *R. maritima*-derived N was higher at 4 days than at 14 days when the habitats were pooled (T4 = 15.09 $\pm$ 0.92, T14 = 29.50 $\pm$ 2.96, χ^2 = 23.22, P < 0.0001). A comparison of

the *R. maritima* utilization (change in $\delta^{15}N$ signatures from background signatures) among major invertebrate groups revealed taxon differences at both 4 and 14 days (Figure 6.4a). Species divided into three significant different groups: (1) highest consumption species: *Paranais litoralis*, (2) middle consumption species: Enchytraidae sp. 1, *Capitella* sp., *Polydora nuchalis*, *Monocorophium insidiosum*, and Turbellaria sp. 1, and (3) low consumption species: Coryxidae sp. 1 (Figure 6.4a).

Slightly elevated ^{15}N (change in ^{15}N of 15‰) was observed in microalgae within 4 days, potentially reflecting leaching of ^{15}N from the labeled *R. maritima* detritus and heterotrophic organic matter uptake by microalgae, but the signals were several orders of magnitude lower than that of the labeled detritus. In addition, a comparison of $\delta^{15}N$ signatures of invertebrates from leaching bag treatments with $\delta^{15}N$ signatures of invertebrates from normal litter bag treatments revealed that uptake of ^{15}N by animals exposed to N leached through 61 μm mesh was significantly less than uptake of ^{15}N by animals exposed to N in either intertidal or *R. maritima* habitats with much lower $\delta^{15}N$ values (Wilcoxon across all species, $\chi^2_2 = 4.75$, P = 0.029). The numerically dominant species found in the leaching treatments, *Paranais littoralis* and *Monocorophium insidiosum* demonstrated the minor N leaching effect (*P. littoralis*: consumer access treatment = 222.18 ± 82.31, leaching = 14.91 ± 2.21, $\chi^2_2 = 6.42$, P = 0.011; *M. insidiosum*: consumer access treatment = 136.78 ± 24.24, leaching = 20.69 ± 5.14, $\chi^2_2 = 5.14$, P = 0.023) (Appendix 6.2).

Species-level comparisons at each time period revealed that several species exhibited greater N uptake than the others. The greatest *R. maritima*-derived ingestion, as indicated by elevation of $\delta^{15}N$ signatures above background ($\Delta\delta^{15}N$) at 4 and 14 days

was by oligochaete species considered to be detritivores (Enchytraidae) or mixed-diet feeders (*Paranais littoralis*) (Figure 6.5). Lesser uptake of ^{15}N label was observed in many other taxa, including microalgal consumers (Figures 6.4 & 6.5). When species were pooled by feeding groups (Table 6.2), we observed significantly greater uptake in detritivores than in microalgal and mixed-diet feeders after 4 and 14 days (Figure 6.4b).

Discussion

Benthic community patterns: *Ruppia maritima* zone communities are distinguishable from neighboring intertidal areas by having higher density and species richness (Table 6.1). In addition, the density of detritivores, such as oligochaetes and crustaceans, and the density of omnivores/carnivores, such as Turbellaria, are much greater in these systems where live *R. maritima* is present. As demonstrated by a lack of relationship between percent cover and macroinvertebrate community parameters ($r^2 <$ 0.15, $P > 0.05$ in all cases), abundance of *R. maritima* does not alone determine the community structure. The reasons behind these macroinvertebrate community differences are more complicated than simple presence/absence of *R. maritima* (Hovel et al. 2002, Brito et al. 2005). An extensive amount of research documents that submerged vascular plants, of which widgeon grass is an example, influence nutrient dynamics and water chemistry, alter water flow and sedimentation (i.e. Fonseca and Bell 1998, Reusch and Williams 1999), modify the structure and dynamics of food webs (i.e. Heck and Orth 1980, Bell et al. 1994), and increase the physical habitat structure (reviewed in Orth et al. 1984 and Jeppensen et al. 1997). Our research does not isolate the mechanisms by which the presence of *R. maritima* structures its associated invertebrate community, but it does highlight differences between habitats (intertidal and subtial *R. maritima* zone) at

different tidal elevations that are consistent with known seagrass effects. The amount of intertidal versus subtidal habitat will change with inlet status as mudflats are often intertidal when the San Dieguito Lagoon inlet is open and subtidal when the inlet is closed. The dynamic *R. maritima* cover within the lagoon is one aspect that should be considered as a mechanism to help explain the dramatic biotic changes observed with different sampling dates and inlet status (Figure 6.1).

Relationship between nutritional dependence and benthic community: Those invertebrate species able to derive N from *R. maritima* were also more abundant in *R. maritima* habitat. Species with greatest *R. maritima* ingestion were detritivores, while microalgal feeders (primarily insects) had lower *R. maritima* consumption. Some *R. maritima* N uptake in microalgal feeders, such as insect larvae and gastropods, may have been due to increased microalgal colonization on the surface of *R. maritima* detritus and subsequent grazing (Figures 6.4 & 6.5). The most abundant species in the *R. maritima* habitat, *Paranais litoralis*, and several other numerically abundant species *Monocorophium insidiosum* and *Polydora nuchalis* were also the largest consumers of ^{15}N-labeled *R. maritima* detritus (Figures 6.2 & 6.5, Table 6.1). In a similar ^{15}N labeling experiment using invasive *Spartina* hybrid, Levin et al. 2006 documented that oligochaetes and capitellid polychaetes were the primary consumers of hybrid *Spartina* detritus while the amphipod *Corophium* sp., and the polychaetes, *Polydora nuchalis*, and *Streblospio bendicti* ingested little *Spartina*-derived N (< 1% of tissue N from labeled detritus). To explain the discrepancy between observed *R. maritima* and *Spartina* hybrid detritus experiments, we hypothesized that *R. maritima* detritus is more labile than *Spartina* detritus.

Paranais litoralis, in particular, was the greatest consumer of ^{15}N-labeled *R. maritima* detritus at T14 (Figure 6.6). Yet, *P. litoralis* has traditionally been considered a deposit feeder, eating mainly diatoms (Giere 1975, Nillson et al. 1997). Our research corroborates more recent research, suggesting that *P. litoralis* is a mixed diet feeder, capable of responding individually and at a population level to patchy input of algal and plant detritus (Kelaher and Levinton 2003, Junkins et al. 2006). This ability of *P. litoralis* to utilize patchy and seasonal input of detritus, such as *R. maritima*, drives its boom-bust population pattern and its temporally shifting growth rates (Levinton and Stewart 1982, Talley and Levin 1999, Junkins et al. 2006).

Monocorophium insidiosum, an introduced gammarid amphipod on the Pacific coast of North America (Bousfield and Hoover 1997), has been observed feeding on deposited particles including detritus and diatoms (Dahl 1973) and has "shredder" mouthparts that can transform leaf material into fine particulate organic matter (Schwoerbel 1993). As in many freshwater ecosystems (i.e. Menendez and Comin 1990, Casagranda et al. 2006), gammarid amphipods are numerically dominant in the *R. maritima* zone (Figure 6.2). This dominant amphipod, *M. insidiosum*, was able to assimilate ^{15}N derived from *R. maritima* detritus (Figure 6.5). Research suggests that these shredders do not digest the detritus itself but instead assimilate living epiphytes (Fenchel 1977). As a shredder, this species contributes to macrophyte decomposition and exists as a link between primary (in this case, *R. maritima*) and secondary production in lagoon ecosystems (Casagranda et al. 2006). Our labeling experiments do not separate the role of *R. maritima* in the food web as either detritus itself or as a structure and a source of organic matter for the growth of epiphytes, another crucial food source for the

system (Harrison 1977, Tomas et al. 2006). Future labeling experiments could be constructed to distinguish between epiphytes and the actual detritus (i.e. Mutcher et al. 2004). However, our experiments demonstrate that this lagoonal seagrass community supports a diverse grazing pathway that includes grazing on live seagrass leaves, consumption of epiphytic algae on seagrass leaves, and consumption of POC from the water around the seagrass patches (Heck and Valentine 2006).

The observed differences in macroinvertebrate communities between the two habitats (Figure 6.2) mirror the abilities of consumers to utilize *R. maritima*, as evidenced by increased N in the diets of detritivore and predatory feeding groups (Figure 6.4). These plant-induced changes in microalgae and macrofauna can have effects that extend to higher trophic levels. For example, structural differences in macrofaunal communities between different seagrass systems have been shown to translate to higher trophic levels by altering foraging patterns of fish (i.e. Heck and Orth 1980, Bell et al. 1994). Although this suggests bottom-up regulation of the community, other factors, including top-down control, grazer access to food sources, predator refugia formed by seagrass, flow regime modifications, and indirect changes in food supply, may also structure this benthic ecosystem.

The lower abundance of *R. maritima* consumers in unvegetated intertidal habitats relative to the *R. maritima* zone follows patterns similar to those observed in freshwater systems (Casagranda et al. 2006) and describes an important role for *R. maritima* in southern California lagoon ecosystems. Despite its being an ephemeral species, *R. maritima* supports macroinvertebrates, such as *Monocorophium insidiosum*, that have key

functions in making macrophyte matter available to different trophic levels through fragmentation and accelerated decomposition (Giere 1975, Casagranda et al. 2006).

Management implications for San Dieguito and other southern California lagoon ecosystems: Within southern California lagoons, the widgeongrass, *Ruppia maritima*, is dynamic and locally abundant (Johnson et al. 2003). Our research suggests that *R. maritima* is important in structuring the associated macroinvertebrate community as a food source (Figure 6.2, Table 6.2 b) and perhaps indirectly important to sustaining ecosystem functions, especially in providing trophic support for larger invertebrates, resident fishes, and migratory and resident birds through consumption of invertebrate community (Zedler 1996b).
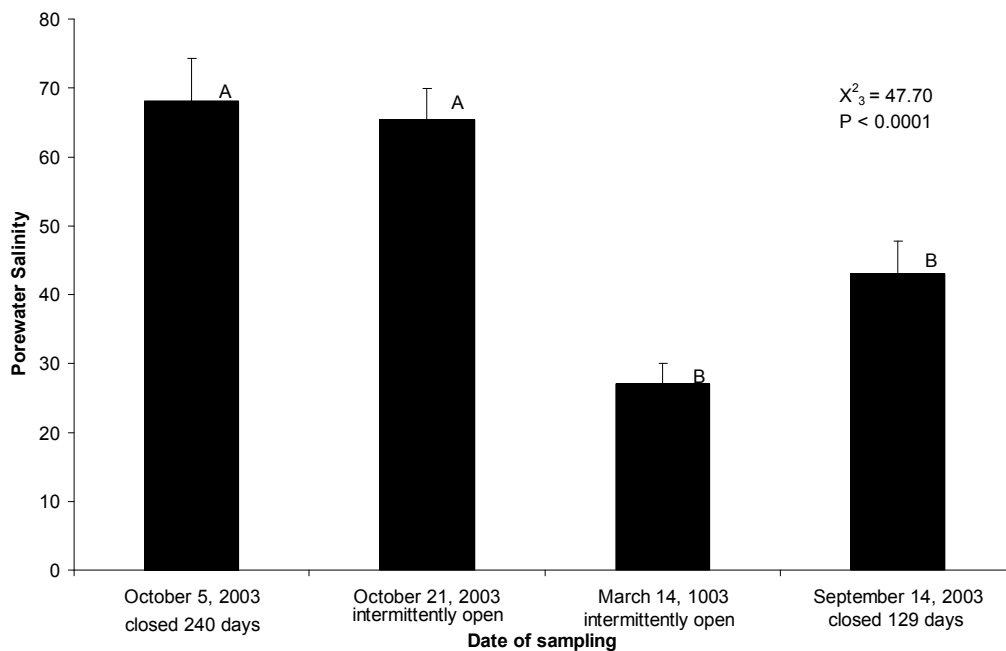
Permanent opening of inlets through the construction of jetties has been a common management strategy to avoid nuisances associated with long periods of closure (Arundel 2003). However, our results suggest that in southern California, lagoons with permanently open inlets may lose important plant species such as *Ruppia maritima*.   It is possible that the structural loss of *R. maritima* could be replaced by *Zostera marina*, and research comparing the two species would be valuable in ascertaining the functions of and value of each seagrass habitat. The coupling of community structure and trophic structure in seagrass systems has been demonstrated with other species (nematodes – Danovaro and Gambi 2002) and offers an explanation as to why invertebrate communities would vary with temporally and with lagoon state. While our study does not predict what will occur if permanent connection to the ocean is created, it does suggest one potential scenario of ecosystem change involving the loss of a trophically important plant, *Ruppia maritima*, within the lagoon ecosystem. These shallow lagoons

are particularly susceptible to stressors such as long-term temperature increases associated with climate change (Short and Neckles 1999, Koch et al. 2007). Sequential consequences of changing seagrass cover are likely. Knowledge of these trophic pathways involving *R. maritima* can increase our ability to predict consequences of climate change for southern California lagoons systems.

Acknowledgements

(a)

Figure 6.1. Variability of (a) porewater salinity, (b) porewater temperature, (c) percent cover of *Ruppia* and *Ulva* sp. and (d) macrofaunal invertebrate community composition among sampling dates within the subtidal *Ruppia* habitat.

(b)

(c)
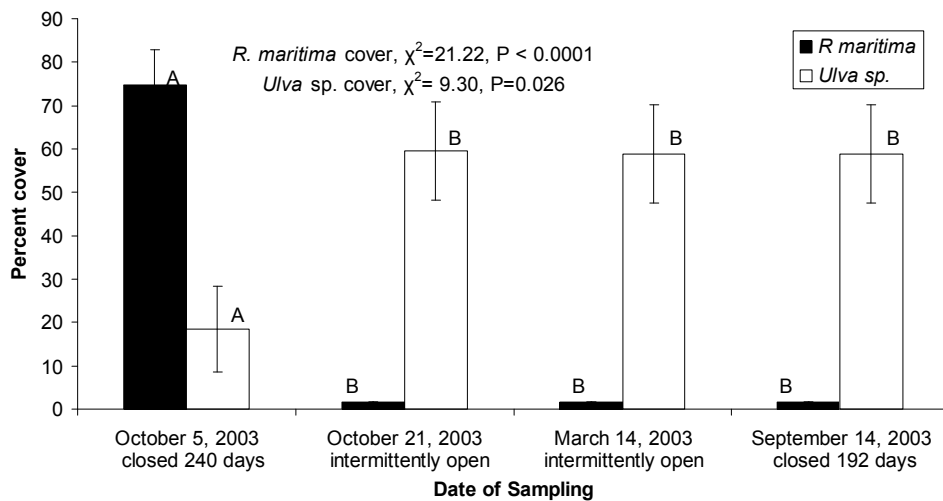
(d)
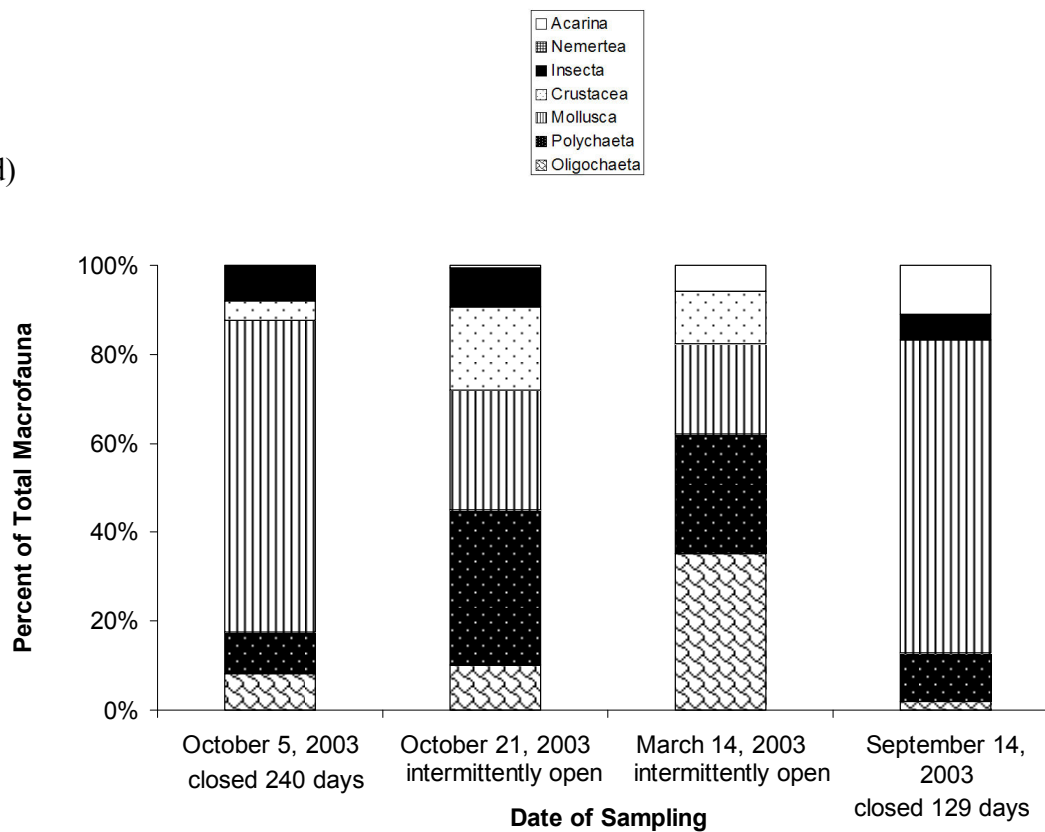
Figure 6.1 (continued)

(a)

(b)
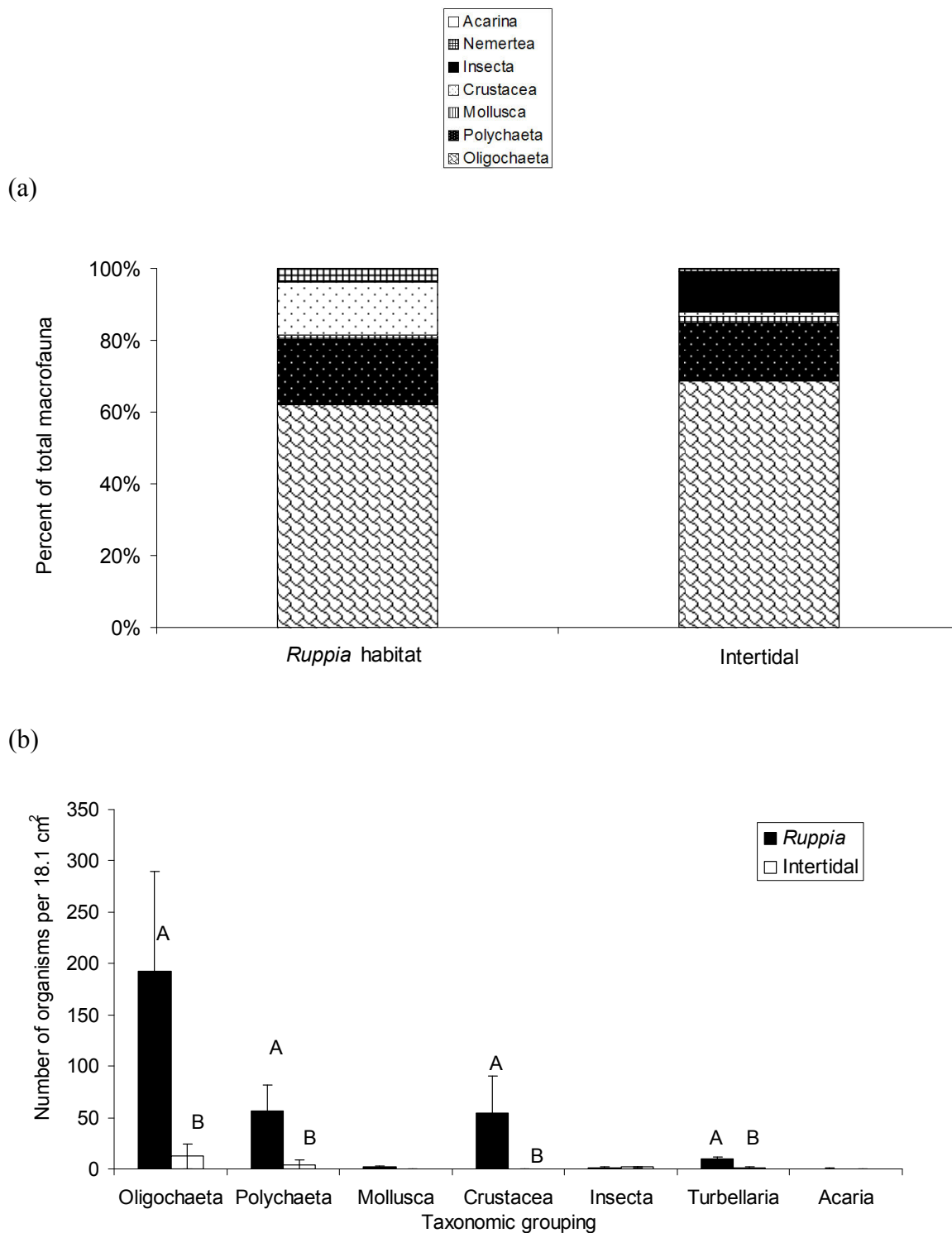
Figure 6.2. Macrofaunal community composition based on abundance (a) and percent compostion (b) in three habitats with two seasons averaged for each inlet status category.

(c)
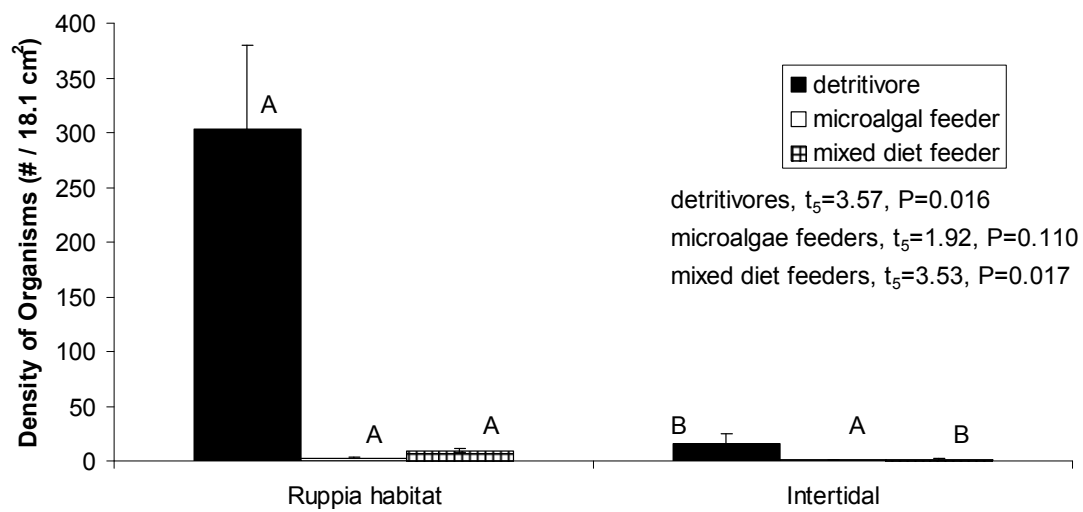
Figure 6.2 (continued)
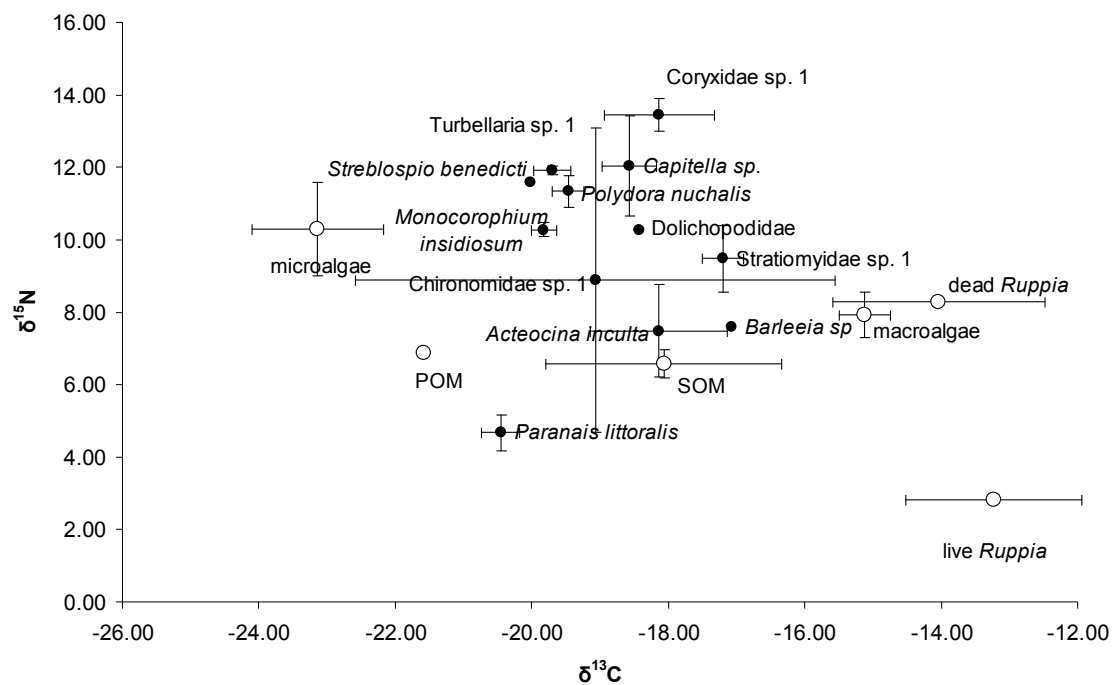
Figure 6.3. Dual isotope plot of natural abundance δ^{13}C and δ^{15}N signatures (mean $\pm$ 1 se) among producers and consumers in San Dieguito Lagoon, subtidal *R. maritima* habitat. Potential food sources are indicated by open circles while consumers are indicated with closed circles.

(a)

(b)
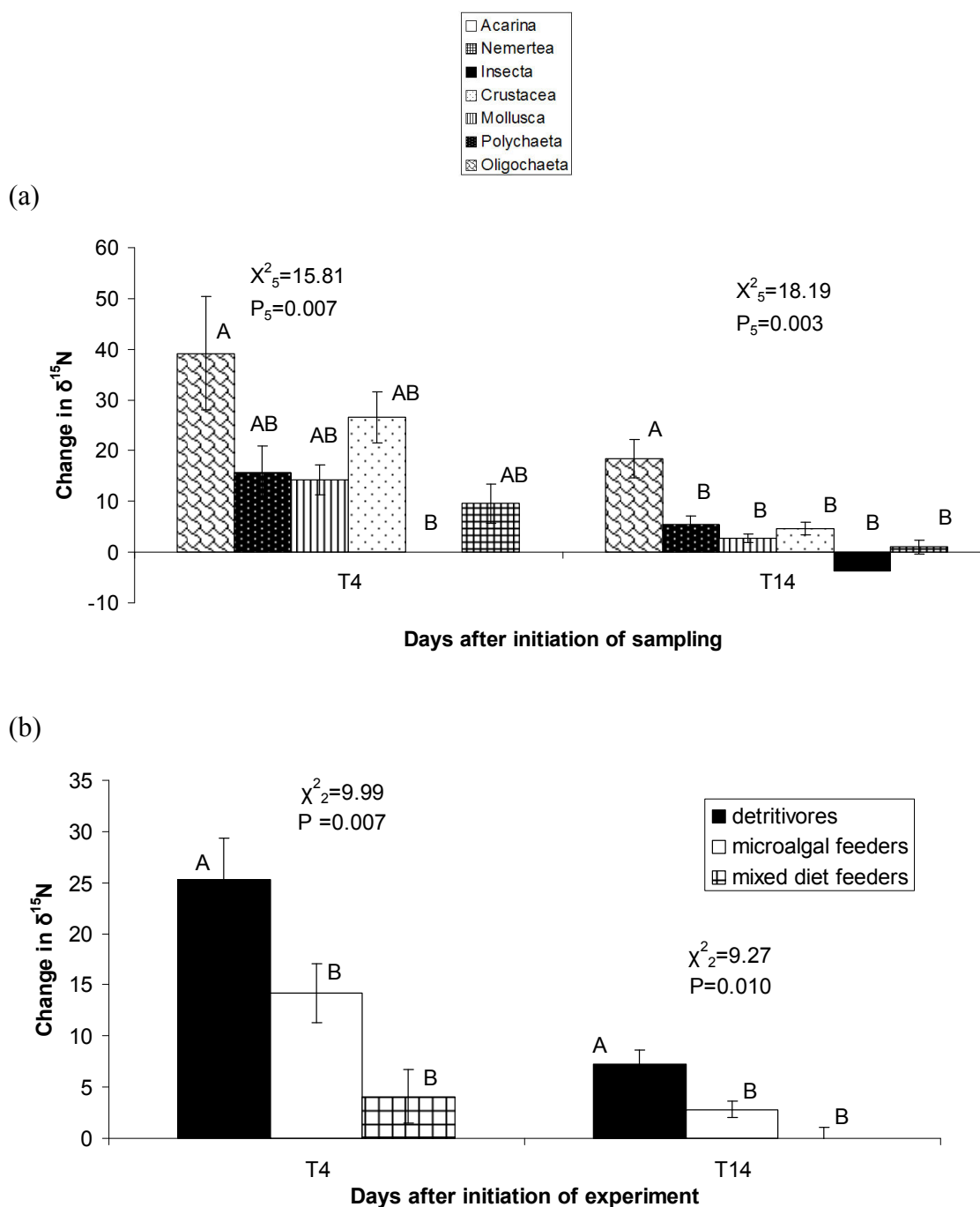
Figure 6.4. Mean ($\pm$ 1 se) Δ $\delta^{15}N$ signatures ($\delta^{15}N_{experiment}$ - $\delta^{15}N_{background}$) of (a) infaunal invertebrate taxa and (b) feeding behavior groups following periods of exposure to ^{15}N-labeled *R. maritima* detritus in litterbags. The absence of error bars indicates very small error terms or n=1. Letters indicate *a posteriori* differences among treatments (P < 0.05).
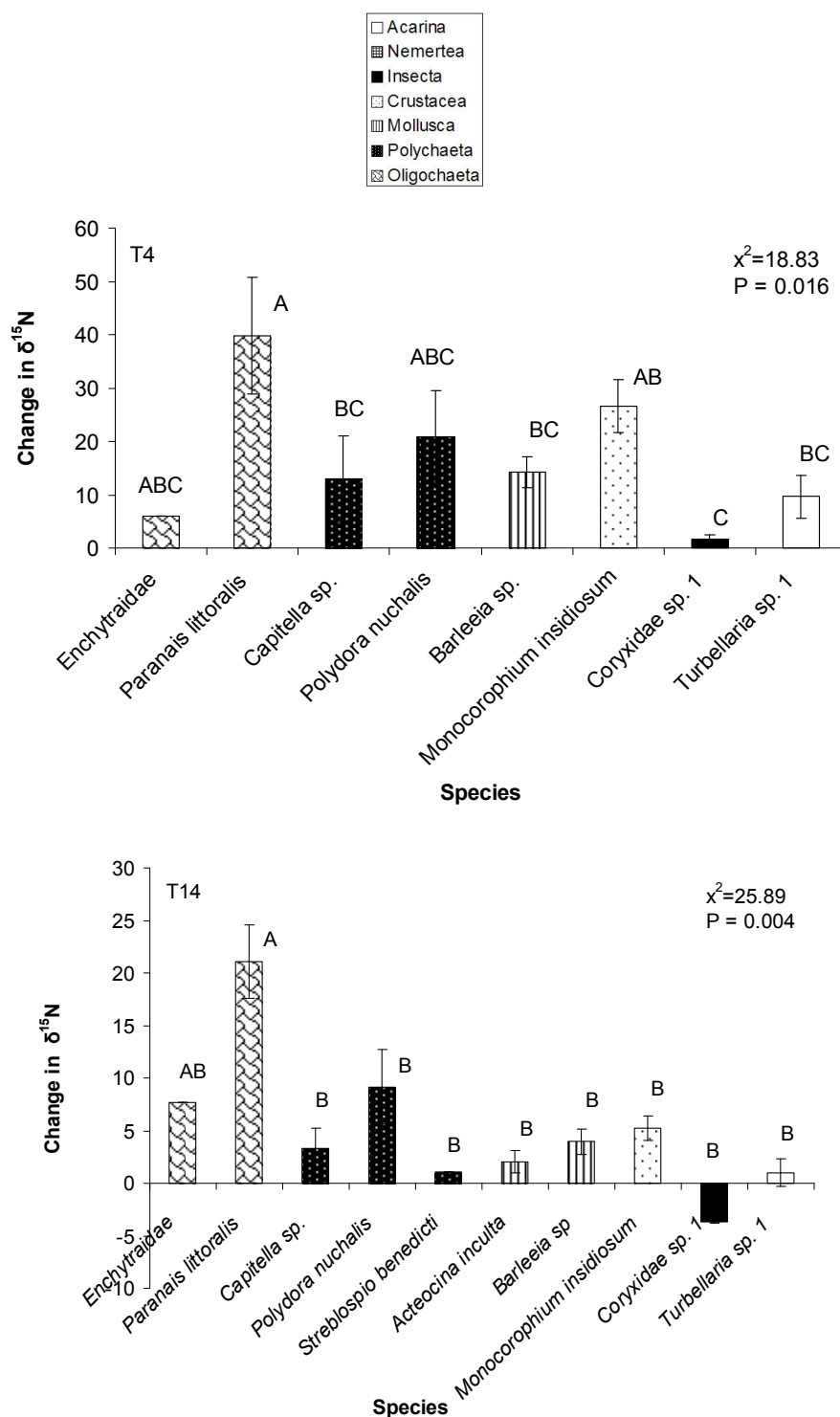
Figure 6.5. Mean ($\pm$ 1 se) Δ δ^{15}N signatures (δ^{15}N$_{experiment}$ - δ^{15}N$_{background}$) of infaunal invertebrate species and families following periods of exposure to ^{15}N-labeled *R. maritima* detritus in litterbags. The absence of error bars indicates very small error terms or n=1. Letters indicate *a posteriori* differences among treatments (P < 0.05).

Table 6.1. Comparison of responses to sampling date and habitat by the macrofaunal community (density and composition) in intertidal *R. maritima* habitats. Mean density per core (18.1 cm²) and percent of total (±1 SE) are reported. Superscripted letters indicate *a posteriori* (Tukey HSD) differences among treatments (P < 0.05).

|	Date of Sampling					
Group	**October 5, 2003**	**October 21, 2003**	**March 14, 2003**	**September 14, 2003**	X^2_3	**P value**
Crustacea						
density	1.40 (0.68)[bc]	9.20 (3.35)[b]	21.67 (3.18)[a]	0.00 (-)[c]	**20.94**	**0.0001**
% of total density	4.45 (3.17)[bc]	18.69 (5.86)[bc]	11.94 (2.20)[ab]	0.00 (-)[c]	**17.87**	**0.0005**
Gastropoda						
density	44.00 (17.51)[a]	17.80 (9.39)[ab]	34.17 (9.59)[ab]	1.89 (0.66)[b]	**14.00**	**0.003**
% of total density	70.17 (15.95)	26.97 (11.61)	20.37 (6.36)	70.37 (14.37)	6.49	0.090
Insecta						
density	1.60 (0.51)[ab]	2.60 (0.68)[a]	0.17 (0.17)[bc]	0.11 (0.11)[c]	**16.38**	**0.0009**
% of total density	7.92 (4.70)	8.73 (4.85)	0.06 (0.06)	5.56 (5.56)	12.72	0.005
Oligochaeta						
density	2.00 (1.38)[b]	5.80 (4.02)[b]	17.67 (25.87)[a]	0.11 (0.11)[a]	**15.78**	**0.001**
% of total density	8.37 (7.65)[b]	10.12 (7.08)[ab]	35.14 (8.66)[a]	1.85 (1.85)[b]	**12.56**	**0.006**
Polychaeta						
density	1.40 (0.75)[b]	15.60 (6.79)[b]	36.83 (15.04)[a]	0.22 (0.15)[b]	**19.57**	**0.0002**
% of total density	9.09 (6.41)	34.89 (14.18)	26.85 (23.00)	11.11 (2.05)	8.31	0.040
Other						
density	0.00 (-)[ab]	0.40 (0.24)[ab]	8.50 (4.53)[a]	0.11 (0.11)[b]	**13.06**	**0.005**
% of total density	0.00 (-)	0.60 (0.38)	5.63 (2.90)	11.11 (11.11)	9.54	0.023
Density (#/18.1 cm²)	50.40 (16.46)[a]	51.40 (11.86)[a]	189.67 (29.83)[b]	2.33 (0.80)[a]	**20.82**	**< 0.0001**
Species richness (#/18.1 cm²)	5.40 (1.63)[a]	7.60 (0.75)[a]	7.83 (0.48)[a]	1.22 (0.22)[b]	**15.77**	**0.001**

a)

Table 6.1 (continued)

April 2006

Group	*Ruppia*	intertidal	t_5	P value
Crustacea				
density	**55.00 (36.59)**[a]	**0.00 (0.00)**[b]	**4.20**	**0.037**
% of total density	**54.17 (21.22)**[a]	**0.00 (0.00)**[b]	**2.56**	**0.050**
Gastropoda				
density	**2.00 (0.58)**[a]	**0.17 (0.17)**[b]	**3.38**	**0.020**
% of total density	0.77 (0.30)	1.28 (1.28)	0.47	0.657
Insecta				
density	0.67 (0.67)	1.00 (0.58)	0.22	0.637
% of total density	0.27 (0.13)	9.32 (5.98)	1.50	0.195
Oligochaeta				
density	**192.67 (46.06)**[a]	**12.17 (6.21)**[b]	**3.73**	**0.014**
% of total density	61.99 (4.38)	57.35 (15.26)	0.26	0.802
Polychaeta				
density	**56.17 (16.40)**[a]	**3.50 (2.58)**[b]	**3.13**	**0.026**
% of total density	18.66 (3.62)	13.60 (6.13)	0.62	0.561
Turbellaria				
density	**12.67 (2.40)**[a]	**1.00 (1.00)**[b]	**3.97**	**0.050**
% of total density	**9.33 (1.89)**[a]	**0.50 (0.50)**[b]	**4.37**	**0.007**
Other				
density	0.17 (0.17)	0.00 (-)	1.00	0.363
% of total density	0.10 (0.10)	0.00 (-)	1.00	0.363

b)

Table 6.2: Feeding behavior for the macroinvertebrates found in isotope samples and percent carbon of varied food sources as estimated from natural abundance three-source mixing model. Feeding designations are based on natural abundance signatures and/or published literature. Blanks indicate species not present or unresolved model data.

Species	Taxonomic Grouping	Feeding behavior	% of C from *R. maritima*	% of C from microalgae	% of C from POC
mite sp. 1	Acaria	mixed diet[1]			
Monocorophium insidiosum	Crustacea	detritivore[2]	9.1	9.5	82.4
Grandidierella japonica	Crustacea	detritivore[2]			
Acteocina inculta	Gastropoda	microalgal grazer[2]			
Acteocina carcinata	Gastropoda	microalgal grazer[2]			
Barleeia sp.	Gastropoda	microalgal grazer[2]			
Cerithidea californica	Gastropoda	microalgal grazer[2]			
Ceratapogonidae larvae	Insecta	mixed diet[3]			
Chironomid larvae	Insecta	microalgal grazer[3]	0	39.5	79.5
Coleoptera sp. 1	Insecta	detritivore[3]			
Coryxidae sp. 1	Insecta	mixed diet[4]			
Dolicopodidae larvae	Insecta	mixed diet[5]			
Ephydra sp. 1 pupae	Insecta	mixed diet			
Muscidae larvae	Insecta	mixed diet[4]			
Poduridae sp. 1	Insecta	mixed diet[6]			
Psychodidae larvae	Insecta	mixed diet[7]			
Staphylinidae adult	Insecta	mixed diet[8]			
Staphylinidae larvae	Insecta	microalgal grazer[4]			
Stratiomyidae larvae	Insecta	detritivore[4]	0	75.4	40.1
Enchytraidae	Oligochaeta	detritivore[9]			
Paranais littoralis	Oligochaeta	mixed diet[10]	21.2	72.1	7.2
Capitella sp.	Polychaeta	detritivore[2]	28.8	31.6	39.6
Polydora nuchalis	Polychaeta	detritivore[2]	20.9	12.9	66.2
Streblospio benedicti	Polychaeta	detritivore[2]	23.9	0	76
Turbellarian sp. 1	Turbellaria	mixed diet	27.4	5.1	67.5

[1] Di Sabatino et al. 2000
[2] Levin and Currin 2005, Dahl 1973
[3] Moseman et al. 2004
[4] Kelts, L.J. 1979
[5] Bickel and Dyte 1989
[6] Hopkin 1997
[7] Schlein and Muller 1995
[8] D. Holway (pers. com.)
[9] Dash and Cragg 1972
[10] Wavre and Brinkhurst 1971

Table 6.3: Percent of N in invertebrate diets that was derived from δ^{15}N labeled-*R. maritima* detritus at 1, 4, and 14 days after deployment of labeled material. Missing values indicate that that species was not collected at that time point. Percentages are calculated from a single isotope, two-source mixing model for δ^{15}N in which labeled *R. maritima* detritus was treated as one food source and unlabeled (background) native food sources (i.e. microalgae, POM and SOM) were treated as a second food source

Intertidal and *R. maritima* habitats			
Species	**T1**	**T4**	**T14**
Acteocina inculta	0.003		0.0005
Diptera sp. 1		0.0002	
Barleeia sp.		0.024	0.037
Capitella sp. complex		0.030	0.012
Cincinalidae sp. 1		0.012	
Monocorophium insidiosum	0.013	0.053	0.012
Grandiderella japonica			0.0007
Coryxidae sp. 1		0.011	0.0008
Enchytraidae sp. 1		0.005	0.008
Paranais litoralis		0.067	0.032
Polydora nuchalis		0.044	0.021
Streblospio benedicti			0.007
Turbellaria sp. 1		0.012	0.007

Appendix 6.1. Comparison the macrofaunal community (density) in *R. maritima* and intertidal habitats in April 2006. Mean density of organisms per core (18.1 cm^2) ($\pm$ 1 SE) are reported. Superscripted letters indicate t-test differences among treatments (P < 0.05).

Species	Group	April 2006 Ruppia	April 2006 Intertidal	t_5	P
Monocorophium insidiosum	Crustacea	**54.17 (21.22)[a]**	**0.17 (0.17)[b]**	**2.56**	**0.051**
Acteocina inculta	Gastropoda	0.50 (0.34)	0.00 (-)	1.46	0.203
Acteocina carcinata	Gastropoda	0.33 (0.33)	0.00 (-)	1.00	0.363
Barleeia subtenuis	Gastropoda	1.17 (0.60)	0.17 (0.17)	1.58	0.174
Chironimidae larvae sp. 1	Insecta	0.67 (0.42)	0.00 (-)	1.58	0.175
Ceratapogonidae larvae sp. 1	Insecta	0.00 (-)	0.33 (0.21)	1.58	0.175
Dolicohopodidae larvae sp. 1	Insecta	0.00 (-)	0.33 (0.21)	1.58	0.175
Muscidae sp. 1	Insecta	0.00 (-)	0.33 (0.33)	1.00	0.363
Poduridae sp. 1	Insecta	0.33 (0.33)	0.17 (0.17)	0.42	0.700
Psychodidae larvae sp. 1	Insecta	0.00 (-)	0.33 (0.33)	1.00	0.363
Enchytraeidae sp. 1	Oligochaeta	0.00 (-)	3.17 (2.04)	1.55	0.181
Paranais litoralis	Oligochaeta	**192.67 (46.06)[a]**	**9.00 (5.13)[b]**	**3.88**	**0.012**
Capitella sp.complex	Polychaeta	35.67 (14.09)	3.17 (2.61)	2.33	0.067
Polydora nuchalis	Polychaeta	**13.33 (4.13)[a]**	**0.33 (0.33)[b]**	**3.10**	**0.027**
Spionidae	Polychaeta	0.00 (-)	0.00 (-)	2.00	-
Streblospio benedicti	Polychaeta	**6.67 (2.01)[a]**	**0.00 (-)[b]**	**3.31**	**0.021**
Turbellaria sp. 1	Turbellaria	**9.33 (1.89)[a]**	**0.50 (0.50)[b]**	**4.37**	**0.007**
mite sp. 1	Acarina	0.17 (0.17)	0.00 (-)	1.00	0.363

Appendix 6.2. Mean δ^{15}N and δ^{13}C signatures of macrofauna ($\pm$1 SE) by sampling time point (days after initiation of experiment) and by habitat (intertidal, *R. maritima* zone). When no SE is reported, n=1.

Background and T0

Species	Taxonomic Group	*R. maritima* zone		intertidal zone	
		δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C
POM	Food source	6.87	-21.58		
SOM	Food source	5.94 (0.43)	-16.41 (2.15)	7.19 (0.50)	-20.27 (2.79)
microalgae	Algae	8.19 (1.27)	-23.11 (0.65)	14.88 (2.68)	-23.27 (1.47)
Ulva sp.	Algae			7.93 (0.63)	-15.12 (0.38)
Monocorophium insidiosum	Crustacea	10.16 (0.30)	-19.95 (0.21)	10.42 (0.26)	-19.68 (0.31)
Acteocina inculta	Gastropoda	7.49 (1.28)	-18.14 (1.00)		
Barleeia sp	Gastropoda	7.59 (1.70)	-17.07 (1.37)		
Chironomidae larvae sp. 1	Insecta	8.88 (4.20)	-19.07 (3.52)		
Coryxidae sp. 1	Insecta			13.44 (0.45)	-18.13 (0.81)
Dolicopodidae larvae sp. 1	Insecta			10.25	-18.42
Fly sp. 1	Insecta			14.48	-16.98
Stratiomyidae sp. 1	Insecta	9.47 (0.91)	-17.20 (0.31)		
Paranais littoralis	Oligochaeta	5.39	-20.82	4.44 (0.70)	-20.34 (0.42)
Ruppia (detritus)	Plantae	8.29 (0.10)	-14.04 (1.56)		
Ruppia (live plant)	Plantae	2.82 (0.04)	-13.23 (1.29)		
Ruppia (without epiphytes)	Plantae	1.85	-12.38		
Capitella sp. Complex	Polychaeta	12.01 (1.68)	-18.35 (0.23)	12.14	-19.65
Polydora nuchalis	Polychaeta	11.33 (0.42)	-19.46 (0.23)		
Streblospio benedicti	Polychaeta	11.59	-20.03		
Turbellaria sp. 1	Turbellaria	11.93 (0.12)	-19.70 (0.27)		

T1

Species	Taxonomic Group	*R. maritima* zone		intertidal zone	
		δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C
microalgae	Algae	12.74 (0.83)	-22.90 (0.15)	12.62 (3.31)	-20.30 (1.82)
Monocorophium insidiosum	Crustacea	1.47	-10.43		
Acteocina inculta	Gastropoda	7.83	-21.07		
Capitella sp. Complex	Polychaeta	5.11	-25.98		

T4

Species	Taxonomic Group	*R. maritima* zone		intertidal zone	
		δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C
POC	Food source	10.80 (5.64)	-16.78 (1.44)	10.80 (5.64)	-16.78 (1.44)
SOM	Food source	8.24 (0.72)	-19.80 (0.75)		
microalgae	Algae	21.36 (2.61)	-24.27 (0.84)	13.57 (2.22)	-23.20 (1.08)
Monocorophium insidiosum	Crustacea	37.28 (5.91)	-18.72 (0.33)	35.90 (11.10)	-18.96 (0.53)
Barleeia sp	Gastropoda	21.80 (2.89)	-16.95 (1.15)		
Cincinalidae adult sp. 1	Insecta			15.7	-20.44
Coryxidae sp. 1	Insecta			15.05 (0.84)	-18.67 (0.73)
Fly sp. 1	Insecta	9.41	-24.91		
Enchytraidae	Oligochaeta			11.96	-19.67
Paranais littoralis	Oligochaeta	23.89	-20.01	48.57 (12.39)	-15.81 (1.81)
Pollen	Plantae	10.69	-13.18	10.69	-13.18
Capitella sp. Complex	Polychaeta	27.70 (9.97)	-16.75 (1.84)	14.05	-18.48
Polydora nuchalis	Polychaeta	24.13 (3.75)	-19.42 (0.38)	56.59	-8.58
Turbellaria sp. 1	Turbellaria	21.52 (3.93)	-18.60 (0.28)		

T4 Leaching

Species	Taxonomic Group	*R. maritima* zone		intertidal zone	
		δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C
microalgae	Algae	14.36 (1.94)	-23.08 (0.45)	14.36 (1.94)	-23.08 (0.45)
Monocorophium insidiosum	Crustacea	30.95	-19.18	10.58	-21.10
Paranais littoralis	Oligochaeta	16.29	-21.76	15.6 (0.61)	-20.07 (0.40)
Polydora nuchalis	Polychaeta	35.72	-20.39		

T14

Species	Taxonomic Group	*R. maritima* zone		intertidal zone	
		δ^{15}N	δ^{13}C	δ^{15}N	δ^{13}C
POC	Food source	5.73 (0.39)	-19.88 (0.02)		
SOM	Food source	7.46 (1.21)	-15.60 (2.94)	5.17 (0.21)	-14.79
microalgae	Algae	13.95 (5.71)	-23.99 (0.57)	12.43 (2.81)	-22.63 (0.84)
Grandiderella japonica	Crustacea			8.45	-17.11
Monocorophium insidiosum	Crustacea	15.98 (1.96)	-18.32 (0.25)	14.98 (1.13)	-19.51 (0.37)
Acteocina inculta	Gastropoda	9.54 (1.04)	-20.82 (0.48)		
Barleeia sp	Gastropoda	28.42 (16.91)	-17.03 (0.62)		
Coryxidae sp. 1	Insecta	9.72 (0.03)	-22.68 (2.80)		
Enchytraidae	Oligochaeta			13.64	-16.80
Paranais littoralis	Oligochaeta			25.77 (3.49)	-18.23 (1.68)
Capitella sp. Complex	Polychaeta	14.65 (2.82)	-18.09 (0.38)	16.83 (1.33)	-18.41 (1.21)
Polydora nuchalis	Polychaeta	20.49 (3.55)	-18.00 (0.49)		
Streblospio benedicti	Polychaeta	12.71	-20.13		
Turbellaria sp. 1	Turbellaria	14.15 (0.63)	-18.81 (0.30)	6.91	-17.08

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CHAPTER VII

CONCLUSIONS

In this dissertation, I tested the hypotheses that changes in plant communities (species, height, density, cover) would have direct and indirect effects on the sediment ecosystem. I developed *apriori* hypotheses, as shown in Figure 1a, predicting that loss of the plant canopy would directly alter abiotic and sediment properties, benthic microalgal community composition, and invertebrate community structure (Figure 7.1 a). In addition, initial hypotheses predicted that changes to food sources (microalgae or detritus) or to the abiotic parameters would have cascading effects on the invertebrate community. Studies of three systems and four plant species demonstrated that changing plant cover in different wetlands structures infaunal communities by distinct mechanisms (Figure 7.1 b-d).

Edaphic characteristics of coastal wetlands exhibit gradients from sudtidal to upland transition zones that correspond with elevation and frequency of tidal inundation (Ellison et al. 1986, Bertness and Ellison 1987). Superimposed along these gradients, marsh plants form distinct zones with physical tolerances, competition and positive interactions affecting zonation (Chapman 1974, Pennings and Callaway 1992). Because physical stresses in marshes are potentially limiting, modification of the habitat by resident marsh plants is a pervasive and critical process mediating the structure and organization of salt marsh communities. Wetlands would not exist without the halophytic plants capable of thriving in the harsh edaphic conditions along the coast. Thus, I hypothesized that the combination of physical and biological stresses along the

marine to terrestrial continuum determine how the plants studied in my dissertation structure their environments and which mechanisms are particularly important (Figure 7.2).

Subtidally, many seagrass species structure their physical environments through general habitat creation and influence their biological associates by providing refuge from predation, enhancing larval retention, and increasing food supply (Bruno and Bertness 2001). Relative to other environments along the marine to terrestrial continuum, subtidal habitats seem to be dominated by biological stressors (predation, food availability, etc.) with fewer physical stressors because the benthic community is continually submerged. While our research did not elucidate exact mechanisms (light reduction and structure), it is clear that widgeongrass (*Ruppia maritima)* structures its immediate environment, such as sediment properties, and the associated benthic invertebrate community (Chapter VI) (Figure 7.1d). Our labeling experiments demonstrate that *Ruppia* might be important as a detrital food source and as a structure for the growth of epiphytes (Figure 7.1d).

In the high and mid salt marsh vegetation zones, two dominant plants (*Spartina foliosa* and *Sarcocornia pacifica* (*Salicornia virginica*)) exert influence on abiotic environmental factors and thus regulate the biotic community (Chapter II). When both plant structure and light reduction capabilities were removed, marsh soils exhibited harsher physical properties, a microalgal community composition shift towards increased diatom dominance, and altered macrofaunal community composition. Plant removal lowered species richness and produced a larger proportion of insect larvae and a smaller proportion of annelids, crustaceans, and oligochaetes compared to shaded (plant removal,

shade mimic) and control treatment plots. Plant cover removal also resulted in parallel shifts in microalgal and macrofaunal isotopic signatures of the most dynamic species. Our experiments demonstrate that the light reduction function provided by the vascular plant canopy is crucial to maintaining the natural biotic community of southern California salt marsh sediments in a zone where physical stressors dominate (Figure 7.1b). Understanding these interactions is important because plant presence, density and height are dynamic, altered by seasonality, climate or sea-level change, habitat degradation, marsh restoration or plant invasion.

In much of western North America, riparian environments or upland transition zones (UTZs) are the only part of the landscape moist enough to allow survival of trees. UTZ landscapes are usually defined as ecotones or corridors between terrestrial and marine realms (Malanson 1993). However, at this interface between marine and terrestrial, these areas are very susceptible to disturbance from both aquatic and terrestrial stressors, including upland plant invasion. One of the most problematic invaders in the western United States has been salt cedar, *Tamarix* spp.. Large stands of different invasive genotypes of tamarisk now reside in the salt marshes and upland transition zones (UTZ) of Tijuana River National Estuarine Research Reserve (TRNERR). Similar to its impacts in freshwater environments, tamarisk invasion into the salt marshes of TRNERR altered physical conditions and invertebrate community assemblages in the middle marsh zones where physical stressors are most significant regulators of invertebrate communities. The mechanisms behind these alterations were not tested explicitly, but tamarisk-invaded areas in all habitats did have reduced light energy reaching the sediment as well as changes in sediment properties, indication both light reduction and

structure as driving mechanisms of change for tamarisk (Figure 7.1c). Overall, these changes in the middle marsh zone increase the speed of the marsh succession towards a more terrestrial environment (Chapter V) (Figure 7.1c). In the low marsh, inundated at least once daily, few differences existed between invaded and native plots, leading us to hypothesize that the effects of tamarisk are ameliorated by constant salt water inundation. Within the upland transition zone, changes in physical and biological parameters between tamarisk-invaded and natural plots were minimal, perhaps indicative of infrequent complete inundation in this zone. Isotope enrichment experiments demonstrate that diets of several native consumers now include N derived from invasive tamarisk, increasing the chances that tamarisk can alter ecosystem functioning in terms of trophic transfer (Chapter IV) (Figure 7.1c).

General Implications of Research

Results of this dissertation contribute to both theoretical and applied ecology and conservation science. It is well known that plants in marine ecosystems are habitat modifiers, and this dissertation research has furthered defined the mechanisms driving these modifications. I have focused on how the structuring ability of plants varies along an elevation and salinity gradient. In addition, the results suggest adaptive management solutions for southern California wetlands that are affected by varied anthropogenic influences (invasion by non-native plants, altered lagoon inlet status).

This research illustrates the use of stable isotope enrichment experiments for several purposes: (1) to describe alterations to a food web under different plant conditions, (2) to trace the fate of a plant invader as it moves through the food web system, and (3) to describe the trophic importance of a native, ephemeral seagrass. This
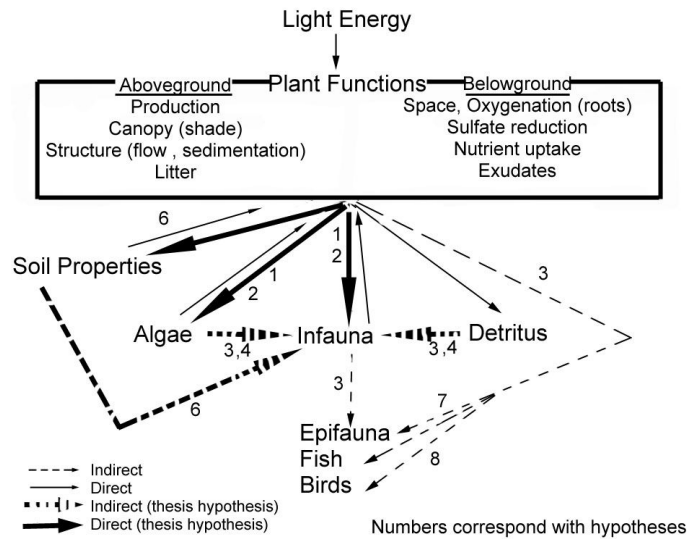
technique has great potential for use in experiments throughout marine ecology, especially to study food webs in systems where natural isotope signatures overlap or where organisms of concern are too small for gut content analysis. While exact methods will depend on the local environmental conditions as well as health of the ecosystem and the type of plant in question, using stable isotope techniques to understand detrital input at the base of the food web will further our knowledge of how trophic shifts can occur and of how best to manage wetland ecosystems.

In addition to methodological and theoretical advances, our research can be applied to adaptive management strategies, particularly for predicting ecosystem response to large-scale perturbations, such as plant species switching, invasion, or flushing regime shifts. We have increased understanding of sequential consequences of changing salt marsh plant cover. Such changes occur with climate change, sea-level rise, coastal development, habitat restoration or plant invasion. In addition, we can predict that intertidal salt marshes of arid climates are a habitat vulnerable to invasion by tamarisk and that the potential impact of tamarisk within this environment is significant. This highlights the need for managers and scientists to be aware of the problems associated with tamarisk invasion of coastal marine habitats and to take early and aggressive action to combat any incipient invasion. Finally, it should be recognized that manipulation of inlet status in southern Californian lagoon systems can drive ecosystem change, involving the loss of an important ecosystem-structuring plant, *Ruppia maritima*, within the lagoon ecosystem.
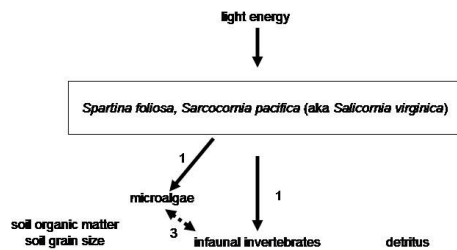
This research develops several experimental methods which isolate mechanisms of wetland plant influence and allow us to make generalizations across important

structuring gradients in salt marsh ecosystems. As wetland ecology progresses as a discipline, our hypotheses about the mechanisms by which marine vascular plants structure the environments will continue to be tested and refined through both comparative and manipulative research.
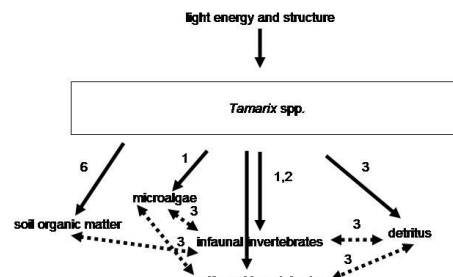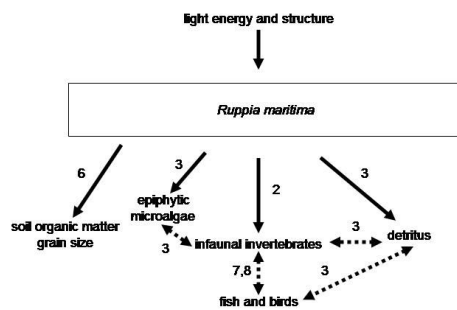
(a)

(b)

(c)

(d)

Figure 7.1: *Apriori* (a) and final (b-d) plant canopy-benthos interaction model with mechanistic hypotheses (1-8) identified. Numbered hypotheses from model listed.

[1] Changes in light regime or structure will alter abiotic or algal properties.
[2] Changes in aboveground plant structure will alter the infaunal community directly.
[3] Changes in algal community or detritus production will alter the infaunal community.
[4] Changes to the algal mat structure will alter the infaunal community
[5] Changes to the infauna will affect plants.
[6] Changes in light regime or structure will affect soil properties.
[7] Changes will affect epifauna and fish indirectly
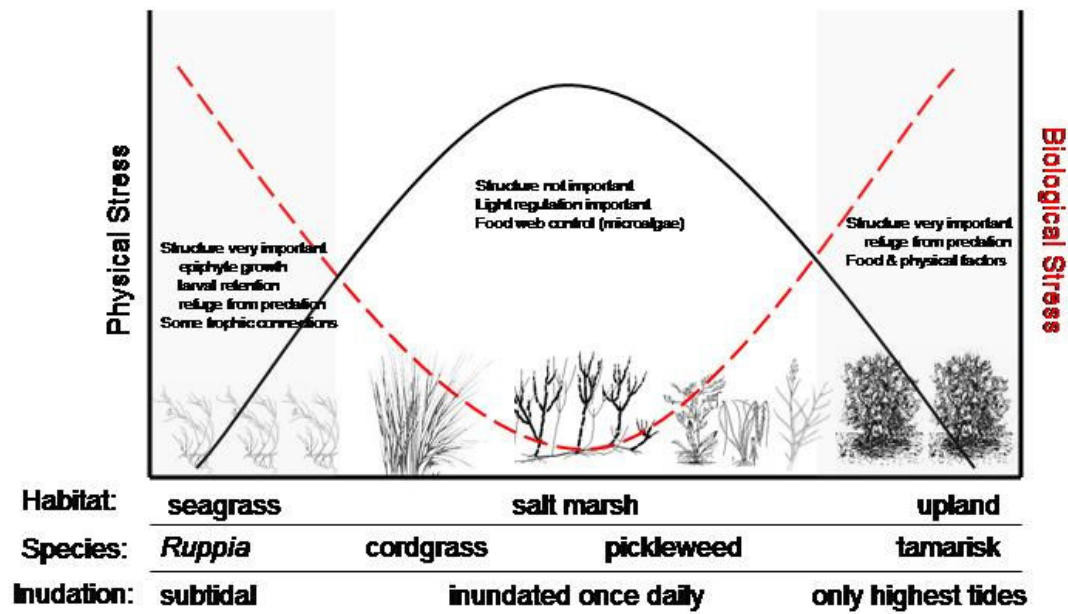[8] Changes will affect birds indirectly

Figure 7.2: Hypothesized physical and biological stressors along a marine to terrestrial continuum by zonation, species, and tidal descriptions

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