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Los Angeles

Community-dependent Positive Interactions in

Southern California Coastal Ecosystems

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Sarah Bryson

2012

ABSTRACT OF THE DISSERTATION

Community-dependent Positive Interactions in

Southern California Coastal Ecosystems

by

Sarah Bryson

Doctor of Philosophy in Biology

University of California, Los Angeles, 2012

Professor Peggy Fong, Co-chair

Professor Richard R. Vance, Co-chair

Ecological interactions are context dependent. The net effect of species interactions includes the

multifaceted impacts of community composition and abiotic influences of the environment. I

examined how both biotic and abiotic stressors, in the form of herbivore composition and salinity

stress, respectively, elicited positive interactions between species. In a kelp forest I examined

how the relationship between kelp and an encrusting bryozoan, *Membranipora membranacea*,

shifted to an associational defense depending on herbivore guild composition. Using a

combination of choice experiments and surveys of grazing damage, I demonstrated that the

mesograzers *Lacuna unifasciata*, *Perampithoe humeralis*, and *Idotea resecata* almost entirely

avoided (<1% of total diet) encrusted kelp. The large snail *Norrisia norrisi* also preferred clean

kelp, but kelp crabs, *Pugettia producta*, targeted encrusted kelp. Field surveys in a mesograzer dominated canopy found 2.5 times more grazing damage on sparsely encrusted kelp than on heavily encrusted kelp and far more grazing in the upper canopy than on the blades from the vertical stipes below the canopy. These results indicate that, when mesograzers are dominant, *Membranipora* provides kelp associational resistance to grazing. Such protection may be more prominent in the upper canopy. Additionally, I examined the role of abiotic stress on positive interactions in a hypersaline salt marsh. Following disturbance that removes established vegetation, salt-tolerant species can ameliorate harsh soil salinities for less tolerant species and therefore promote secondary succession. However, when abiotic stress is extremely high amelioration may be inadequate to improve growth of associated neighbors. Using clipping manipulations of *Batis maritima*, an early successional halophyte, I tested whether *B.maritima* facilitates secondary succession in an excessively hypersaline salt marsh in southern California. Experimental plots with *B.maritima* present recovered faster (27% compared to 14% revegetation by matrix species) and had lower increases in soil salinity. *Salicornia pacifica* and *Arthrocnemum subterminale* were the dominant recovery species in both treatments and no differences were found in species richness, diversity, or evenness of recovery species between treatments.

Overall, my research indicates positive interactions play a prominent role in these coastal ecosystems though that role will depend on the specific nature of the community.

The dissertation of Sarah Bryson is approved.

Richard F. Ambrose

Cheryl Ann Zimmer

Richard R. Vance, Committee Co-Chair

Peggy Fong, Committee Co-Chair

University of California, Los Angeles

2012

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INTRODUCTION OF THE DISSERTATION

Stress is defined as any detrimental effect on a biological entity (Parker et al. 1999). Resource limitation (Grime 1989), toxicity (Zhu 2001), and threats to physical integrity (Hay et al. 2004) are basic stressors that reduce the growth, reproduction, and/or survival of organisms. Such forms of stress can arise from abiotic factors of the environment (Parker et al. 1999). These factors can include, amongst others, salinity, desiccation, or temperature (reviewed in Bertness and Leonard 1997). Stress can also arise from the presence of other species, in the form of competition (Brooker et al. 2005) and consumption (Barbosa et al. 2009). Organisms cope with stress via physiological tolerance, either through evolutionary adaptation (Pennings et al. 2003) or plasticity (Callaway et al. 2003), or species can associate with stress ameliorators (Leslie 2005). Therefore an association between species that negatively impact each other under benign conditions may be beneficial under elevated stress (Bertness and Callaway 1994, Brooker et al. 2008).

This pattern of shifting interactions with levels of stress was first described by Bertness and Callaway (1994) and has come to be known as the Stress Gradient Hypothesis (SGH). The shift in direction and magnitude of the interaction occurs when an ameliorator species improves reproduction, growth, and/or survival for a neighboring beneficiary species, even though they may compete for limited resources (Stachowicz 2001, Holmgren and Scheffer 2010). Such interactions expand keystone species' habitats by enabling their persistence under conditions too harsh for independent survival (Bruno

et al. 2003). Thus, it is important to understand when and how such interactions arise since, when stress is elevated, they act as ecological buffers to the community as a whole. The objectives of this research are to examine the positive interactions that result from both biotic and abiotic stress sources and identify when these context-dependent interactions are likely to occur.

Both biotic (Hay et al. 2004) and abiotic (Brooker et al. 2008) sources of stress can give rise to community-protecting positive interactions between neighbors. Intense herbivory pressure can elicit association between neighbors that protect against consumption (first described by Atsatt and O'Dowd 1976). This type of interaction, termed associational resistance to grazing, has been observed in many marine communities (Hay 1986, Fong et al. 2006, Levenbach 2009). Similarly, the physical stress gradients of intertidal habitats can give rise to associations amongst neighbors that reduce physical stress. These interactions, called facilitations, protect and promote the resident species (Bertness and Leonard 1997). Vascular plants are sensitive to salinity (Zhu 2001) and often in intertidal habitats their association with neighbors can reduce stress via passive shading of the soil (Bertness and Ewanchuk 2002, Whitcraft and Levin 2007). In two separate marine habitats, I will investigate whether positive interactions, in the form of associational resistance and facilitation arose in response to herbivory and salinity stress respectively. In Chapter 1 and 2 I will examine if a positive biotic association between giant kelp, *Macrocystis pyrifera*, and the bryozoan epibiont, *Membranipora membranacea*, mediated grazing pressure from kelp herbivores. In Chapter 3 I will

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examine facilitation between salt marsh plants in response to the abiotic stress associated with elevated soil salinity during secondary succession.

Many have found that positive interactions are highly context-dependent (reviewed in Hay et al. 2004). Much remains unknown as to when and under what conditions these interactions effectively buffer their local communities. Therefore it is important to identify where in both geographic space and along a stress continuum positive interactions are likely to occur. In the case of herbivory, the SGH suggests that positive interactions will increase when pressure from consumers is high (Bertness and Callaway 1994). The presence of a positive interaction such as associational resistance requires pressure from consumers that are deterred by the associated neighbor. Yet grazers and their ability to consume fluctuate greatly in time and space (Lubchenco and Gaines 1981). Using the community of a giant kelp canopy, in Chapter 1, I will identify which canopy grazers reduced consumption of kelp in the presence of the kelp-associated epibiont, *Membranipora*. Additionally, in Chapter 2, in a natural kelp forest I will examine where in the canopy the mesograzers, which may be particularly sensitive to the presence of *Membranipora*, are located and cause grazing damage. These findings will indicate where in the canopy associational resistance to herbivory by mesograzers is likely to occur.

In the case of physical stress, the presence of predictably high levels of stressors can also influence the effectiveness of a positive interaction. Highly stressed habitats are typically inhabited by stress-tolerant species (Grime 1989). Recent analysis of the SGH

(Holmgren and Scheffer 2010) and empirical studies (Pennings et al. 2003) suggest that facilitation may be rare amongst species adapted to harsh physical conditions because such species may not benefit from amelioration by neighbors to growth and reproduce. Salt marshes in Mediterranean-type climates experience hot, dry summers and are characterized by much saltier soils than higher latitude salt marshes (Zedler 1982, Callaway et al. 1990) where much of the previous work on species interactions and zonation have taken place. In Chapter 3 I will examine whether *Batis maritima* is an effective facilitator of recovery from disturbance for these salt-tolerant species (Pennings and Callaway 1992, Kuhn and Zedler 1997) when bare patches are excessively hypersaline. Though a few empirical studies have examined competitive and facilitative interactions at the extreme end of the stress gradient, whether facilitation can promote secondary succession in extremely high stress regimes amongst tolerant species is unknown.

Through these studies I will examine how herbivory and salinity stress alter species interactions between primary producers and their community and when positive interactions that protect the primary producers are likely to arise.

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I Community-dependent associational resistance in a kelp canopy

ABSTRACT

By altering feeding preferences of consumers, epibionts can enhance or reduce consumption of their host. While previous studies have documented how a single consumer species responds, few studies have examined how multiple grazer species change their consumption of a host when an epibiont is present. In particular, how the small but abundant members of the mesograzer community respond to epibionts has been largely unexplored. Using a combination of choice experiments and in situ estimates of grazing, I evaluated whether an encrusting epibiont, *Membranipora membranacea*, promotes or deters consumption of its host, the giant kelp *Macrocystis pyrifera*, by invertebrate canopy grazers. In lab choice experiments, four of the five grazers, the snails *Lacuna unifasciata* and *Norrisia norrisi* and the crustaceans *Perampithoe humeralis* and *Idotea resecata*, preferentially consumed unencrusted kelp. Of these, the mesograzers (*Lacuna*, *Perampithoe*, and *Idotea*) almost entirely avoided (<1% of total diet) *Membranipora*-encrusted kelp. Kelp crabs, *Pugettia producta*, the largest of the crustacean grazers, targeted encrusted kelp. Field surveys compared relative grazing damage between densely and sparsely encrusted kelp in a canopy dominated by amphipod and isopod mesograzers. I found 2.5 times more grazing damage on sparsely encrusted kelp than on densely encrusted kelp. These results indicate that *Membranipora* provides associational resistance to grazing when these mesograzers are dominant consumers. Thus, whether *Membranipora* reduces or promotes grazing on kelp will depend on the species composition of the grazing guild.

INTRODUCTION

Due to close proximity, an epibiont can strongly influence its host. These species living directly on the surface of another organism are common in marine systems, and much attention has been paid to the direct negative effects epibionts typically impose on the host (reviewed in Wahl 1989). Such effects include reduced nutrient transfer between the host and ambient water (e.g. Hurd et al. 1994), increased blade loss (e.g. Fong et al. 2000, e.g. Saunders and Metaxas 2009) and reduced growth (e.g. Littler et al. 1995, Stachowicz and Whitlatch 2005, Rohde et al. 2008). Less attention has been given to how an epibiont affects the host indirectly by changing interactions with other members of the community.

One important interaction is consumption, which can be modulated, positively or negatively, by the presence of an epibiont (Wahl and Hay 1995). Epibionts can reduce consumption of the host (e.g. Vance 1978, Durante and Chia 1991, Gray et al. 2005, Fong et al. 2006, Thornber 2007). These relationships, termed associational resistance (described by Atsatt and O'Dowd 1976), can protect a host by interfering with a consumer's attachment mechanism or detection abilities, or defending the host chemically and/or physically (reviewed in Wahl 2008). Alternatively, a palatable epibiont may be harmful by attracting consumers (e.g. Karez et al. 2000, e.g. Enderlein et al. 2003, e.g. da Gama et al. 2008) a phenomenon termed "shared doom" by Wahl and Hay (1995). Since palatability is species-specific (Lubchenco and Gaines 1981, Duffy and Hay 1990) some consumers may reduce grazing on the host while others may increase their consumption when an epibiont is present.

Most studies examining the interaction between giant kelp and the encrusting bryozoan *Membranipora membranacea* have documented negative impacts on the kelp host. *Membranipora* reduces nutrient transfer (Hurd et al. 1994) and decreases light penetration to the underlying tissues (Wing and Clendenning 1971). When present in high abundance, *Membranipora* accelerates blade loss on *Macrocystis pyrifera* (Dixon et al. 1981) and other kelp species (Lambert et al. 1992, Saunders and Metaxas 2009), causes blade deformities (Neushul and Haxo 1963), and, as an invasive species along the northern Atlantic coast of the United States, *Membranipora* reduces growth and percent cover of native kelps (Levin et al. 2002). However, at moderate abundances and within

its native range, *Membranipora* does not appear to reduce growth of the host (Hepburn and Hurd 2005). The potential positive effect of associational resistance to grazing has yet to be examined.

I hypothesized that different species of canopy grazers have different magnitudes of attraction to or avoidance of *Membranipora*. *Membranipora* is common in giant kelp beds along the coast of California (Woollacott and North 1971), at times covering almost all of the surface area of the algal host (Jones 1971, Harvell et al. 1990, Chess and Hobson 1997). Mesograzers, the small (< 2.5cm) canopy-dwelling grazers (Brawley 1992) and intermediate-sized grazers (defined here as between 2.5 cm and 10 cm in length) are present in giant kelp canopies (Jones 1971, Leighton 1971, Coyer 1984, Kushner et al. 1995, Hobday 2000, Sala and Graham 2002) and likely encounter the bryozoan regularly. *Membranipora* colonies contain calcium carbonate (Ryland 1970) and individuals produce defensive spines when preyed upon (Harvell 1998), both of which may deter some consumers. Lidgard (2008) noted that typical bryozoan consumers were either large enough to tolerate their defenses or specialize on removing only the soft tissue portions of colonies. I predicted that mesograzers may have difficulty penetrating the colonies. However, since most herbivores are thought to benefit from nitrogen-enriched food sources (reviewed in Fong and Paul 2011), consumers not deterred by defenses may receive additional nutritional benefits over eating kelp alone.

In this study, I examined whether *Membranipora* alters the feeding preferences of several common invertebrate kelp grazers. Using choice experiments I tested whether 5 grazer

species (2 gastropods and 3 crustaceans) present in southern California kelp canopies

prefer to consume encrusted or unencrusted portions of *Macrocystis pyrifera*. Further, to

assess if grazing was reduced on heavily encrusted kelp when mesograzers were

dominant, I surveyed relative levels of grazing pressure between densely and sparsely

encrusted kelp in a local kelp bed.

METHODS

Grazer preference assays

To determine if invertebrate grazers preferentially choose unencrusted or encrusted kelp

surfaces for consumption, grazers were collected, starved, and then exposed within

replicate arenas to partially encrusted kelp blades. Experiments took place from June

through November 2006 at the Cabrillo Marine Aquarium near Los Angeles, California.

I collected adult grazers prior to the day of experiment (Table 1). The two larger species,

Pugettia producta (kelp crabs) and *Norrisia norrisi* (Norris' top snail), were collected on

snorkel from kelp canopies at Cabrillo Beach, 40 km south of Los Angeles, CA. The

mesograzers, *Lacuna unifasciata* (One-band *Lacuna* snail), *Perampithoe humeralis*

(amphipod kelp curlers), and *Idotea resecata* (kelp isopods) were either removed from

kelp while on kayak inside the Cabrillo Harbor or in the lab from collected blades.

Grazers were kept in flow-through seawater tables prior to each experiment. Since I was

interested in preference and therefore wanted to reduce the duration of the experiments

and minimize autogenic changes and degradation of the kelp (per Peterson and Renaud

1989), most grazers were not fed for several days (see Table 1). However, individuals of

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Perampithoe were used immediately upon collection because they did not survive starvation in the lab. All five grazing species are found in southern California kelp beds, but do not necessarily co-occur at all beds and all times (Kushner et al. 1995, pers. obs.). Jones (1971) noted from observation that in southern California kelp beds, of all the invertebrate canopy grazers, *Perampithoe* and *Idotea* probably consume the most kelp.

Plastic containers arranged in an indoor seawater table were used as experimental arenas. The larger species, *Norrisia* and *Pugettia*, were placed in 40 x 27 x 16cm (L x W x H) containers while 15 x 15 x 9cm (L x W x H) containers were used for *Idotea*, *Perampithoe*, and *Lacuna*. Each container had a roughly 5 x 5cm section of each side removed and replaced with plastic mesh to allow water flow. To increase replication, most experiments were conducted in two separate trials on different days (See Table 1).

Macrocystis pyrifera blades were collected from Cabrillo Harbor on the day of each experimental trial. Since the distal portion of a blade is older than the proximal portion (Abbott and Hollenberg 1997) and grazers can show preferences due to blade age (Durante and Chia 1991, Van Alstyne et al. 2001), I targeted kelp with a relatively even distribution of *Membranipora* along the length of each blade to minimize the confounding effects of kelp age (Fig. 1). Larger species, *Norrisia* and *Pugettia*, received one whole blade (tattered end removed), rubberbanded at the pneumatocyst to a glass slide anchor. To determine if, despite precautions, kelp blade age confounded my results, using two-sided Wilcoxon signed ranked tests, I tested for differences in *Membranipora* cover (*Norrisia*: $p = 0.28$, *Pugettia*: $p = 0.31$) or grazed area (*Norrisia*: $p = 0.74$,

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Pugettia: p = 0.38) between the older and younger halves of each blade and found no significant differences. The three smaller species received cut pieces of kelp, on average 26cm^2 (Table 1), with encrusted and unencrusted areas of the same age present to minimize age effects on grazer preferences (Fig. 1). Since the pieces were small and hence tissue age differences minimal, I did not test for age effects. Cut pieces were rubberbanded flat on two sides to a glass slide and placed in an experimental arena. One individual grazer was haphazardly placed in each experimental unit except for *Lacuna* for which I employed 3 snails per arena to increase replicates with grazing. Each species was left to graze for a short duration not longer than 24 hours such that most replicates had grazing activity (Table 1). I did not use no-grazing treatments to control for autogenic changes used since the proportion of encrusted kelp did not visibly change during the experiments.

I quantified initial percent cover of *Membranipora* and area of grazing damage in both encrusted and unencrusted regions by comparing before and after photos of the experimental kelp pieces using NIH ImageJ software. *Lacuna*, *Norrisia*, *Perampithoe*, and *Idotea* left scars that did not penetrate through the entire blade and were located predominately on a single side of the kelp. Therefore I only used photos of the heavily grazed side to determine grazed area. *Pugettia*, however, shred and consume whole pieces, and so I used photos of both sides of the kelp to determine grazing damage.

For each grazer species, preference for encrusted or unencrusted kelp was analyzed by comparing the proportion of encrusted kelp eaten to the proportion of encrusted kelp

available to the consumer using a Wilcoxon signed rank test since the data did not meet

the assumptions of a paired t-test. Per replicate, I compared:

$$\frac{A_e}{A_t} \quad \text{to} \quad \frac{A_{ee}}{A_{te}}$$

where A_e is the area of kelp encrusted, A_t is the total area of the piece of kelp, A_{ee} is the

area eaten that was encrusted, and A_{te} is the total area eaten. If the average proportion of

encrusted kelp consumed was significantly less than the proportion of encrusted kelp

available, the species was considered to show avoidance of encrusted areas.

Alternatively, if the average proportion of consumed kelp that was encrusted was

significantly greater than the proportion of encrusted area available, the species was

considered to show a preference for *Membranipora*-encrusted kelp. Since I was

comparing grazing rates, replicates in which kelp was never consumed were not included

in the analysis (Table 1). Data from trials occurring on different days were pooled since I

found no differences in the proportion of *Membranipora*-encrusted kelp consumed

between days for all species (*Lacuna*, p = 1.0, *Norrisia*, p = 0.26 *Idotea*, p = 0.15,

Pugettia, p = 0.14, Wilcoxon rank-sum test).

Grazing patterns in the field

To determine if *Membranipora* colonies reduced grazing damage on kelp blades, I

conducted a field survey of grazing damage on densely and sparsely encrusted kelp in

August 2007. This study was conducted in the canopy of a *Macrocystis pyrifera* forest at

Lunada Bay (33°77'19.52"N, 118°42'79.47"W), on the northern side of the Palos Verdes

Peninsula, approximately 46 km southwest of Los Angeles, California. Collection took

place on the seaward edge of the bed where *Membranipora* is typically most abundant

(Bernstein and Jung 1979, pers. obs.). Active grazers at the site included gammarid amphipods, *Idotea*, and *Norrisia* (Bryson, unpubl. data), all of which leave visible grazing scars (pers. obs.). On snorkel, I collected individual kelp blades with visible differences in *Membranipora* cover between the two sides.

After collection and prior to analysis, the distal tattered end (~30%) of each blade was removed. As comparisons were made between two sides of the same blade, the kelp was the exact same age on both sides of the blade. Each blade, including patches of *Membranipora* and grazing scars, was traced onto a sheet of clear plastic. Images were scanned, and total area, encrusted area, and grazed area were quantified using NIH ImageJ software. From experience with the grazing preference experiments and observations in the field, I identified most of the grazing scars encountered on this survey as amphipod and *Idotea* bites. Both species leave small, ~ 0.12 cm^2, irregularly distributed scars that do not entirely penetrate though the kelp blade. The scars from each species could not be distinguished from each other reliably, and therefore I combined these scars together to quantify mesograzer damage. Only fresh, crisp scars with the kelp's yellow medulla tissue still present were counted so as to quantify only recent grazing damage with respect to recent levels of encrustation. A total of 499 fresh scars were included in the analysis while 109 older tattered holes that penetrated all the way through both sides of the kelp were omitted from the 21 blades analyzed. Using a paired t-test, I compared the area of mesograzer-inflicted damage between the sparsely encrusted, (sparse side) and densely encrusted (dense side) sides of the blades. The data were log transformed to fit the assumptions of the test. Only one blade had grazing

damage from another species, that of *Norrisia*, which leaves much larger, ~4.0cm^2, meandering swaths across the blade. This blade was excluded from analysis.

RESULTS

Grazer preference assays

Both gastropod species, *Lacuna* and *Norrisia*, strongly targeted areas of kelp blades without *Membranipora* (Fig. 2ab). Almost half of the kelp offered to *Lacuna* was encrusted with *Membranipora*, yet none was consumed. While *Norrisia* did not entirely avoid eating encrusted kelp, over 80% the diet was composed of unencrusted kelp compared to the approximately 60% that was available (Fig. 2b).

The two smaller crustaceans, *Perampithoe* and *Idotea*, strongly avoided consuming portions of kelp blades covered with *Membranipora*. These species included almost none of the encrusted kelp in their diets (Fig.2cd) even though these grazers were offered 30% and 47% encrusted kelp on average respectively. *Pugettia producta*, in contrast, preferentially selected *Membranipora*-encrusted kelp. Proportionately, the diet of the crabs consisted of almost twice as much encrusted kelp as was available (Fig. 2e).

Grazing patterns in the field

Confirming my selection of surveyed blades, the side designated as the dense side of the blade was significantly more encrusted than the sparse side (p < 0.0001, Wilcoxon signed rank test). On average, the dense and sparse sides were 41.6% ± 3.7% (mean ±SE) and 11.1% ± 2.1% encrusted, respectively, with the minimum difference being 14.7%

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between the two sides of one blade. Small crustaceans consumed more than double the area on the sparsely encrusted side than on the dense side (Fig. 3). All grazing scars were located in unencrusted areas.

DISCUSSION

My results demonstrated that *Membranipora* modified the palatability of kelp, with the direction of this effect dependent on grazer species. All 5 species I tested showed significant alterations of grazing rates with respect to the presence of *Membranipora*, 4 negative and 1 positive. Previous studies have found examples of epibiotic bryozoans protecting their hosts (Durante and Chia 1991, Gray et al. 2005), but studies of *Membranipora*'s effects on host consumption to date have only found *Membranipora* to attract consumption. For example, the presence of *Membranipora* made the unpalatable alga *Zonaria tournefortii* palatable to the generalist sea urchin, *Arbacia punctulata* (Wahl and Hay 1995). Further, the omnivorous fish, *Oxyjulis californica* has been observed to consume *Membranipora*-encrusted portions of *Macrocystis* blades (Yoshioka 1973, Bernstein and Jung 1979, Chess and Hobson 1997). My study expands these others by showing that the effects of *Membranipora* on grazers can be either positive or negative, depending on the species, and, at times, acts to protect the kelp host.

Membranipora is an especially effective deterrent to small-sized consumers. All three of the mesograzers strongly avoided encrusted kelp in both the lab experiments and in the field. The calcium carbonate ($CaCO_3$) in the colonies may protect the underlying algal tissue from mesograzers. Previous studies have documented $CaCO_3$ being a deterrent for

similar species. Hay et al. (1994) found that $CaCO_3$ deterred feeding by a species of amphipod when incorporated into artificial food. Steneck and Watling (1982) noted that the genus *Lacuna* has a morphological type of radula not typically used for grazing calcified algae. Additionally, Gaines (1985) found that *Idotea wosnesenskii* was deterred by the relatively harder outer cuticle of the red alga *Iridaea cordata* suggesting that *Idotea* may, in general, be deterred from grazing by hard substances. Thus, size may be a more important predictor than taxonomic affiliation in determining the direction of the effects of *Membranipora* on grazers.

While I observed a clear associational defense in a natural kelp canopy, it does not automatically follow that *Macrocystis* benefits from this defense. *Membranipora* may have both positive and negative impacts on the kelp host. The indirect benefits of reduced consumption can outweigh negative direct impacts when consumption is high (Fong et al. 2006) or when negative impacts are minimal. I did find a reduction in grazing damage at the level of the blade and Hepburn and Hurd (2005) found no effect of *Membranipora* cover on kelp growth rates, suggesting that even relatively small benefits from hosting colonies may exceed costs if colonization is modest. Still, the grazing pressure I observed in the field was low, 1.5% of the sparse side of the blade was damaged. Given the high growth rates of *Macrocystis*, 2% dry-mass increase daily (Reed et al. 2008), *Macrocystis* can likely tolerate low levels of grazing quite well. However, grazing rates by mesograzers can be much higher than I observed in my field surveys. Rare but destructive infestations, which may result from reduced fish densities (Tegner and Dayton 1987) since predatory fish moderate mesograzer densities and behaviors

(Duffy and Hay 2000, Davenport and Anderson 2007, Perez-Matus and Shima 2010), can severely defoliate kelp (Jones 1965, Tegner and Dayton 1987, Graham 2004). I predict that during these times of increased abundances of mesograzers *Membranipora* could be an important factor limiting overgrazing, acting as a buffer to the community.

One important implication of my results is that the species composition of the canopy grazing guild will likely affect the direction of the interaction between *Membranipora* and kelp. Local abundances of grazers change seasonally and from site to site (Wicksten and Bostick 1983, North 1987, Kushner et al. 1995) and several species other than the mesograzers I observed at my site have been documented to be significant kelp consumers in other locales (i.e fish, Bernstein and Jung 1979, kelp crabs, Bracken and Stachowicz 2007). Clearly, *Membranipora* reduced grazing on kelp in my site but may promote grazing in other sites, especially if larger species dominate the grazer community. Shifts in indirect interactions from positive to neutral or negative have been documented in marine communities (Berlow 1999, Hay et al. 2004, Wahl 2008). I predict that as the grazing guilds in kelp forests change from dominance by mesograzers to macrograzers the associational resistance to grazing provided by *Membranipora* will likely shift to shared doom.

OLDER

YOUNGER

~ 6cm

~ 4 cm
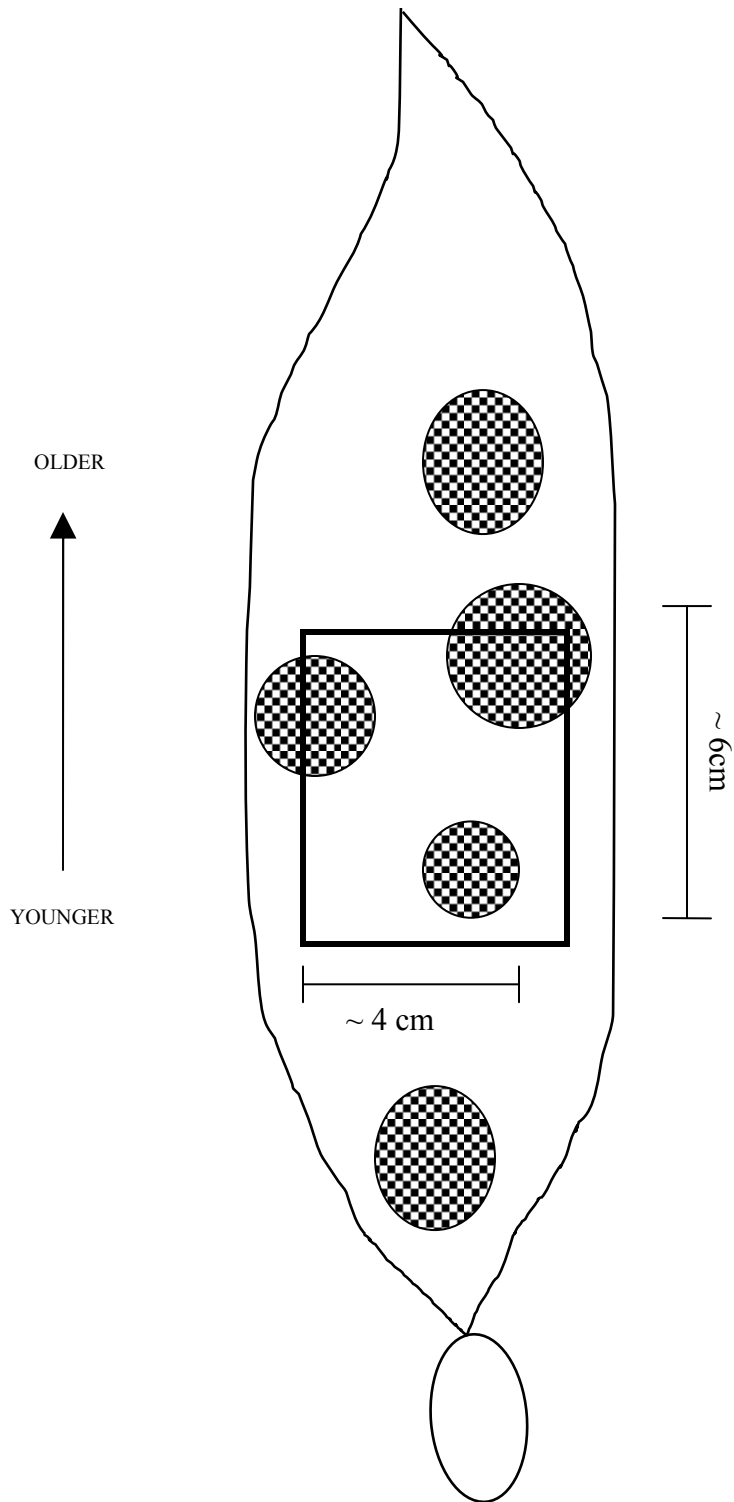
Fig. 1. Example of experimental kelp for small grazers**.** Pieces were cut to incorporate same aged areas with and with out *Membranipora*. *Membranipora*-encrusted areas depicted here as checkerboard patches.

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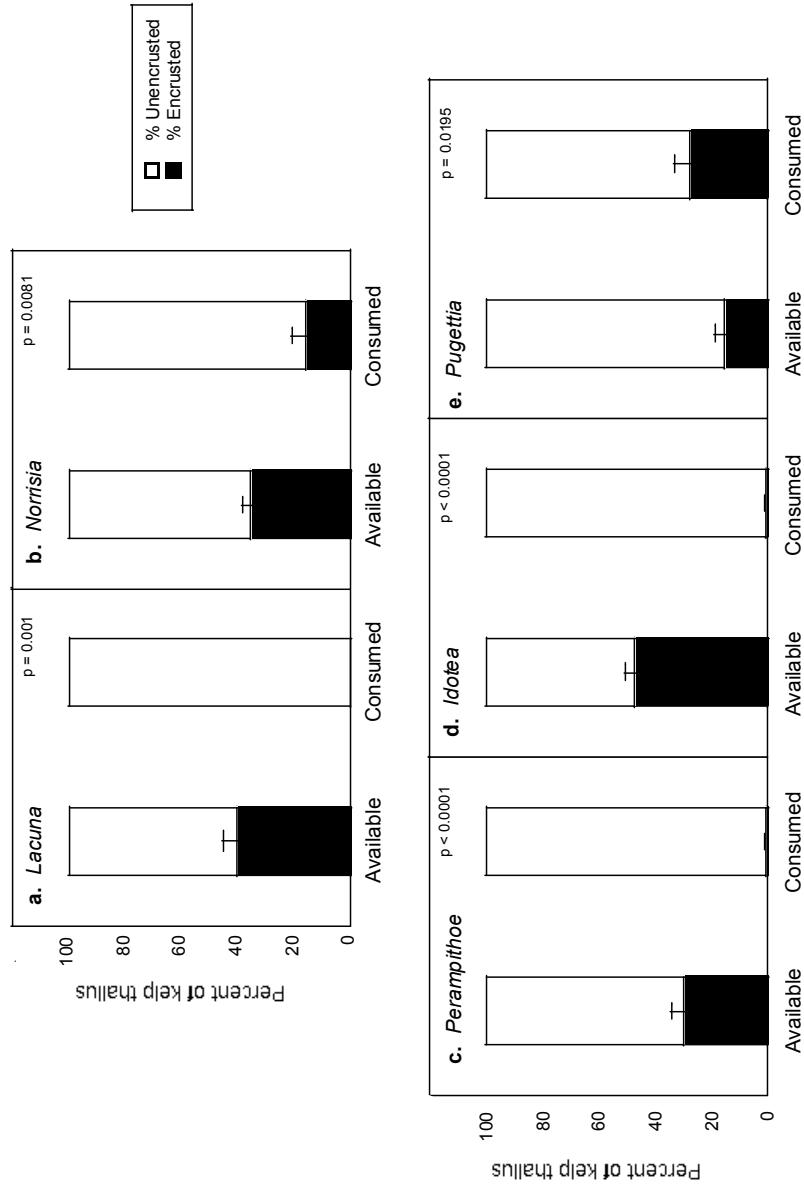
Fig. 2a-e. Preference for encrusted or unencrusted kelp of the five grazers. The left bar in each panel is the percent of encrusted and unencrusted kelp available. The right bar is the percent of encrusted and unencrusted kelp eaten. Reported p-values from Wilcoxon signed ranked tests. a-b. Gastropods arranged from small-bodied (left) to large-bodied (right). c-e. Crustaceans arranged in same way.

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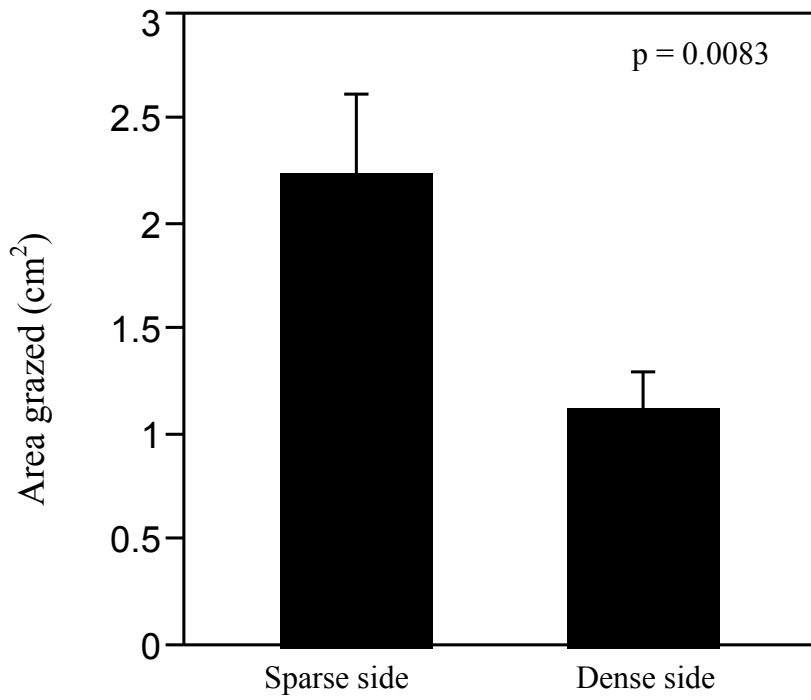
Fig. 3. Area grazed on the sparse and dense sides of kelp blades collected during field sampling. Bars are means ± SE.

Table 1. Specifications from preferences assays. Length refers to the anterior-posterior distance of the organism. When experiments were run on two dates, I report combined averages for size of kelp and consumption rate.

Species	Length (mm)	Days Starved	Date of Trial(s)	Size of Kelp	Replicates (eating)	Not eating	Duration (hr)	Consumption Rate
Lacuna unifasciata	3.6*	3-5	09/25/2006 09/28/2006	27.67cm² ± 1.49	6 4	4 5	24 24	0.00065 cm²/hr ± .00028
Norrisia norrisi	42.3 ± 1.58	10-13	06/22/2006 08/1/2006	144.7cm² ± 20.9	6 6	0 0	22 24	0.95 cm²/hr ± 0.22
Perampithoe humeralis	18.1 ± 0.97	0	10/11/2006	20.6cm² ± 1.25	15	0	23.5	0.084cm²/hr ± 0.0073
Idotea resecata	19.3 ± 0.67	3-5	09/06/2006 09/12/2006	29.7cm² ± 0.60	8 13	7 2	2 2.5	0.24 cm²/hr ± 0.050
Pugettia producta	33.9 ± 4.2	5-7	11/02/2006 11/14/2006	148.3cm² ± 18.5	5 5	0 0	1 1	11.1 cm² ± 3.7

Lacuna test subjects were not measured for length, a measurement from Jones (1971) is included for comparative purposes.

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II   Mesograzer abundance and grazing damage in a giant kelp forest canopy

ABSTRACT

Mesograzers are often abundant members of marine communities that link higher trophic levels to primary productivity, yet little is known about their grazing patterns. In a giant kelp forest canopy in southern California I conducted two surveys to determine mesograzer abundance, levels of grazing damage on kelp blades, and level of cover by *Membranipora membranacea*, a kelp epibiont known to deter consumption by mesograzers. I found the two dominant mesograzer taxa, the isopod *Idotea resecata* and an assemblage of gammarid amphipod species, and the majority of grazing damage to vary with depth. Grazing damage, measured as abundance of grazing scars, and the abundance of *Idotea*, were higher in the upper horizontal portion of the kelp canopy, while significantly less grazing was found in the deeper, middle portion of the kelp canopy where amphipods were more common. I also found a trend of reduced grazing by mesograzers when the bryozoan, *Membranipora membranacea* was present in sufficient abundance. My findings suggest that mesograzer consumption disproportionately impacts the more photosynthetically active blades in a kelp forest. However such impacts may be moderated by the presence of other kelp-associated species.

INTRODUCTION

Although herbivory is well documented to be a strong force in structuring many marine communities (e.g Estes and Palmisano 1974, Lubchenco and Gaines 1981, Hay and Fenical 1988, Hughes 1994, Babcock et al. 1999, Graham 2004, Heck and Valentine 2007), less is known about mesograzers and their activities and impacts in these habitats.

These small (<2.5 cm), mobile epifauna are often present in extremely high densities but are difficult to study due to their small size (reviewed in Brawley 1992). While "mesograzers" denotes a wide variety of species with different feeding habits the term generally refers to a guild of consumers that specialize on epiphytes (Brawley 1992, Duffy and Harvilicz 2001), though some species consume host tissue (Farlin et al. 2010). Two studies assessing the influence of mesograzers in early successional processes found a strong influence on the developing community via top-down control (Brawley and Adey 1981, Duffy and Hay 2000). However, little is known about mesograzers and their activities in a fully developed algal canopy (but see Davenport and Anderson 2007, Poore et al. 2009).

While giant kelp forests, dominated by *Macrocystis pyrifera*, support a diverse suite of mesograzers species (Jones 1971, Coyer 1984, Hobday 2000), the role these grazers play in the community is understudied. Of the mesograzers that live in the kelp canopy, some are known to consume kelp directly (Leighton 1971, Sala and Graham 2002, Bryson, Chapter 1). Such consumption by mesograzers is moderated by the presence of microcarnivorous fishes (Davenport and Anderson 2007, Perez-Matus and Shima 2010). However, consumption of kelp by mesograzers has been known to spike to destructive levels on rare occasions (for examples see Jones 1965, Tegner and Dayton 1987, Graham 2002). Outside of the recognition that consumption by mesograzers does not often devastate kelp biomass (North 1987), the grazing pressure exerted by mesograzers in the canopy remains largely unknown.

The bryozoan *Membranipora membranacea* is a kelp epibiont (Fig. 1) that has been

shown to deter grazing by mesograzers (Bryson, Ch.1). *Membranipora* is a common

invertebrate present in the kelp canopy (Woollacott and North 1971) that can become so

dense as to cover most of the kelp thallus (Jones 1971, Harvell et al. 1990, Chess and

Hobson 1997). With such a strong presence in kelp beds, *Membranipora* may frequently

interact with kelp consumers. Because *Membranipora* reduces consumption of kelp by

mesograzers, the presence of the bryozoan may affect grazing damage patterns in the

field.

My objectives were to **1.** examine spatial patterns of grazing intensity measured as the

accumulation of grazing scars from mesograzers in a natural *Macrocystis* canopy, **2.**

relate grazing intensity to abundances of mesograzers, and, **3.** evaluate whether the

presence of *Membranipora* reduced grazing pressure from mesograzers.

METHODS

To accomplish my objectives, I conducted two surveys in the kelp forest at Lunada Bay

(33°77'19.52"N, 118°42'79.47"W) on the north side of the Palos Verdes Peninsula,

approximately 46 km southwest of Los Angeles, California, USA. The kelp bed at this

site occupied about 21.0 hectares of ocean bottom, but fluctuated in size seasonally

though it persisted year round. Water depth ranged from 7.5m to 12m. Like all southern

California kelp forests, *Macrocystis pyrifera*, or giant kelp, was the dominant structural

kelp of the community. The kelp occurred at a density of 2.2 holdfasts/m^2 (Bryson,

unpublished data); this relatively high density is typical of a frequently disturbed

community (North 1987). Surveys and collections took place on the seaward side of the kelp bed where encrusting *Membranipora* colonies were most abundant (pers. obs.). *Membranipora* was present on virtually all kelp thalli.

To evaluate spatial patterns of grazing with depth I quantified grazing within two depth ranges (top and mid) of the kelp bed. The top range was comprised of the upper canopy, from the surface to approximately 1.0m depth, defined as where the kelp lies horizontally on the surface. Most kelp blades existed in this region, as noted elsewhere (North 1987), and blades were usually spaced < 0.05m apart. The mid depth occurred between 2.5m-4m depths, where kelp stipes were vertical and blades fewer and spaced at approximately 0.2m intervals. Deeper depths were not considered since few blades were present below 4m at this site.

Preliminary grazer surveys confirmed the dominance of two mesograzer taxa, a mixed assemblage of gammarid amphipods and the isopod *Idotea resecata*, in the kelp canopy at Lunada Bay. Both are common in southern California kelp forests (Jones 1971, Kushner et al. 1995). There are many species of gammarid amphipods associated with kelp; Coyer (1984) found 20 species in kelp forests at Santa Catalina Island, on average approximately 2-3mm in length. Some of these kelp-associated gammarids are kelp consumers (Light 1975, Davenport and Anderson 2007, Cerda et al. 2009). The isopod, *Idotea resecata*, is larger, up to 39mm in length (Morris et al. 1980), and is known to consume kelp (Jones 1971). This species may be less abundant than the gammarid amphipods (Coyer 1984).

On May 11, 2007, I collected portions of kelp thalli to assess grazing damage and quantify mesograzer abundance. Two series of random numbers were generated to designate collection points in the top and mid depths along a haphazardly placed transect in the seaward side of the bed, parallel to the bed edge. In the top depth, at each sampling point I collected the nearest stipe with attached blades at 0m (n = 10). Similarly, a second swim was conducted to collect stipes with attached blades in the mid range at 3.3m depth (n = 11). A stipe with attached blades was collected only if it came from a frond long enough to reach the surface to ensure it was old enough to have accumulated *Membranipora* and grazing scars. Each section of stipe, approximately 1.3m in length, was cut, gently disentangled from neighboring stipes, and placed in 9.4 liter reclosable plastic bag. Prior experience with sampling revealed that mesograzers cling to kelp and that quick handling of the short stipes from cutting to placement in plastic bags ensured that few if any mesograzers were lost in the process. None were observed to escape. Bags of kelp were placed in a cooler and transported to the lab.

To determine if mesograzer abundance varies with depth, I counted mesograzers collected with the kelp from both the top and mid depth ranges. Each stipe segment was considered a replicate. To estimate mesograzer density per blade, I counted the number of blades that were longer than 40 cm in length. I excluded immature blades near the apical meristem, here defined as those less than 40cm in length, because they are much smaller than the mature blades and do not contribute substantially to total kelp surface area (Jackson et al. 1985). Stipe segments were rinsed in fresh water, agitated, and the

invertebrates strained through 60 micron mesh and placed in 65% ethanol/seawater preservative (adapted from Coyer 1984). All species of gammarid amphipods were pooled and counted due to the difficulty in identifying gammarids to species. Individual *Idotea resecata* were also counted. To obtain estimates of mesograzer abundance, for amphipods and *Idotea* separately, I calculated total number of individuals per blade longer than 40cm on each stipe section. I analyzed differences in amphipods/blade between the top and mid depths using a Student's t-test following a log-transformation of the data to meet the assumptions of the test. Since transformations of *Idotea*/blade did not improve the fit to the assumptions of a t-test, differences between depth ranges were analyzed using a Wilcoxon rank-sum test.

I counted grazing scars to determine if damage on kelp blades from mesograzer consumption differed between depths in the canopy. Each blade over 40cm in length was assigned an identification number, and, using a series of random numbers, five blades were selected for assessment of grazing damage. Grazing scars produced by both amphipods and *Idotea* were small, ragged, approximately $0.12cm^2$ (n = 7) in area, and did not penetrate through the kelp blade. Because scars could not be reliably distinguished by grazer identity they were pooled. These scars occurred only in the unencrusted spaces between *Membranipora* colonies, confirming previous findings (Bryson, Ch.1) that the colonies prevent almost all grazing by mesograzers on underlying kelp. Only fresh, crisp scars with the medulla of the kelp blade intact were counted. As a frond grows, the depth of an individual blade will change as the apical meristem approaches the surface of the water (North 1971). Recently created fresh scars are more indicative of the grazing

pressure on the blade at its current depth in the water column. Scars on both sides of the blade were counted and I averaged data from the five blades of each sampled stipe to generate average grazing scar counts per blade for each replicate. I compared mean grazing scar counts/blade between depths using a two-sided t-test following a square root transformation to ensure that the data satisfied the assumptions of the test. I also assessed *Membranipora* cover on these blades. However, due to greatly uneven distribution of cover categories between depth ranges I could not assess grazing differences with respect to *Membranipora* from data garnered from this survey. This aspect is examined on the survey discussed below.

I compared mesograzer abundance and grazing damage on a per blade basis using blades per stipe as a proxy for the surface area available to grazers (as described above). This comparison assumes all blades to be of equal size. Since I employed short stipe segments all attached blades from a single stipe were similarly sized. However, blades from different stipes, and in particular, between depths appeared to differ, with the smaller, younger blades more common in the top depth as expected (Parker 1971, Jackson et al. 1985). To generate rough estimates of area differences between blades in the Top and Mid depth ranges, I haphazardly selected a single blade per stipe and approximated blade area using the formula: $\frac{2}{3}$ * blade length * width based on the shape of the blade. On average, blades in the Mid had 1.4 times the surface area than blades from the Top. Therefore, measures I employed will tend to underestimate abundance of grazers and grazing scars per actual surface area in the top relative to the mid depth.

On May 6, 2007, I conducted an *in situ* survey of grazing damage and *Membranipora* cover in the field. On SCUBA, I surveyed blades in the top depth (n = 28) at 0m and within the mid depth (n = 32) at 3.3m at randomly selected points along a haphazardly placed transect. Selected thalli were tall enough to reach the surface. At each predetermined sampling point, considered to be a single replicate, three sequential blades along the selected stipe were surveyed. I visually estimated *Membranipora* cover and placed each replicate into one of three cover categories: low (0-5%), medium, (6%-39%), and high (40%+). Since the three blades were almost identical in age and adjacent to each other along the stipe, they were always in the same cover category; cover category did vary between replicates. Grazing scars from the three blades were counted and averaged for each replicate as described above. Since transformations did not effectively improve the fit of the data to the assumptions of the test I was unable to compare average grazing scar counts between depths and *Membranipora* cover categories simultaneously. Consequently, I conducted two separate analyses. I analyzed differences in grazing scar counts between depths with a Wilcoxon rank-sum test. Then, from data collected from the top depth only, I compared average grazing scar counts/blade between the three different categories of *Membranipora* cover using a one-way ANOVA following a square-root transformation of the data. All three cover categories were not well represented by my sampling in the mid depth and therefore data from this depth range could not be analyzed with respect to *Membranipora* cover.

RESULTS

Overall, amphipods were more abundant than *Idotea* (Fig. 2). From all the mesograzers collected, I found amphipods to be about 12 times more abundant than *Idotea* overall (1763 vs. 142 individuals respectively). I also quantified a partitioning of mesograzer taxa between depths in the kelp canopy. Amphipods were significantly more abundant (> 2 times more abundant) in the Mid than the Top depth (Fig. 2a). However, *Idotea* was almost an order of magnitude more abundant in the top depth (Fig.2b). Almost all (214 of 224) *Idotea* individuals were found in the top of the kelp canopy. Natural variation in blade size will tend to lessen the differences found in amphipod abundances but amplify differences in *Idotea* abundance between depth ranges.

Mesograzers exerted the majority of their grazing impact within the top portion of the kelp forest (Fig. 3). I found this pattern using both survey techniques. Mesograzer scars were approximately 9 and 6 times more abundant in the top than the mid depth on the *in situ* and kelp collection surveys respectively even though kelp blades in the top depth were smaller than those at deeper depths. Average grazing scars/blade were approximately 4 times greater on the kelp collection survey than the *in situ* survey with 8.6 ± 2.0 grazing scars/blade (±SE) and 2.0 ± 0.39 grazing scars/blade (± SE) on average respectively.

There was a trend of less grazing scars when *Membranipora* was abundant (Fig. 3a). Blades from the top depth with high levels of *Membranipora* cover had fewer scars than blades with medium or low cover though this difference was only marginally significant.

And, even though there were few scars on blades from the mid depth, blades with low

Membranipora cover appeared to have more grazing scars than blades with medium and

high levels of cover.

DISCUSSION

My results suggest that *Idotea* may be driving the overall grazing damage pattern. I

found far more grazing in the top depth of the kelp canopy where *Idotea* individuals were

predominated located than in the mid region where most of the amphipods were found.

Coyer (1984) also found higher abundances of amphipods, four times more, in the middle

third portion of the kelp forest, but did not quantify grazing pressure. Since many

amphipods consume epiphytes rather than the host macrophyte (Duffy 1990, Brawley

1992, Heck and Valentine 2006, Christie et al. 2009, Farlin et al. 2010) it is possible the

amphipods I collected may not be kelp consumers. Additionally, while fewer *Idotea*

individuals were collected, they were much larger, up to 39mm in length (Morris et al.

1980) compared to the average amphipod, approximately 2-3mm in length (Coyer 1984).

With a size difference of this magnitude, the sparse population of *Idotea* may actually

consume more kelp than the relatively dense population of amphipods.

It is possible that different species or even size classes of amphipods have different

vertical distributions within the kelp forest and that those in the top depth consume more

kelp. Vast differences in modes of eating and life styles exist between gammarid

amphipod species. Some consume their macrophyte host and others do not (Hay et al.

1987, Duffy 1990, Brawley 1992, Poore et al. 2008, Farlin et al. 2010). The tube-

building amphipods of the genus *Perampithoe* (Cerda et al. 2010) are known to eat kelp (Jones 1971, Cerda et al. 2009), however some of the other species are likely to be epiphyte consumers (Farlin et al. 2010). Additionally, Coyer (1984) noted that larger individuals were present in the canopy and found several amphipod species, *Hyale frequens* and *Perampithoe plea*, that tended to reside in the upper canopy rather than at deeper depths. These species are from genera known to consume kelp (Farlin et al. 2010). Jorgenson and Christie (2003) described different mesograzer species compositions between different depths along the thalli in Norwegian kelp beds and suggest that local factors of complexity and longevity of the host strongly influence the composition of the epifauna community. Such differences could separate those amphipods that actively consume kelp and those that do not, leading to greater amphipod grazing damage in the upper depth range of the kelp canopy.

Finally, it is likely that the presence of fishes strongly affects rates of mesograzer consumption. Few fishes were visually observed in the top while many more were present in the mid and bottom regions (pers. obs.), a pattern also noted in other California kelp beds (Limbaugh 1955, Coyer 1984). Microcarnivorous fishes reduce mesograzer abundances, movement, and consumption in marine communities (Nelson 1979, Duffy and Hay 2000, Davenport and Anderson 2007, Perez-Matus and Shima 2010). Of the fishes known to consume mesograzers (Quast 1971, Bray and Ebeling 1975, Bernstein and Jung 1979), senoritas, *Oxyjulis californica*, were abundant at this site along with juvenile kelp bass, *Paralabrax clathratus* to a lesser extent (pers. obs.). Per the extensive surveys of kelp-associated fishes along the Pacific coast of North America both these

species tend to reside within kelp stipes but are not common in the upper canopy (Stephens et al. 2006). It is possible that even with high amphipod abundances in the mid region, the risk of predation may be too high for active foraging by amphipods. There are many factors that change with increased depth in a kelp forest, such as reduced irradiance (Arkema et al. 2009), reduced numbers of blades (Jackson et al. 1985), increased age of the blades (North 1971), and reduced flow speed (Bertness et al. 2001) that may directly or indirectly influence mesograzer consumption rates. However, I expect the presence of predatory fishes to strongly impact the ability of mesograzers to actively consume kelp.

The presence of *Membranipora* may also play a role in mediating grazing by mesograzers. I found support for previous findings that *Membranipora* reduces damage from mesograzers on kelp (Bryson, Ch.1). Depending on grazer identity, *Membranipora* can deter grazing (for *Perampithoe humeralis*, *Idotea*, and the snails *Lacuna unifasciata* and *Norrisia norrisi* , Bryson Ch.1) or promote grazing (for the fish *Oxyjulis californica*, Bernstein and Jung 1979, sea urchins, Wahl and Hay 1995, kelp crabs, Bryson Ch. 1). Since *Membranipora* is common (Woollacott and North 1971) and often densely abundant (Jones 1971, Harvell et al. 1990, Chess and Hobson 1997) in kelp forests along the coast of California, it may regularly interact with mesograzers to reduce their consumption of kelp.

Whether natural abundances of mesograzers regularly influence host growth and survival is largely unknown. In Australian algal beds, Poore et al. (2009), using experimental removal via pesticides, found that the associated amphipods did not affect the growth rate

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of the brown alga *Sargassum linearifolium*. The authors concluded that grazing pressure by the amphipods was low enough to have no detectable effects on the host growth rate. Whether this result can be generalized to other algal beds is unknown. I found grazing damage on kelp, but only a small portion of the blade was lost to grazing by mesograzers. Similarly, Davenport and Anderson (2007) reported approximately 1.0% of the blade consumed over a one and half month time period with natural levels of mesograzers present. However, even modest levels of grazing can impact kelp if grazing targets important structures of the alga (Duggins et al. 2001, Bracken and Stachowicz 2007). The kelp blades in the top depth are more photosynthetically active and contribute more to algal production than blades at deeper depths (North 1971, Colombo-Pallotta et al. 2006). Damage to these blades could disproportionately affect the alga. Additionally, Cerda et al. (2009) demonstrated defensive growth strategies in *Macrocystis integrifolia* when grazed by amphipods indicating an evolved response to such grazing. While it is unclear if the level of grazing I observed represents a sizable impact, further study is needed to understand how the kelp-associated mesograzers influence their host.

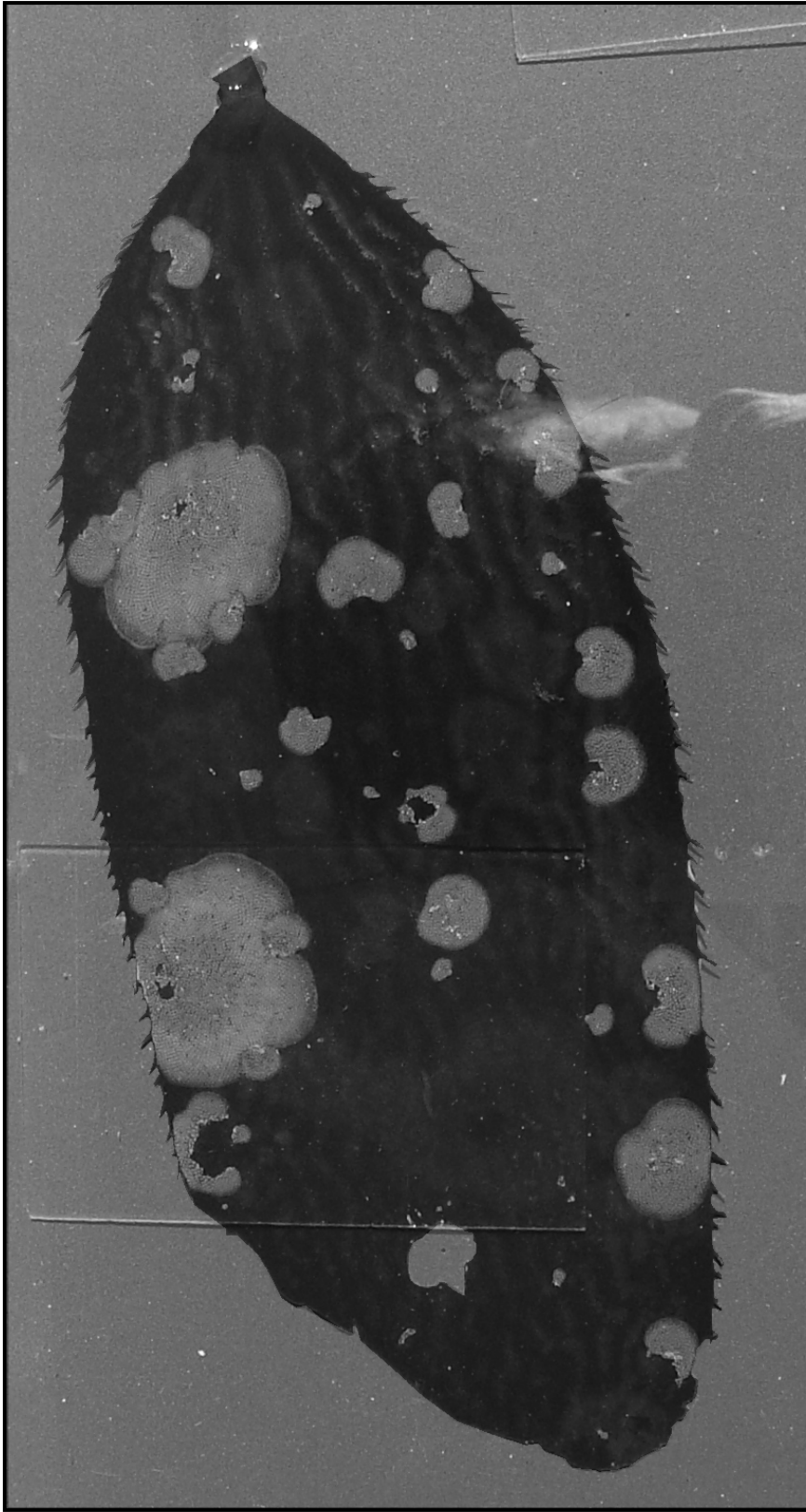**Fig. 1** *Membranipora membranacea* colonies on a kelp blade.
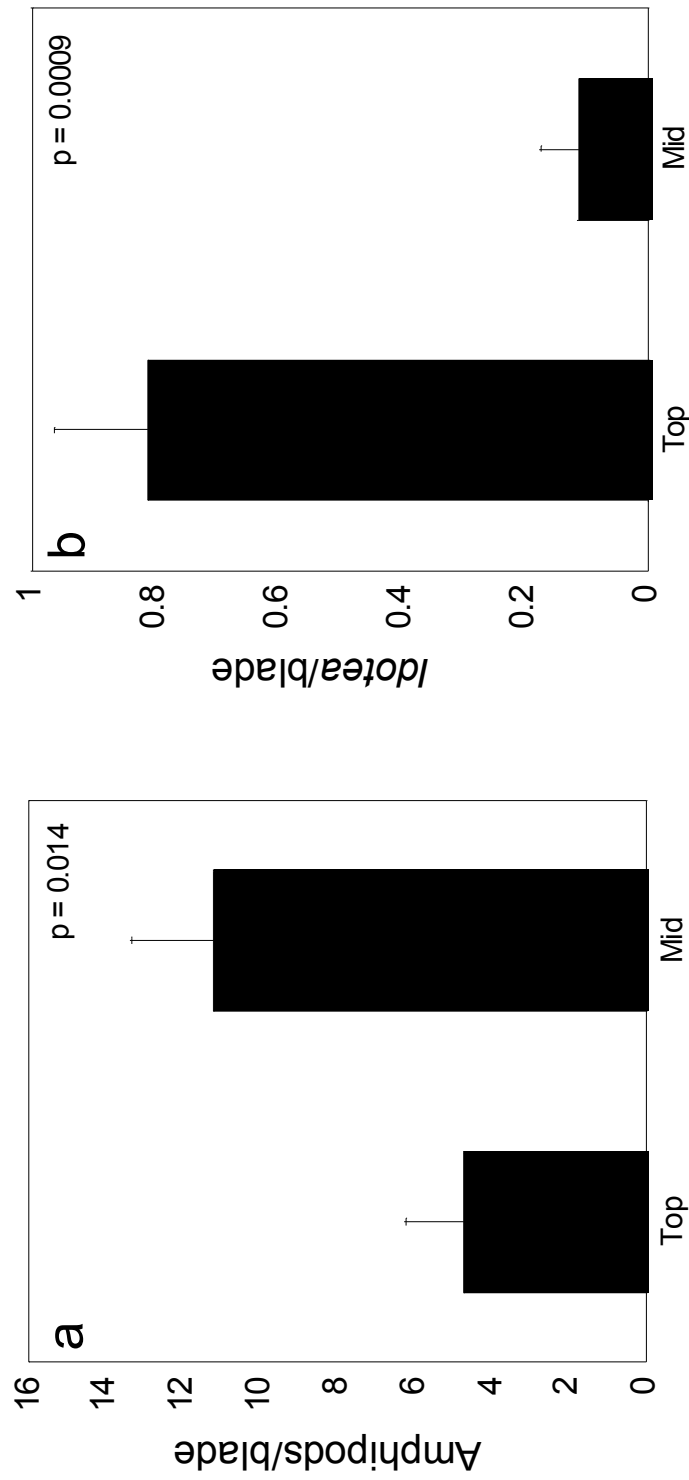
Fig. 2. Abundance of **a**. amphipods and **b**. *Idotea resecata* (individuals/blade) collected from two depth strata (Top, n = 10, Mid n = 11) within the kelp canopy. Bars represent mean ± SE. Amphipod data were log-transformed and analyzed with t-test and *Idotea* data were analyzed by a Wilcoxon rank-sum test. Note different scales.
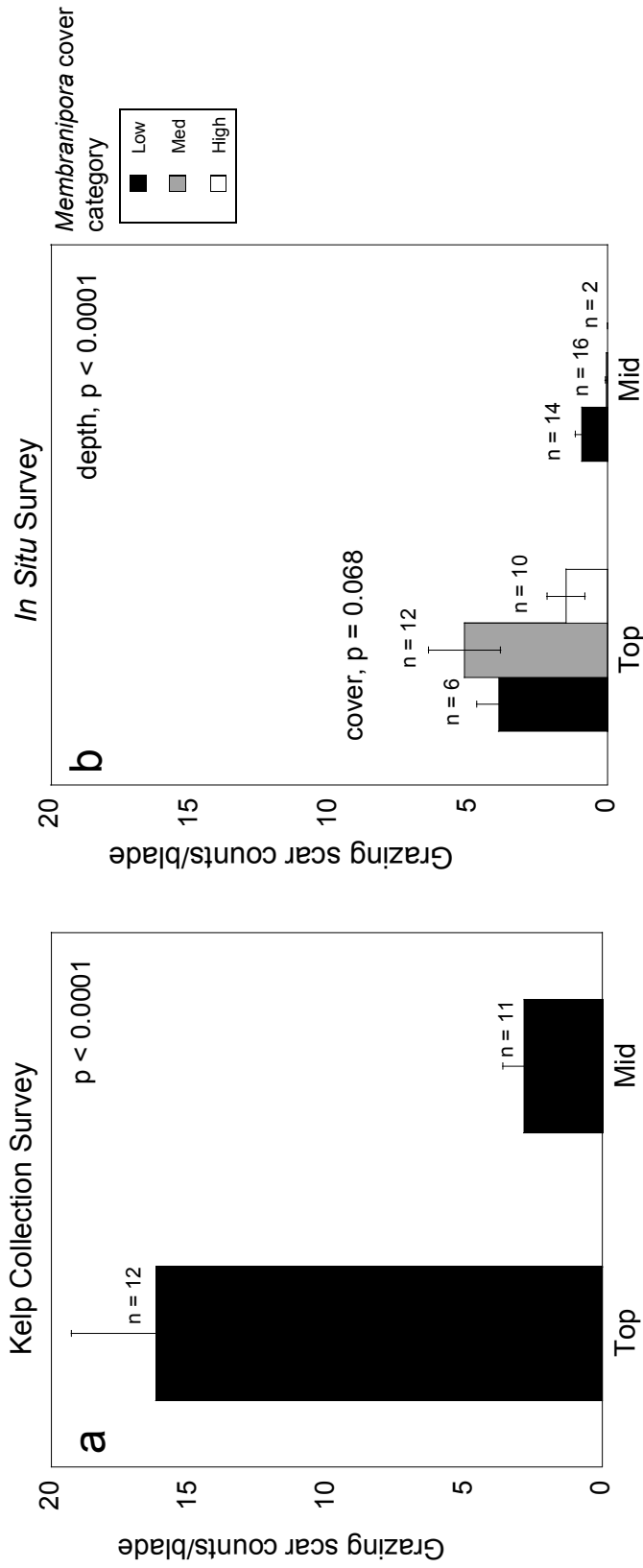
Fig. 3 Differences in grazing scar counts per blade between depth strata. Bars represent mean ± SE. **a**. the kelp collection survey. Data analyzed by a two-sided t-test after a square-root transformation. **b**. *In Situ* survey. Depth comparison analyzed by a Wilcoxon rank-sum test, and grazing scar counts between blades with different levels of *Membranipora* compared by a one-way ANOVA after square-root transformation of the data.

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III   Facilitation of secondary succession in an ultrahypersaline salt marsh in

southern California

ABSTRACT

Facilitation by early colonizers is an important mechanism promoting secondary succession

in salt marshes. These salt-tolerant pioneers shade bare patches and ameliorate harsh soil

salinities, thereby promoting the growth of less-tolerant species. However, this process has

not been evaluated in warm-climate marshes where positive interactions between highly salt-

tolerant species may be rare. Using manipulations of the presence of the early colonizing

halophyte, *Batis maritima*, I examined whether this species facilitated secondary succession

in experimentally cleared patches in a mediterranean-type climate salt marsh (southern

California). Only 4% cover of *B. maritima* was present in the experimental plots in which *B.*

maritima was allowed to grow, yet these plots had significantly more cover of marsh matrix

vegetation, 27% compared to 14% in the treatment lacking *B. maritima*. Soil salinity

increased in all plots over the growing season (spring through fall), though this increase was

less in the *B. maritima* present (55 ± 4 ppt) than in *B. maritima* clipped (72 ppt $\pm$ 6)

treatment. The most abundant colonizers were *Salicornia pacifica* and *Arthrocnemum*

subterminale in both treatments. I found no evidence that *B. maritima* promoted particular

species as indicated by non-significant differences in species richness, diversity, evenness,

and the composition of recolonizing species between treatments. Most importantly,

facilitation was seen to promote recovery of salt-tolerant plants under severe soil salinities

typical of salt marshes exposed to mediterranean-climatic conditions.

INTRODUCTION

The Stress Gradient Hypothesis (SGH), originally described by Bertness and Callaway (1994), predicts an increase of facilitative interactions when abiotic stress is elevated, yet recent work questions the generality of this prediction under conditions of extreme abiotic stress (Brooker et al. 2008, Maestre et al. 2009). Under moderately elevated stress (relative to low levels) the benefits of neighbors can outweigh the negative effects of competition if the association ameliorates stressful conditions (reviewed in Stachowicz 2001, Bruno et al. 2003, Brooker et al. 2008, Maestre et al. 2009, Holmgren and Scheffer 2010). Numerous studies have documented species-species interactions shifting from competitive to facilitative when abiotic stress levels are elevated (i.e. Callaway 1994, Bertness and Leonard 1997, Leslie 2005, Pennings et al. 2005). However, recent research failed to find facilitation when abiotic stress is extremely high (Abbott and Hollenberg 1997, Tielborger and Kadmon 2000, Pennings et al. 2003, Maestre and Cortina 2004). In a recent review of the SGH, Holmgren and Scheffer (2010) suggested that facilitations may be less common and less important in habitats predictably characterized by extremely high levels of abiotic stressors because the resident species are adapted to the local conditions and can thrive without amelioration. If and when facilitation occurs in very stressful habitats needs further study.

Salt marsh plant communities are ideal to study the relationship between stress and facilitation because they are characterized by soil salinity gradients (Zedler 1982, Vince and Snow 1984, Bertness and Ellison 1987, Callaway et al. 1990, Alberti et al. 2010) that strongly influence the spatial arrangement of plant species (Pennings and Callaway 1992, Bertness and Pennings 2002, Greer and Stow 2003, Wetzel et al. 2004, Pennings et al. 2005)

and affect the direction of species interactions (Bertness 1991, Bertness and Shumway 1993, Pennings et al. 2005). Several studies have documented beneficial associations between tolerant and intolerant plant species in areas of the salt marsh with elevated soil salinities, though interactions between the same species are competitive or neutral in regions with lower salinity (Bertness 1991, Pennings et al. 2005). In this study, I examined whether facilitation occurs within a salt-tolerant plant community living in ultrahypersaline soils characteristic of salt marshes in mediterranean-type climates.

Stress-ameliorating facilitation may be of key importance during secondary succession in salt marshes. Secondary succession occurs following any disturbance such as wrack burial (Brewer et al. 1998), ice scouring (Ewanchuk and Bertness 2003), or attack by parasitic plants (Pennings and Callaway 1996) that opens relatively small bare patches in marsh vegetation. Disturbance-generated bare patches commonly occur in the northeastern United States (Brewer et al. 1998), and recovery rates depend on salinity regime (Crain et al. 2008). This phenomenon is less studied in west coast marshes and may be less common in southern California because lower latitude marshes do not experience winter die-offs and associated heavy accumulations of wrack (Pennings and Richards 1998). However, in especially stormy years thick mats of smothering wrack accumulated onto the salt marsh plain (pers. obs.), and Pennings and Callaway (1996) documented the frequent occurrence of patches created by mortality following attacks by parasitic plants. If vegetation is removed, resulting patches have higher soil salinities than the surrounding vegetated marsh as demonstrated in both east and west coast marshes (Bertness 1991, Shumway 1995, Whitcraft and Levin 2007). Higher salinities have been attributed to higher rates of evapotranspiration (Zedler 1982, Pennings

and Bertness 1999), which can hinder bare patch recovery (Bertness 1991, Bertness et al. 1992). However, recovery can be facilitated by plants that tolerate high soil salinities and act as nurse plants by providing shade, reducing evaporation and hence soils salinities, and speeding establishment of less tolerant species (Bertness and Shumway 1993, Callaway 1994). Whether facilitation of secondary succession of bare patches in ultrahypersaline conditions occurs has never been studied.

Salt marshes in mediterranean-type climates provide an ideal opportunity to expand our understanding of the relationship between facilitation and stress tolerance during secondary succession. Many acknowledge that regional climate can affect the frequency of facilitations (Bertness and Ewanchuk 2002, Pennings et al. 2003). Due to hotter climates, lower latitude marshes have strikingly higher soil salinities than salt marshes in the northeastern United States (Bertness and Pennings 2002) which is true in southern California salt marshes experiencing a mediterranean-type climate with hot, dry summers (Zedler 1982, Callaway et al. 1990). Callaway (1990) documented ultrahypersaline soils, 40-100 ppt under vegetation in the upper marsh which is substantially saltier than soils in the upper marsh of a New England salt marsh, 14-18ppt under vegetation (Bertness 1991). And, in general, warmer-climate marshes are composed of more salt tolerant plants (Kuhn and Zedler 1997, Pennings and Bertness 1999) that may not benefit from ameliorators. Indeed, Pennings et al. (2003) found facilitation rare amongst the salt-tolerant species in the warm climate of the southeastern United States. Yet, even salt-tolerant species are sensitive to salinity. Pennings and Richards (1998) found wrack deposition to facilitate growth of marsh vegetation in part due to moderation of salinity. In southern California, Zedler (1996) noted that tolerant marsh

plants establish more easily during brief reductions of extreme salinity following freshwater input. Therefore I predict that the presence of a salinity-reducing neighbor with weak competitive abilities may be beneficial even to the salt-tolerant inhabitants of the upper marsh in southern California.

I examined whether the presence of the early colonizing halophyte, *B. maritima,* promoted the initial phase of secondary succession in the upper zones of a hypersaline mediterranean-type salt marsh in California, USA. I hypothesized: **1.** following disturbance, *Batis maritima* facilitates recolonization of vegetation into bare patches of the upper marsh; **2**. facilitation by *Batis maritima* is associated with lower soil salinities; and **3**. *Batis maritima* disproportionately promotes particular species during recovery. To address these hypotheses, I manipulated the presence of *B.maritima* in artificially cleared plots and monitored regrowth rates, soil salinities, and species composition during vegetative recovery.

METHODS

Site and Species Description

The experiment was conducted at Mugu Lagoon, 87 km west of Los Angeles, CA, USA (Fig. 1). Located on the Naval Base Ventura County, Point Mugu, the salt marsh is 597 hectares, relatively large compared to other southern California salt marshes (Onuf 1987). The experiment took place near the upper limit of the fully vegetated marsh (Fig. 1), or high *Salicornia* zone (sensu Pennings and Callaway 1992), within the tidal reach of high spring tides with inundation at ≈ 5 days/mo (pers. obs.). Observed tidal flooding agreed with that observed by Callaway (1990) in a similarly vegetated zone of a nearby marsh.

The subshrub, *Frankenia salina* and the succulent *Salicornia pacifica* were the spatially dominant species of the marsh matrix vegetation at this elevation. *Batis maritima* (Bataceae) was also present in this zone. *B. maritima* is a decumbent (with stems lying on the ground), salt-tolerant succulent found in mid and high intertidal zones throughout its range (Lonard et al. 2011) and common to salt marshes of the area (Zedler 1982). As an early colonizing species (Milbrandt and Tinsley 2006, Lonard et al. 2011), *B. maritima* quickly expands into open areas (Zedler 1982, Pennings and Richards 1998).

To evaluate whether there are facilitative effects of *B. maritima* on the early phase of secondary succession, I conducted an experiment that varied regrowth of *B. maritima* into cleared plots. I monitored the respective rates of revegetation during the growing season from April 2008 to August 2008. Experimental plots with naturally occurring *B. maritima* were randomly chosen using a table of random compass headings and numbers of walked steps. No plots were closer to each other than 2m and maximum distance between neighboring plots was 10m. A circular ring approximately $0.25m^2$ was placed on each plot and percent cover of plant species within the ring was measured using the point-intercept method (rectangular quadrat over a circular area, 43 points $\pm$ 2 SE). To determine if there were differences in pre-experiment species composition, I used estimates of percent cover prior to clearing to calculate the proportion each species comprised of the total vegetation. A MANOVA evaluated if proportional species composition prior to experimental clearing differed between the *B. maritima* present and *B. maritima* clipped treatments.

From each plot, all aboveground and near-surface (depth of 1-2cm) belowground

vegetation was gently removed by hand or with a hand shovel. Four markers were placed

around each perimeter to designate the original area cleared. Five cleared patches were

randomly assigned to each of 2 treatments: *B. maritima* permitted to recolonize the

cleared plot (*B. maritima* present) and *B. maritima* clipped monthly to prevent *B.*

maritima recolonization (*B. maritima* clipped). I monitored revegetation rates in plots

with digital analysis of photos using NIH ImageJ software. A level, overhead photo was

taken of each plot at the beginning and end of the growing season. The regrowth rate in

each plot was calculated by totaling the percent cover of each matrix species present,

excluding the manipulated *B. maritima*, at the final time point. The difference in the

regrowth rates between treatments was statistically analyzed using a one-sided Student's

t-test since I expected faster rates of regrowth when *B. maritima* was present.

To quantify pore water salinity, soil cores (5cm deep and 2cm in diameter) were collected

near the center of the plot on initial and final dates. Soil samples were stored in sealed

plastic bags, put on ice in a cooler during transportation to a lab, and placed in a freezer

until processed. Frozen soils were weighed, dried in a drying oven, reweighed to

determine water content, and ground to a fine powder with a mortar and pestle. Soil

subsamples (5g) were placed in a beaker with 20ml of distilled deionized water, stirred,

and allowed to extract for 30 minutes. Salinity of the supernatant was measured with a

refractometer and original pore water salinity calculated for the initial amount of water

present in the core. Because soil salinity at the end of the growing season is highly

dependent on initial soil salinity we calculated the difference in soil salinity in each

replicate and employed a one-sided t-test to determine whether the increase in soil

salinity differed between the *B. maritima* present and *B. maritima* clipped treatments.

Final total soil salinities of both treatments are also presented.

To evaluate if the presence of *B. maritima* altered the pattern of recovery by matrix

vegetation, I determined whether proportional species composition differed between the

two treatments at the end of the experiment. I calculated the proportion of total

vegetation, not including *B. maritima*, represented by each species in each treatment

through image analysis (see above) and conducted a MANOVA to detect any differences

between treatments. Additionally, excluding *B. maritima*, I calculated species richness,

Shannon's diversity index (H), and species evenness on the final date. For each measure,

I examined treatment differences by Wilcoxon rank-sum tests because the data did not fit

the assumptions of a t-test.

RESULTS

Prior to clearing, *F. salina* and *S. pacifica* dominated the plots, making up 73% of all the

vegetation (Fig.2). Initial species composition did not differ between treatments (p =

0.70, MANOVA). Overall mean soil salinity at the onset of the experiment was 59 ppt ±

5 (±SE) and did not differ significantly between treatments (p = 0.82, two-sided t-test).

The presence of *B. maritima* promoted growth of vegetation (Fig. 3). In plots with *B.*

maritima, percent cover by matrix species was almost twice that in the *B. maritima*

clipped plots (Fig. 3a). An additional 4% ± 1.3% (± SE) of the plot in the *B. maritima*

present plots was covered by *B. maritima* (Fig. 3b). None of the encroaching *B. maritima* stems were rooted in the plots, rather they were decumbent on bare soil. In plots of both treatments, almost all plant cover appeared to result from local vegetative growth. Only *Cressa truxillensis*, accounting for 1.5% ± 1% (±SE) of the final vegetation, appeared to grow from seeds.

Increases in soil salinity were lower when *B. maritima* was present (Fig.4). Over the course of the season, soils became saltier under both treatments, 113 ± 7 ppt (±SE) for *B. maritima* present and 132 ± 10 ppt (±SE) for *B. maritima* clipped at final sampling. In *B. maritima* clipped plots, the increase in soil salinity over the course of the experiment was 30% higher than in plots with *B. maritima* present (Fig. 4).

I did not find evidence that the presence of *B. maritima* promoted particular species (Fig.5). Species composition did not differ significantly between treatments ($p = 0.93$ MANOVA). *S. pacifica* and *A. subterminale* were the most and second most common species for both treatments at the season end sampling. Species richness ($p = 0.41$), Shannon's Diversity Index (H) ($p = 0.92$), or evenness ($p = 0.92$) also did not differ significantly between treatments.

DISCUSSION

Facilitation was a prominent mechanism accelerating secondary succession in this extremely hypersaline marsh. The presence of *B. maritima* promoted more rapid recolonization of plant species, presumably by reducing soil salinities in the experimental

plots. Two studies in the northeastern United States demonstrated similar facilitation in the process of bare patch closure (Bertness 1991, Bertness and Shumway 1993). In the upper marsh, Bertness and Shumway (1993) reported bare patch closure rates in the presence of facilitating neighbors of approximately 50% cover after two growing seasons, which is similar to the 31% cover I observed after one growing season with *B. maritima*. Although recovery rates were comparable, salt marshes in the northeast experience a milder and cooler climate. In these marshes there is less evaporation from soils and therefore far less saline soils, 30 ppt in bare patches (Bertness 1991, Bertness et al. 1992), than I observed in the upper marsh at Mugu Lagoon. While recent empirical findings (Pennings et al. 2003) and expansions of the Stress Gradient Hypothesis indicate that extremely high levels of stressors should produce less and weaker facilitations in stress-tolerant communities (Brooker et al. 2008, Holmgren and Scheffer 2010), my experiment demonstrated that salinity stress-induced facilitation can be an important process during secondary succession within the plant communities of mediterranean climate marshes.

A small amount of *B. maritima* played a very effective role in facilitating the early phase of secondary succession. Only 4% of the plot was covered by *B. maritima* at final sampling, yet more matrix vegetation cover and lower soil salinities were found in these plots. In contrast, during secondary succession in the northeast, the facilitator species *Distichlis spicata* covered more than 50% of the plot in the first year of recovery (Bertness 1991). Mechanisms that have been posed in such facilitations include sequestering of salts and shade provision (Bertness et al. 1992). In my study, biological compartmentalizing of salt ions was unlikely since *B. maritima* was not rooted in the

cleared plots. Shade provision, which has been demonstrated elsewhere (Bertness et al.
1992, Whitcraft and Levin 2007), is a more likely means of lowering soil salinities.
However, since *B. maritima* does not appear to cast shade broadly (Pennings and
Richards 1998, pers. obs.) the effect of *B. maritima* on soil salinity is probably indirect.
While the dense, but small prostrate mats appeared to heavily shade the soils directly
underneath, reducing salinity by 66 ppt directly below *B. maritima* in other locations
(Bryson, in prep), this highly localized salinity reduction would not be detected by the
salinity sampling protocol employed in this study. An alternative explanation is that
these extremely local changes in soil salinity permitted faster growth of the larger, shade-
casting plants like *Salicornia pacifica* that can reduce light at the soil surface by 85% (per
Whitcraft and Levin 2007). Pennings and Bertness (1999) posited that a feedback exists
between soil salinity and matrix vegetation in warm climates, via shading, that reduces
soil salinities and further enables the growth and survival of vegetation. During
secondary succession, *B. maritima* may trigger the development of this feedback.

The presence of *B. maritima* did not appear to promote particular species
disproportionately; rather it appeared that the locally resident species encroached faster
when *B. maritima* was present. The vast majority of revegetation by matrix species
resulted from vegetative growth, mostly through observable encroachment of
aboveground vegetation from outside the cleared plot (pers. obs.). Most plant growth in
hypersaline zones of southern California marshes is vegetative (reviewed in Zedler et al.
2003). Hypersaline soils substantially reduce seedling germination (Noe and Zedler
2000) and survival (Zedler et al. 2003). In this early phase of recovery, it appears that *B.*

maritima promoted vegetative expansion of local residents. I expect, then, that later successional phases will approach compositions similar to the immediately local community.

Specific features of *B. maritima* may enable facilitation at higher soil salinities than other benefactor species. The nature of the particular species and type of stress may influence when facilitation is functional in highly stressful habitats (Michalet et al. 2006, Maestre et al. 2009). Clonally integrated species, like *B. maritima*, are those that expand into new territory with runners physically connected to rooted adults. Ideal for early colonizers, this morphology allows runners to share water with physically connected portions in less extreme habitats while invading harsh, exposed soils (Shumway 1995, Pennings and Callaway 2000). Also, as a decumbent species, *B. maritima* is likely a poor competitor for light. Therefore the cost to benefit ratio of associating with *B. maritima* may be low, and so even salt tolerant species like *S. pacifica* and *A. subterminale* (Pennings and Callaway 1992, Kuhn and Zedler 1997) benefit during secondary succession. Two other studies documented facilitations in warm climate marshes (Callaway 1994, Pennings et al. 2003) though Pennings et al. (2003) found competition far more common. However, in both these studies the beneficiary species were relatively salt-intolerant. The properties of *B. maritima* appear to expand facilitation to tolerant species. While facilitation may be less common in highly physically-stressed regimes, a well-suited benefactor can facilitate even highly stress-tolerant species.

Photo courtesy of the US Navy

Fig. 1 Location and close-up of Mugu Lagoon in southern California. Experiment site in the upper marsh indicated with oval and arrow.
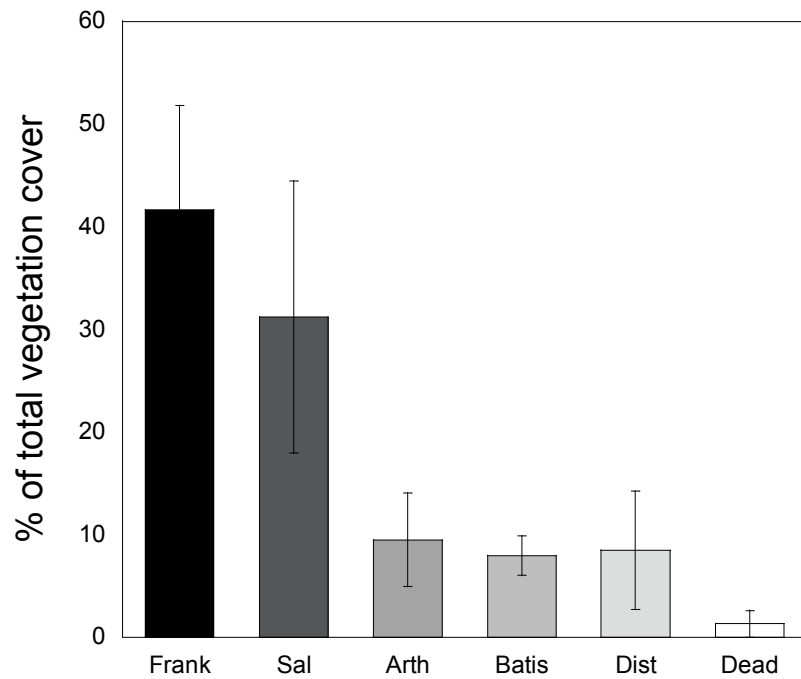
Fig. 2. Mean percent of total vegetation cover of each species present prior to clearing. Species abbreviations are Frank (*Frankenia salina*), Sal (*Salicornia pacifica*), Arth, (*Arthrocnemum subterminale*), Batis (*Batis maritima*), Dist (*Distichlis littoralis*), and Dead (combined dead species). Bars are means ± SE.
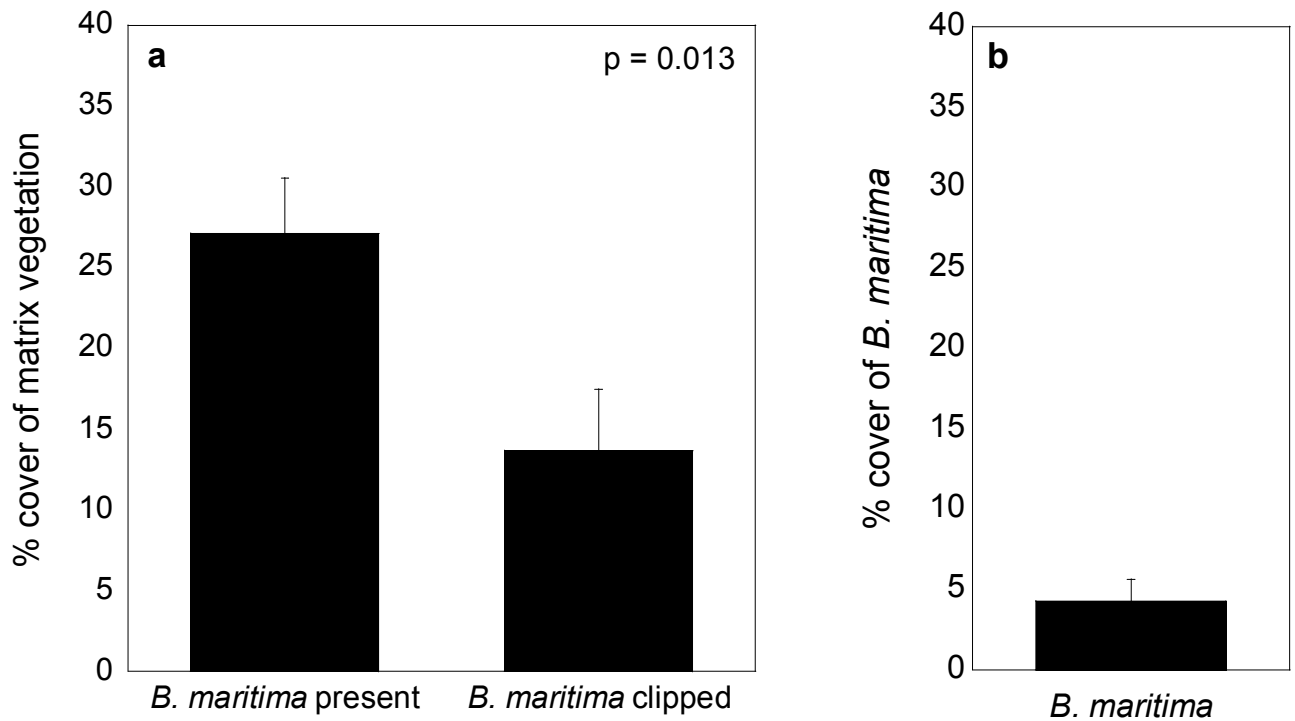
Fig. 3 Percent cover of vegetation at final sampling for **a**. matrix vegetation, not including *B.maritima* and **b**. *B.maritima* alone. Reported p-values from a t-test. Bars are means ± SE.
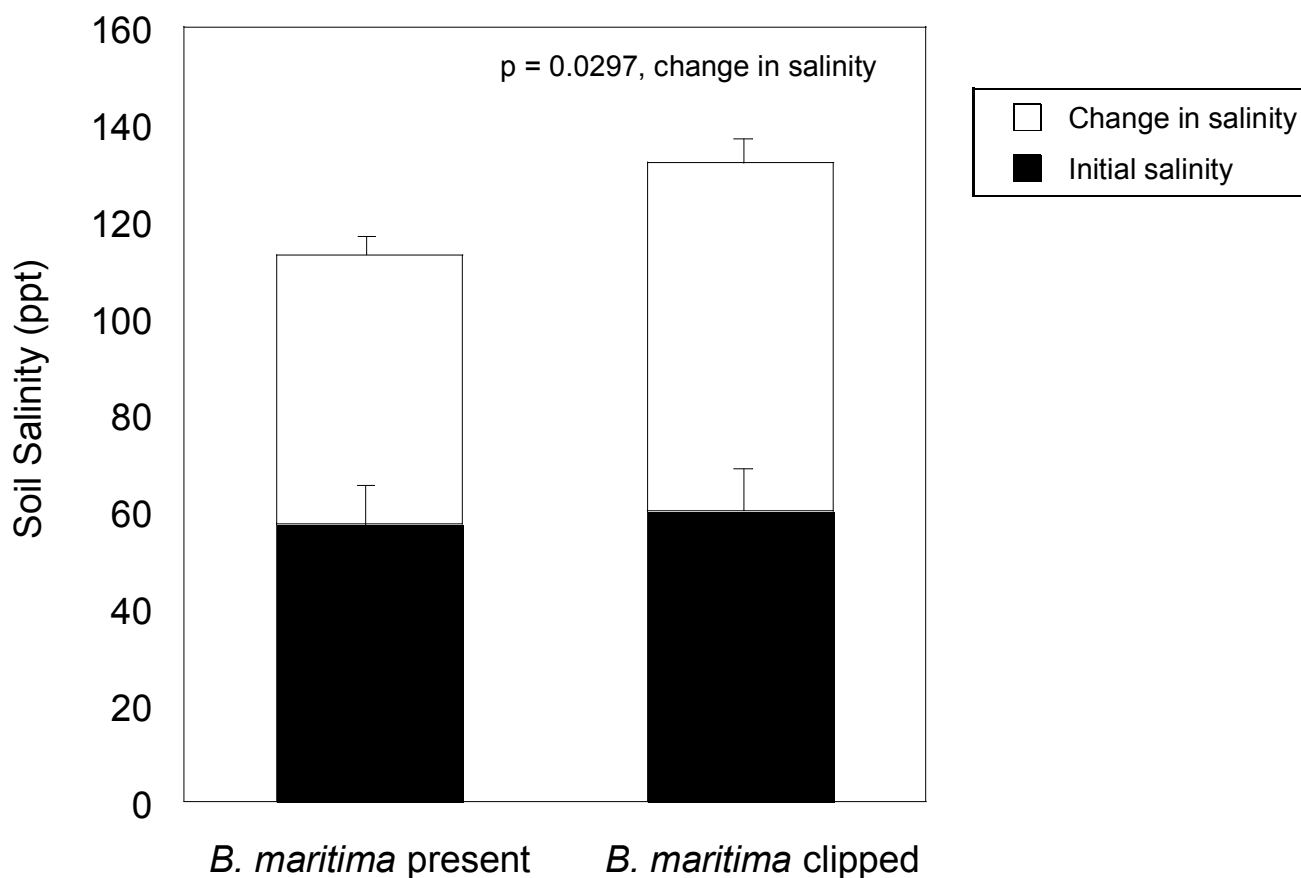
Fig. 4. Soil salinity differences between *B. maritima* present and *B. maritima* clipped treatments. Black bars are initial salinities. White bars stacked on top initial salinities are change in salinity from the initial and final sampling . Reported p-value from a t-test on change in salinity between treatments. Bars are means ± SE.
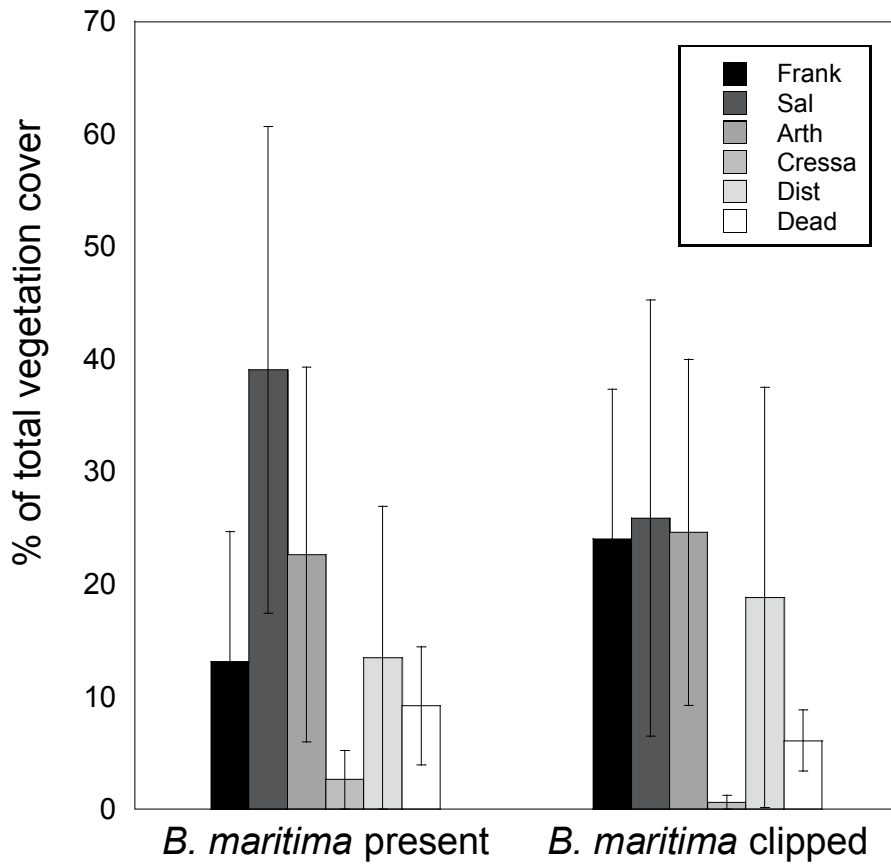
Fig. 5 Final species composition. No differences in composition between treatments (p = 0.93, MANOVA). Species abbreviations as in Fig. 2, additionally Cressa (*Cressa truxillensis*). Bars are means ± SE.

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CONCLUSIONS OF THE DISSERTATION

I found that positive species-species interactions occurred in response to both biotic (herbivory) and abiotic (salinity) factors. Associational resistances and facilitations can protect primary space holders of the community (Stachowicz 2001). In a kelp forest, a common epifaunal invertebrate, *Membranipora membranacea*, conferred associational resistance to herbivory by mesograzers. In a salt marsh, I found facilitation to ameliorate salinity stress between plant species during secondary succession. Both of these conditional positive interactions may contribute to community persistence in the presence of stress.

The two interactions differed in the strength of their effects on local primary producers. The associational resistance to mesograzer herbivory reduced grazing damage on giant kelp. However, with fast growth rates (Reed et al. 2008), kelp can probably tolerate moderate herbivory pressure from mesograzers. Therefore, even though the presence of the encrusting bryozoan reduced grazing damage, the benefit conferred to kelp in terms of increased biomass is probably quite small. In contrast, I observed almost a doubling of matrix species percent cover when the facilitator, *Batis maritima*, was present. This effect reflected a substantial increase in plant biomass whereas the effect in the kelp forest was much more modest. Whether associational resistance tends to be weaker relative to facilitation in physically stressful habitats is unknown. This trend, if it exists, would depend on, in part, whether the negative consequences of biotic stressors tend to be less than that of physical stressors, and on the ability of neighbors to ameliorate each type of stress. This topic would be an interesting area of future research.

The results of my studies also suggested that the temporal consistency of the interactions differ. Kelp canopies contain a number of grazing species (Jones 1971, Coyer 1984, Sala and Graham 2002) whose feeding behaviors are influenced differently by *Membranipora membranacea* (Bernstein and Jung 1979, Wahl and Hay 1995, Bryson, Ch.1). Therefore whether *Membranipora* promotes or deters grazing is likely to change in space and time. However, previous research in higher latitude salt marshes found that early salt-tolerant colonizers promote revegetation by matrix species (Bertness 1991, Bertness and Shumway 1993), similar to the findings presented here. The temporal pattern of recovery described as disturbance, elevation of soil salinities, colonization by tolerant species, amelioration of soil salinity, followed by facilitation of the matrix, was consistently observed in these studies. This commonality between systems is despite recent empirical evidence that facilitation is less common in high salinity regimes with salt-tolerant species (Pennings et al. 2003) which occur in southern California salt marshes (Zedler 1982). Though seasonal (Callaway et al. 1990) and inter-annual (Zedler 1983) variation in soil salinities do exist and may influence the effectiveness of this process, I predict that facilitation during secondary succession of the salt marsh to be much more of a general occurrence than the associational resistance to mesograzer herbivory I documented in a kelp canopy.

I propose that the difference in the temporal consistency between the two positive interactions reported here is the result of differences in the predictability of the stresses. Algal herbivores and the level of grazing damage they inflict vary greatly in time and space (Lubchenco and Gaines 1981) as do the abundances of epibionts (Wahl 1989). However, vascular plants regularly perform less optimally in saline conditions (Zhu 2001) and even salt marsh plants are

extremely sensitive to changes in soil salinity (Zedler 1996). Thus, plants living in saline conditions, even within their tolerance range, may benefit from amelioration of soils following disturbance. Thus, I speculate that neighbors that reduce salinity stress with minimal competitive effects will be beneficial whereas the benefits of a species-dependent deterrent neighbor will be transitory.

Overall I found two sets of positive interactions in two coastal communities, one biotic and one abiotic, but the effects and consistency of each interaction differed between the two systems probably due to the predictability of the stressors.

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