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Linking ecology, restoration science, and mitigation policy to guide management of rocky intertidal habitats affected by oil spills

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LINKING ECOLOGY, RESTORATION SCIENCE, AND MITIGATION POLICY TO GUIDE MANAGEMENT OF ROCKY INTERTIDAL HABITATS AFFECTED BY OIL SPILLS

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in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Kristin L. de Nesnera

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Abstract

Linking ecology, restoration science, and mitigation policy to guide management of rocky intertidal habitats affected by oil spills

by

Kristin L. de Nesnera

Solving the environmental problems created by the increasing impact of humans on our planet will require a collaborative effort between scientists, practitioners, and policymakers. In this dissertation, I provide an example of how ecologists can contribute to and benefit from environmental problem solving. I focus on rocky intertidal habitats along the coast of central California (USA), which have high levels of biological diversity and provide a rich environment for education, research, and recreation. These habitats are negatively affected by a number of anthropogenic activities and, as a result, there is a growing interest in restoration strategies, particularly for addressing the impacts of oil spills.

In the following chapters, I explore connections between ecological concepts, restoration science, and mitigation policy to guide management of rocky intertidal habitats. In my first data chapter, I experimentally test the success and benefits of using adult mussel transplants to restore mussel bed communities following disturbance events. Results show mussel transplants provide restoration benefits in areas where recovery is slow but that these benefits are limited by local mussel recruitment dynamics and likely many other environmental and biological characteristics. In my second data chapter, I examine the importance of positive species interactions (i.e. facilitation) during the mussel recruitment stage. These interactions have not been well-described and may provide important insights for mussel bed restoration. I use a combination of field surveys and experiments to evaluate how environmental stress, mussel ontogeny, and organismal movement interact to determine the importance of facilitation during mussel recruitment. I show these interactions shift from neutral to positive with increasing tidal elevation and that ontogenetic shifts in recruit survival and growth modify interactions with different facilitator species. This suggests mussels may move between multiple facilitators throughout the juvenile stage. In the third data chapter, I examine and challenge the mitigation policy and science guiding compensatory restoration of rocky intertidal habitats following oil spills. I do this by reviewing Natural Resource Damage Assessment (NRDA) cases for oil spills in California. I summarize NRDA documentation and show, while tools for injury assessment in rocky intertidal habitats have increased in recent decades, there remain few proposed restoration projects to compensate the public for these injuries. I suggest a more cooperative and flexible approach will be needed to advance compensatory restoration in marine habitats. Finally, I conclude by discussing the key insights from this work and future research directions for rocky intertidal restoration and management.

This body of work is dedicated to:

My grandparents, Tom and Darlene Mahalak,

who fostered my early curiosity and fascination with coastal biology.

-and-

My parents, Jeff and Margie Mahalak,

whose commitment and sacrifice for their education, and my own, has been a constant source of inspiration.

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Introduction

Broad context

Our planet is facing unprecedented environmental change, species loss, and habitat degradation. Solving these environmental problems will require a synergistic effort from scientists, practitioners and policymakers. But historically, information flow between these entities has been poor (Sutherland et al. 2004).

Ecologists are uniquely positioned to help tackle environmental problems as their understanding of how organisms interact with each other and the environment have direct applications to the central goal of resource managers and policymakers; to protect and restore natural resources in a changing environment. For example, studies of ecological succession provide insight into the dynamic processes that regulate changes in species composition and associated environments over time and generate models of community assembly that can be emulated for restoration practice (Choi 2004, Walker et al. 2007). Ecologists also benefit from being involved in environmental problem solving as conservation and restoration projects provide an opportunity to test ideas, reveal gaps in our basic understanding of natural systems and motivate new research questions (Bradshaw 1983, Palmer et al. 1997).

Despite all sides recognizing the benefits of bridging connections between ecology, applied environmental science, and policy, differences in goals, culture, and communication continue to be barriers to progress (Briggs 2006, Burbidge et al.

2011). In the next three chapters, I provide an example of how linking ecological theory, restoration science, and environmental mitigation policy can inform the management of an ecological system and give rise to novel insights into ecology. I do this focusing on rocky intertidal habitats affected by oil spills. Rocky intertidal habitats are found worldwide and are particularly abundant along the west coast of North America. These habitats have high levels of biological diversity and, due to their accessibility relative to other marine habitats, provide a rich environment for education, research, and recreation. However, the location of these habitats at the coastal interface exposes them to a number of human-based disturbances.

Oil spills, marine debris, subsistence harvesting, and visitation-based disturbances, like trampling, all threaten the health and biodiversity of rocky intertidal ecosystems (Murray et al, 1999; Paine et al., 1996; Smith et al., 2008; Suchanek, 1993). But despite documented widespread and persistent human impacts on rocky shores (Thompson et al. 2002), restoration in this system remains relatively unexplored. This is in part because this system is seen as resilient and capable of recovering naturally, since most populations can be replenished by propagules from outside a degraded system (Hawkins et al. 1999). However, there is growing interest in developing restoration strategies to address regions where recovery is slow (Ambrose and Smith 2005, Whitaker et al. 2010).

In addition, restoration projects have been used for the past two decades to compensate the public for the loss of rocky intertidal resources following oil spills.

Oil spills and subsequent clean-up methods result in significant mortality of rocky intertidal species, the consequences of which are felt at the community and ecosystem level (Paine et al. 1996, Peterson 2001). While oil spills are not the most common or even the most damaging human disturbance event that occur in rocky intertidal habitats, they are certainly the most visible and because of legislation like the Oil Pollution Act, there is a legal mandate to address oil spill impacts.

The motivation for this work is linked to the Torch/Platform Irene Oil Spill that occurred off the coast of California, near Point Arguello, when an undersea pipeline ruptured in September 1997. While rocky intertidal injury levels following this spill were not greater than 10%, an effort to address the low level of injury was deemed necessary and was seen as an opportunity to conduct research on restoration strategies that could benefit rocky intertidal habitats in future spills. Given the importance of the mussel, *Mytilus californianus*, as a foundation species in California's rocky intertidal (Lohse 1993a, 1993b) and slow rates of mussel bed recovery in the region (Kinnetic Laboratories Inc. 1992, Conway-Cranos 2012), it was decided that injuries to rocky intertidal habitats from the spill would be addressed by a restoration project that developed a strategy to restore mussel cover. This project along with subsequent explorations of ecological concepts and policies relevant to restoring rocky intertidal habitats affected by oil spills, make up the body of research presented in the following chapters.

Dissertation outline

In **Chapter 1**, I experimentally test the success and benefits of using adult mussel transplants to restore mussel bed communities in central California following disturbance events. This strategy incorporates and evaluates ideas from the concept of ecosystem engineering in ecology and measures the intra- and interspecific positive effects of *M. californianus* transplants to determine the ability of this approach to accelerate the recovery of mussel beds and the species they facilitate. I show mussel transplants result in long-lasting increases in mussel presence at study sites and serve as a point of attraction for mussel recruits. However, I also show the presence of mussel transplants does not result in mussel bed expansion and has no effect on the recovery of an associated algal and invertebrate community. These results suggest mussel transplants will benefit some areas and some restoration goals but not all. They also underscore the importance of continued research efforts to identify where and when ecosystem engineers will and will not be important.

Motivated by the restoration goals in Chapter 1, **Chapter 2** takes a step back to address a critical knowledge gap in the current understanding of mussel ecology and focuses on the importance of positive species interactions (i.e. facilitation) during the recruitment stage. Specifically, I incorporate recent hypotheses and ideas related to facilitation in ecological communities to determine how environmental stress, ontogeny, and animal movement influence interactions between mussel recruits and habitat-forming neighbors. I show these interactions shift from neutral to positive with increasing tidal elevation in the mussel zone and that ontogenetic shifts in recruit survival and growth modify interactions with different facilitator species. I then discuss the possibility that recruit movement between different facilitators is driven by these ontogenetic shifts. These results add to a growing body of literature on the role of positive interactions in nature and suggest organismal movement may be an important factor to incorporate in future facilitation research.

In **Chapter 3**, I return to the original motivation for this work and examine and challenge the mitigation policy and science guiding compensatory restoration of rocky intertidal habitats following oil spills. I explore six Natural Resource Damage Assessment (NRDA) cases following oil spills that affected rocky shore habitats in California. I summarize the documentation related to these cases and show, while tools and strategies for injury assessment in marine habitats have increased in recent decades, there remain few restoration strategies proposed to address these injuries. I suggest this is a result of limited restoration science in rocky intertidal habitats and propose future NRDA restoration projects be designed and monitored as long-term experiments to address some of the more pressing research questions. I also discuss how the current policy guiding NRDA project selection may exclude projects that could be more effective at addressing rocky intertidal injuries. This suggests a more flexible approach to mitigation project selection may benefit compensatory restoration efforts in marine habitats.

Chapter 1

The role of mussels in the recovery of rocky intertidal communities: implications for the use of ecosystem engineers in restoration strategies

Abstract

The positive ecological effects of many ecosystem engineers make them potential target species for restoration efforts. However, there are few experimental tests to determine where and under what conditions ecosystem engineers will predictably benefit restoration. This study focuses on *Mytilus californianus*, a dominant engineer in rocky intertidal communities along the west coast of North America that has intra- and interspecific positive effects that may benefit restoration approaches in regions where recovery is slow following disturbance events. In a four-year experimental mussel restoration project we evaluated whether adult mussel transplants would increase the presence of this dominant ecosystem engineer and speed up the recovery of mussel beds and an associated invertebrate and algal community. To do this, we set up control plots and experimental disturbance plots with and without mussel transplants at two sites along the central California coast. We measured transplant loss and mussel cover to track the presence of mussel engineers in each plot. We also used measures of mussel cover and recruitment to determine if adult mussel transplants acted as a point of attraction for conspecific recruits, thereby accelerating mussel bed recovery. Finally, we compared community composition in control plots to treatment plots to determine if recovery of the associated algal and invertebrate community was faster in the presence of mussel engineers. We found transplants resulted in increased mussel presence in disturbed areas for the entire four year study period, suggesting this strategy may be effective in areas where mussel recovery is slow. We also found evidence that mussel transplants where a point of attraction for mussel recruits. However, we saw no expansion of mussel patches, likely because of transplant loss and low recruitment rates. We also did not see an effect of mussel transplants on the recovery of the associated algal and invertebrate community, as similar communities recovered in plots regardless of mussel presence. These results suggest mussel engineers will not benefit all restoration goals. While ecologists have focused on determining where engineers are ecologically important these results emphasize the need to also identify where they are not in order to optimize restoration success.

Introduction

Single species can play a critical role in structuring the communities they inhabit. For example, keystone predators affect the composition of ecological communities by controlling the abundance of otherwise dominant prey species (Paine 1966, Estes et al. 1978). Likewise, ecosystem engineers can have a profound effect (positive or negative) on populations, communities, and ecosystems by maintaining, modifying, or creating habitat (Jones et al. 1994, Jones and Lawton 1997, Wright et al. 2002, Wright and Jones 2004). The habitat created by ecosystem engineers can be autogenic, a result of their own physical structure (e.g. forests and coral reefs), or allogenic, a result of transforming other living or non-living structures (e.g. beavers) (Jones et al. 1994). This structural change affects other species by either directly or indirectly altering abiotic and/or biotic properties of the system (Jones and Lawton 1997, Jones et al. 2010).

The ability of ecosystem engineers to regulate the abiotic environment has prompted researchers to recommend incorporating them in restoration efforts (Crain and Bertness 2006, Byers et al. 2006, Halpern et al. 2007). This concept is already successful in terrestrial environments where restoration approaches utilize nurse plants, which buffer closely associated plant seedlings from environmental stress (Gómez-Aparicio and Zamora 2004, Padilla and Pugnaire 2006, Gómez-Aparicio 2009). Many seagrass and salt marsh restoration projects also target habitat-forming species; although, they often are not designed to leverage the positive engineering effects of these species, instead focusing on mitigating competitive interactions. (Halpern et al. 2007, Silliman et al. 2015). However, recent experimental work in salt marshes has shown restoration is enhanced when positive interactions are incorporated into project design, which suggests this approach should be integrated more broadly into coastal restoration projects (Silliman et al. 2015).

Ecosystem engineers can aid restoration efforts through both intra- and interspecific positive effects (Stachowicz 2001, Halpern et al. 2007). For example, for many habitat-forming species, like seagrass, marsh plants, mangroves, corals, and shellfish, neighboring individuals buffer each other from harsh environmental conditions (Bertness and Leonard 1997, Bruno and Bertness 2001, Stachowicz 2001 and refs within). These interactions benefit habitat restoration approaches when recovery of a habitat forming engineer is slow or limited by dispersal (Zedler and Kercher 2005, Silliman et al. 2015, van Katwijk et al. 2016). Restoration efforts in aquatic environments can further benefit from positive intraspecific interactions when propagules of ecosystem engineers respond to conspecific cues. In this case, the availability of adult habitat can promote the recovery of a species, through a recruitment cascade, where adults serve as point of attraction for new recruits that then serve as a point of attraction for subsequent recruits, resulting in the rapid expansion of the population (Halpern et al. 2007). Interspecific positive effects of ecosystem engineers can also be leveraged to restore ecological communities. For example, when community recovery is likely to be slow, the use of engineering species can speed up natural successional dynamics (Walker et al. 2007). And in cases where degradation has resulted in a persistent alternate state, ecosystem engineers can help lower the threshold necessary to move that system back towards a more desirable condition (Byers et al. 2006).

However, engineers can also have negative effects on species diversity and abundance, particularly at small scales (Callaway and Walker 1997, Jones and Lawton 1997); and a growing body of literature suggests the importance of positive interactions (relative to negative interactions) vary in both space and time and are dependent on a number of environmental and biological factors (Crain and Bertness 2006, Hastings et al. 2007). Thus, predicting when and where the use of ecosystem engineers will benefit restoration approaches remains a key challenge. Ecological theory (i.e. the stress gradient hypothesis) suggests they will have significant positive effects where environmental stress is high, either through ameliorating harsh abiotic conditions or providing refuge from consumer pressure (Bertness and Callaway 1994, Bertness and Leonard 1997, Bruno and Bertness 2001, Crain and Bertness 2006)). Individual characteristics, like size and age, and population level characteristics, such as density, cover, spatial arrangement, and complexity, may also influence the intra- and interspecific effects of engineers (Bruno and Bertness 2001). For example, studies indicate a certain threshold density of seagrass is necessary for beds to provide a predation refuge (Heck and Orth 1980, Fonseca et al. 1996). Experimental tests that uncover how and under what conditions engineers benefit ecological communities will greatly enhance the ability to successfully harness these effects for conservation and restoration purposes.

Here, we explore the role of the mussel *Mytilus californianus* as an ecosystem engineer in rocky intertidal habitats and its effect on the recovery of mussel bed communities. *Mytilus californianus* is an autogenic ecosystem engineer that creates three dimensional habitat by secreting byssal threads and forming dense aggregations along rocky shores of the west coast of North America. Mussel beds can have both intra- and interspecific positive effects by creating structural, abiotic and biotic change in the environment (Gutiérrez et al. 2003, Jones et al. 2010). Complex habitat formed by *M. californianus* has been shown to maintain community diversity and increase survival and recruitment of epifaunal species (Lohse 1993a, 1993b). Mussels in rocky habitats also support a diverse array of infaunal species that live in the interstitial spaces between shells (Tokeshi and Romero 1995, Borthagaray and Carranza 2007). Mussel aggregations increase survival of conspecifics by reducing predation and desiccation stress (Okamura 1986) and promoting byssal attachment by reducing water flow (Carrington et al. 2008). Mussel recruits also respond to conspecific settlement cues and are commonly found on byssal threads of adults, suggesting juveniles benefit from intraspecific associations (Bayne 1964, Paine 1974, Seed 1976, Petersen 1984a). However, *M. californianus* has also been shown to negatively affect neighboring species due to its superior ability to compete for space (Paine 1966, 1974). And while mussel aggregations increase individual mussel survival, dense aggregations have been shown to decrease mussel growth (van de Koppel et al. 2008).

The question we set out to explore was whether the balance of the positive and negative effects of *Mytilus californianus* would result in a net benefit to restoration efforts in California's rocky intertidal habitats. We focused in particular on the central/southern California region, which experiences high levels of human disturbance from visitation based impacts (i.e. trampling, bait collection, and recreational harvesting) and pollution events, like oil spills (Murray et al. 1999, Thompson et al. 2002, Ambrose and Smith 2005, Smith and Murray 2005). Disturbances in this region of California are more likely to have long-lasting effects on mussel beds (relative to regions in the northern extent of this mussel's range) due to low levels of larval recruitment (Connolly et al. 2001, Broitman et al. 2008) and recovery times that can exceed 20 years (Kinnetic Laboratories Inc. 1992, Conway-Cranos 2012). Thus, there is a growing interest in beginning to explore restoration approaches that reestablish habitat forming species and accelerate recovery in rocky intertidal habitats (Ambrose and Smith 2005, Torch/Platform Irene Trustee Council 2007, Whitaker et al. 2010).

In this study, we experimentally tested the efficacy and benefits of using adult mussel transplants to restore mussel bed communities in central California following disturbance events. To do this we set up control and experimental disturbance plots with and without mussel transplants at two sites in late 2009. We then measured transplant success, species percent cover, and mussel recruitment for a four year period to test whether the mussel transplant strategy would: (1) increase the representation of the dominant engineer (2) speed up mussel recovery and (3) speed up and/or positively alter the recovery trajectory of an associated algal and invertebrate community. We predicted, given the success of mussel transplantation in past ecological experiments (e.g. Navarrete and Menge 1996), that transplants would successfully attach and there would be persistent benefits to transplant presence due to slow mussel recovery in the region (i.e. disturbed areas without transplants would not fill in quickly with mussels). We also predicted adult mussels would serve as a point of attraction for new mussel recruits leading to mussel bed recovery through the expansion of transplant patches. Finally, we predicted, by altering abiotic conditions (e.g. reducing wave forcing and/or desiccation stress), mussel transplants would positively affect the recovery (i.e. increase similarity to a control state) of algal and invertebrate species that settle on and around mussel beds (hereafter referred to as the epibiotic community). While *M. californianus* is known to have positive effects on infauna (Lohse 1993a, Borthagaray and Carranza 2007), this study focused exclusively on epibionts in order to avoid using destructive sampling methods.

This experiment also explored the effect of transplant patchiness on community recovery by comparing plots with 100 mussel transplants grouped in either one or three patches (Fig. 1.1). Patchiness may affect the engineering role of mussels by altering their ability to mediate abiotic and biotic change in the environment (Jones et al. 2010, Silliman et al. 2015). We hypothesized that increased patchiness would either (a) strengthen the positive effects of *M. californianus* on recovery by creating more edge space for recruitment and attachment or (b) weaken these effects by reducing the ability of *M. californianus* to ameliorate wave, wind, or heat stress for associated species.

Methods

Study sites and experimental setup:

This study was conducted at two intertidal sites (Pothole and Occulto) located along the coastline of Vandenberg Air Force Base (Fig. 1.2). These sites were characterized by different abiotic and biotic conditions allowing the effects of mussel transplants on recovery rate to be evaluated in two different environments. Pothole (N 34.71483, W 120.60725) consists of gently sloping ridges of Monterey shale and experiences moderate to heavy wave action with a southwest coastal orientation (cbsurveys.ucsc.edu). Occulto (N 34.8812, W 120.63594) is composed of highly exposed benches made of conglomerate rock with a west/northwest orientation. Biologically, Pothole is more algal dominated with patchy mussel distribution throughout the middle intertidal zone. In contrast, Occulto is mussel dominated with 60-70% cover in the mid-intertidal zone. Experimental plots for this study were established at Pothole and Occulto in December 2009 and April 2010 respectively and were monitored through February 2014.

Each site contained four replicate blocks of four plot types, for a total of sixteen 50 x 50 cm plots per site. Plots were placed in natural spaces within the mussel bed in the mid intertidal zone. Plot types included a control plot that consisted of natural mussel bed and three treatment plots. Treatments plots were initially cleared of all visible biota using paint chisels and wire brushes. The three treatments included (1) a cleared plot with no mussel transplants (used to simulate a situation where a disturbance occurred and no restoration action was taken), (2) a plot with one large mussel patch containing 100 transplanted mussels, and (3) a plot containing 100 transplanted mussels divided into three small mussel patches. The latter two treatments were used to determine if the spatial configuration (i.e. patchiness) of mussel transplants had any effect on plot recovery (Fig. 1.1).

Mussel transplants were collected from Ellwood Pier, Santa Barbara, CA, cleared of epibionts, and notched with a metal file to allow for easy identification and growth measurements, prior to placement in experimental plots. To promote attachment, mussels were placed into cleared plots with their byssal organ oriented downward, and then secured with vexar mesh. Vexar was loosened after one month to allow mussels to reorient, and after two months, the vexar was completely removed.

Evaluating transplant success

The success of transplanted mussels was monitored for one year by counting the number of remaining live and dead mussel transplants in each plot every month. After one year, we stopped counting transplants because transplant loss appeared to be levelling off and it was becoming more difficult to identify the notch on transplanted mussels as their shells weathered and became covered in epibionts. For the duration of the study, decreases in mussel transplants were evaluated using mussel cover from percent cover estimates.

Estimating changes in mussel cover due to recruitment

Estimating the contribution of mussel recruitment to mussel cover during this study was challenging because we were not able to simply count the number of new mussels that entered each plot. This was because, as previously mentioned, mussel transplants became difficult to identify as their shells became weathered and covered in epibionts and new mussel recruits were often difficult to accurately count because they were between interstitial spaces of transplant mussels. Further, we often observed pulses of new mussel recruits in plots that did not persist. Since ultimately we were interested in whether mussel transplants facilitated recruits that contributed to additional mussel cover, not the number of new mussels in a plot at a given time, we used mussel cover rather than mussel count as our overall metric.

However, to determine if the recruitment of new mussels contributed to any change in mussel cover in transplant plots, it was necessary to first account for the loss and growth of transplanted mussels, since all three factors – recruitment, loss, and growth – affect overall percent cover. To do this we had to make several assumptions. First, we assumed the number of mussel transplants remaining in plots, when they were last counted at one year, stayed relatively the same for the duration of the study. We determined this was a reasonable assumption, since transplant loss appeared to level off around one year and even if some plots lost more transplants this only results in an underestimate not an overestimate of recruitment. We also assumed, since mussel cover was consistently around 30% for plots with 100 transplants at the beginning of the study, percent cover of remaining mussel transplants could be accurately estimated by multiplying the number of transplants remaining by 0.3. Then, since we were unable to get direct measures of transplant growth using the original shell notches, we measured the shell length of 20 random mussels in each transplant plot at the end of the study. We assumed these mussels were original transplants based on their appearance and size. We then compared the size range of these mussels to the size range of mussel transplants at the beginning of the study to estimate an average growth factor (e.g. if mussels on average doubled in length the growth factor would be estimated as two). This calculation likely overestimates the amount of percent cover change due to transplant growth but again results in an underestimate, not an overestimate of mussel cover due to recruitment.

Finally, percent mussel cover at the end of the study that was not accounted for by the loss and growth of the original mussel transplants was assumed to be due to new mussel recruits in the plot. This conservative estimate was calculated using the following equation:

$$\begin{aligned}&\%\ \text{mussel cover due to recruitment}\\ &\qquad = \%\ \text{mussel cover} - [\#\ \text{transplants remaining} * 0.3 * \text{growth factor}]\end{aligned}$$

For the purpose of this analysis, we only included transplant plots where transplantation was deemed successful (see Results).

To estimate site-wide mussel recruitment, we placed eight mussel recruitment collectors or Tuffys (S.O.S. Tuffy dishwashing pad, The Clorox Company, Oakland, CA) (Menge 1992) at each site. These collectors are intended to mimic mussel byssal threads, which are known to attract mussel recruits. Two recruitment collectors were associated with each treatment block, one was placed adjacent to a mussel bed and one was placed away from the mussel bed surrounded by bare rock. This placement allowed us to determine if there were differences in potential recruitment due to the presence of conspecifics. Recruitment collectors were retrieved and replaced each month. Collected Tuffys were processed in the laboratory using a standard rinsing protocol (Menge 1992). The resulting content was strained through a 250 μm sieve and preserved in 95% ethanol. The preserved material was then sorted under a dissecting microscope and mussels in the Mytilidae family were counted. We processed and counted mussel recruits for eight of the sample months that were collected for a total of 122 Tuffy samples.

Comparing epibiotic community composition and recovery

To determine the effect of mussel transplants on the recovery rate and trajectory of mussel bed communities, percent cover was estimated either in the field or from plot photos using a point contact grid with 100 points. At each point, we identified organisms to the lowest taxonomic level possible. We accounted for habitat complexity by recording both primary substrate and epibionts (if present); therefore, for a given point, multiple species could be recorded. Sampling at each site occurred monthly throughout the first year of the study, after which, sampling continued on a quarterly basis.

To ensure there was no significant difference in percent cover estimates based on scoring method (i.e. field vs. photo), we scored control plots in April 2011 using both methods. Controls plots are the most complex and therefore most likely to show differences between the two methods. We used a linear regression analysis (Systat v.13) to compare species counts from both methods and found field vs photo estimates were highly correlated (Adjusted squared multiple R = 0.929, $P < 0.001$).

For the purpose of our analysis, points where two species were recorded (i.e. mussel and an epibiont) were counted as two points: one for each species present. For this reason, the total number of data points for a plot could be higher than the number of points sampled (100). To look directly at the effect of mussel presence on the epibiotic community, we removed all points of mussel from the percent cover data, leaving only points of invertebrates or algae settled on mussel or rock substratum. We also removed all points of barnacle from the data since we did not count barnacles as epibionts on mussels, and they were therefore not counted consistently between cleared plots and plots with mussels. Raw species counts were then square-root transformed and used to generate a Bray-Curtis similarity matrix (PRIMER v.6).

To evaluate statistical differences in plot community composition based on plot type (i.e. control, cleared, and two transplant treatments), we used one-way analysis of similarity (ANOSIM) tests for each site (PRIMER v.6). Then, to evaluate changes treatment plot community similarity to control communities over time, we selected from the Bray-Curtis matrix the Bray-Curtis similarity value for the pairwise comparison of every treatment plot to each of the four control plots at a site. For each treatment plot type (i.e. cleared, one patch, three patches), this resulted in sixteen estimates (four per replicate block) of similarity to the control community per month. We then used these estimates to calculate the mean similarity of treatment plots to control plots each sampling month. We also selected Bray Curtis similarity values for comparisons of the control plots to each other and defined the recovery threshold as a point in time when the mean similarity of the treatment plots to the control plots was equal to the similarity of the control plots to each other (Kinnetic Laboratories Inc. 1992, Conway-Cranos 2012). The mean similarity values of treatment plots to control plots and control plots to each other were then plotted over time for each site. In addition to the analyzing community composition, we also examined patterns in individual species presence and abundance to determine if there were differences between treatment plots relative to control plots over time.

Evaluating the effect of mussel transplant patchiness

For each of the above factors: transplant success, mussel cover and recruitment, and community composition we also compared the two transplant treatments (one patch and three patches) to determine if mussel patchiness had any effect on recovery.

Results

Transplant success

At Pothole, an average of 60% of original transplants remained after one year (Fig. 1.3). The only exception was one block where both transplant plots lost nearly all mussel transplants due to a predation event (*Pisaster ochraceus* observed feeding in plots). A similar event occurred at a later date in a control plot. These plots were excluded from the remaining analyses since the effects of transplants could no longer be evaluated.

The success of transplants at Occulto was considerably more variable. Five of the eight transplant plots lost at least 50% of original transplants after one year and mussel cover continued to decline in these plots for the duration of the study (Fig. 1.3). However, one replicate block of plots retained greater than 70% of transplants during the same time period. We suspect that major transplant loss was due to heavy wave pressure at this site. Since the effect of transplants on the epibiotic community and mussel recruitment depend on transplants remaining established, plots at Occulto were grouped by the success or failure of transplants rather than treatment type (i.e. one of three transplant patches) for community composition analyses and failed transplant plots were removed for the mussel cover analysis.

In plots where transplants succeeded at both sites, mussel cover stayed relatively constant for the duration of the study (Fig. 1.3). Cleared plots gained no mussel cover with the exception of a few plots were there were very small increases due to the encroachment of mussels from outside the plot (Fig. 1.3).

Changes in mussel cover due to recruitment:

Transplants that survived to the end of the study period grew on average by a factor of 1.75 and 1.5 at Pothole and Occulto respectively. This corresponds to an average mussel growth rate of 0.4 mm/month at Pothole and 0.3 mm/month at Occulto. Accounting for mussel transplant loss and growth, successful transplant plots saw ~2.7% (+/- 1.97 95% CI) increase in mussel cover attributable to mussel recruitment in plots during the four-year study period. While small mussel recruits were occasionally observed in cleared plots no new mussel recruits established in cleared plots at either site during the study period (personal observation).

Monthly mussel recruitment rates measured by Tuffy collectors were relatively low, compared to regions, like Oregon, where mussel recruitment is an order of magnitude or more higher, but consistent with past measures of recruitment in central California (Menge et al. 2004, Broitman et al. 2008). Recruitment was slightly higher at Occulto where we found 80.1 +/- 15.9 (mean +/- SE) recruits per collector per month compared to 48.5 +/- 4.8 recruits per collector per month at Pothole. Monthly mussel counts ranged from 2 - 855 recruits per collector at Occulto and 5 - 174 recruits per collector at Pothole. There was a significant site by treatment interaction for Tuffys placed adjacent to and away from mussel beds (F = 8.001, df = 115, *P* = 0.006) such that treatment (i.e. Tuffy placement) had no effect on mussel recruitment at Pothole but was higher for collectors placed adjacent to mussel bed compared to collectors surrounded by rock at Occulto (Fig. 1.4).

Epibiotic community composition and recovery:

We saw significant differences in plot community composition based on plot type at both Pothole (ANOSIM: R = 0.781, $P < 0.001$) and Occulto (ANOSIM: R = 0.831, $P < 0.001$) (see Appendix A.1.1: Figs. S1, S2 for MDS plots); however, changes in the similarity of treatment plot communities relative to control communities over the study period suggest transplants did not accelerate or alter the recovery trajectory of the epibiotic community (Fig. 1.5). Instead, the epibiotic community in transplant and cleared plots reached the recovery threshold almost immediately at both Pothole and Occulto (Fig. 1.5). Differences in community composition between plot types, therefore, appear to be due to the overall variability of the epibiotic community at these sites, rather than differences in plot community recovery between transplant and cleared plots. This appears to be particularly true at Pothole where control plots were as similar to each other as they were to treatment plots for the entire study period (Fig. 1.5a).

There were also no consistent patterns in species presence during the study period (Fig. 1.6) or species abundance over time (Appendix A.1.1: Figs. S3, S4) to suggest transplant plots experienced accelerated recovery or increased in similarity to the control community faster than cleared plots.

The effect of mussel transplant patchiness

We did not observe any differences in mussel transplant success, mussel cover/recruitment, or epibiotic community composition related to transplant patchiness. Due to the small overall effect of transplants on mussel recruitment and the absence of an effect of transplants on epibiotic communities we did not evaluate this statistically.

Discussion

Incorporating ecosystem engineers into restoration planning has been proposed as a way to restore damaged ecosystems; however, there have been few empirical tests evaluating this approach. In this study, we found the success and benefits of adult mussel transplants in rocky intertidal habitats were conditional; however, these results also suggest this approach may be a valuable for restoring areas were mussel bed recovery is slow and/or recruitment is episodic.

Transplant success

The persistence of successfully established mussel transplants and the lack of mussel recovery in plots without transplants for the entire four year study period suggest this may be useful approach for increasing the presence of a dominant engineer following a disturbance event. These results are consistent with past studies of mussel recovery (Kinnetic Laboratories Inc. 1992, Conway-Cranos 2012) and indicate, without intervention, disturbances that affect mussel beds will result in long-lasting loss of *M. californianus* in central California regions.

Our method for mussel transplantation was less successful than we expected with much lower transplant success rates at Occulto. Heavy losses of transplants at this site were likely due to site characteristics, including wave exposure and the conglomerate rock type, which is easily broken and sheared off. Future transplant efforts may be improved by increasing the time for attachment before vexar is removed and using an alternative method to attach vexar where drilling holes into the rock is likely to increase sheering. Loss due to predation at Pothole also suggests a certain amount of transplant loss should be factored into restoration strategies based on site predation rates.

There also remain considerable challenges to making mussel transplant strategies feasible and cost-effective at a larger-scale. In particular, concerns about negative effects on donor populations suggest generating transplants through propagation may be necessary.

Effect of engineers on conspecific recruits

It was difficult to determine the effect of mussel transplants on recruiting conspecifics because recruitment rates were low at both sites, although not unusually low for this region (Broitman et al. 2008). However, two pieces of evidence suggest adult mussel transplants may positively impact mussel recruitment. First, there were higher recruit numbers in Tuffy recruitment collectors placed next to mussel beds compared to those placed in bare areas at Occulto (Fig. 1.4), suggesting the presence of adult mussels increases settlement. The absence of this pattern at Pothole may be due to lower recruitment rates or patchiness of the natural mussel bed at the site, which made it difficult to detect a difference between treatments. Second, approximately 2.7% (+/- 1.97 95% CI) of mussel cover was attributed to new recruits entering transplant plots during the study period, while, no recruits established in cleared plots.

Despite evidence that transplants facilitated mussel recruitment, mussel cover did not increase in transplant plots (Fig. 1.3), most likely because the addition of new recruits could not outpace mussel loss. Based on our measurements of mussel cover and recruitment we estimate that recruitment rates would need to be more than three times the average rate observed in this study in order to see a mussel bed expansion. This result suggests the ability to leverage a recruitment cascade (Halpern et al. 2007) to reestablish a stable population will likely depend on local recruitment dynamics. If recruitment rates are relatively high and consistent, species that respond to conspecific cues can be used as restoration targets to attract new recruits and expand the existing population. In this scenario, small numbers of adults can be used to “seed” areas and facilitate recovery of the population. In contrast, if recruitment is low or episodic, as it was in this study, then the presence of conspecifics may only maintain the population at its initial size. In this case, small numbers of conspecific adults are unlikely to seed damaged areas but may nevertheless be beneficial if they persist till an episodic recruitment event. Further, this strategy may be a particularly worthwhile investment if the absence of a species increases the likelihood of an alternative state. For example, where levels of mussel extraction are high in South Africa, intertidal communities shift towards algal dominated states that appear to persist even after extraction has ceased (Erlandsson et al. 2011). Persistent shifts are also observed in urbanized areas, where canopy forming algae often disappear and are replaced by disturbance-tolerant turf algae (Benedetti-Cecchi et al. 2001). Transplanting conspecific adults in this scenario may be necessary just to maintain a community in a desired state but will likely require more than a small number of adults to be successful. Thus, restoration strategies that aim to harness the attraction of recruits to conspecifics will need to evaluate recruitment dynamics to identify a reasonable project goal, timing, and approach.

Effect of engineers on epibiotic communities

Contrary to our hypothesis, there was no evidence that mussel transplants affected recovery of epibiotic communities (i.e. algal and invertebrate species that settle on rock and mussel shells). We predicted that differences in the recovery of transplant and cleared plots would arise if mussel shells provided better attachment sites compared to rock or by providing refuge from biotic or abiotic stress (e.g. reduced herbivory or desiccation stress) (Jones et al. 1994, Gutiérrez et al. 2003). Instead, similar biotic communities recovered quickly in plots whether transplants were present or not, suggesting these effects were not significant (Fig. 1.5).

While unexpected, these results help to clarify the factors that determine where and when mussel engineers will and will not be important. They may also provide insights into other ecosystems where engineers create biogenic habitats (e.g. coral reefs, oyster beds, kelp forests, seagrass beds, and terrestrial grasslands and forests). The role of habitat-forming engineers, like mussels, depend on several factors, including (1) the degree to which responding species specialize on the resource an engineer provides (2) the quality of resources in non-engineered habitats (3) the relative strength of abiotic and biotic stressors that engineers modulate (Gutiérrez et al. 2003). The epibiotic community we sampled was entirely composed of generalist species that are capable of settling on both rock and mussel. Mussel engineers are therefore, less likely to be important to the recovery of this community than a community that includes species that specialize on mussel habitat to survive (e.g. much of the infaunal community) (Gutiérrez et al. 2003). Also, if the effect of mussel engineers depends on the modulation of abiotic or biotic stressors, then the importance of mussel engineers will depend on the strength of these forces at a given site (Gutiérrez et al. 2003, Jones et al. 2010). For example, on wind-swept Patagonian shores, desiccation stress is so severe that all intertidal organisms rely on protection provided by mussel habitat to survive (Silliman et al. 2011). Therefore, *M. californianus* may play a more important engineering role in areas within its range where factors like desiccation, wave stress, and herbivory are more intense.

Mussel bed characteristics, such as bed depth and mussel size composition, also play a significant role in determining the engineering effects of mussels. These factors influence habitat complexity, which has been shown to affect the density of associated species (Beck 1998). Mussel beds in this study were composed of a single layer of mussels of relatively similar size, and these characteristics have been shown to result in lower fractal dimension, a measure of habitat complexity (Snover and Commito 1998, Commito and Rusignuolo 2000). Thus, the engineering effects of mussels may be different in areas where mussel beds are more complex.

In the absence of strong effects of mussel transplants on mussel recruitment and the epibiotic community, we were not able to evaluate the role of mussel transplant patchiness in this study. However, evidence from studies in other systems suggest it will be important for the recovery of mussel beds and the species that depend on their facilitative effects. For example, recent work in salt marsh systems show large patches of *Spartina* transplants are more resilient and capable of expansion compared to small patches following disturbance (Angelini and Silliman 2012). Also, patch configuration of restored seagrass beds has been shown to affect patterns in epifaunal diversity and community composition (Healey and Hovel 2004). Additionally, patchiness may interact with other mussel bed complexity factors, like cover, depth, and size composition. We suggest future studies evaluate all variables separately and together in order to better understand mussel engineering effects.

Conclusions

It is generally accepted that ecosystem engineers have positive effects on biodiversity on a landscape scale (Jones and Lawton 1997); but this study and others (see Wright and Jones 2004 for examples) have shown that the effects of ecosystem engineers vary at the scale of most restoration projects. Thus, it should be carefully considered whether the scale of restoration project goals align with the scale at which positive engineering effects can be expected. On a similar note, the effects of habitat-forming engineers often increase when they are in aggregations rather than solitary individuals. For example, the density and cover of shell aggregations affects water flow and wave attenuation in benthic environments (Gutiérrez et al. 2003). Capturing the positive effects of mussel beds due to wave attenuation may require the restoration of an entire mussel bed, rather than a few small mussel patches, and may not be feasible. Similar challenges exist for salt marsh restoration, where plants need to be a certain height and density to ameliorate soil conditions and therefore require restoration of large areas of vegetation (Pennings and Bertness 2001, Silliman et al. 2015).

Another important consideration is whether ecosystem engineers that are climax species will be effective restoration targets. It seems likely that any successful restoration application with climax species will be both labor and cost intensive due to the challenges of establishing these species in damaged environments. Further, these species are more important to the maintenance rather than recovery of communities. This may be why epibiotic communities in this study did not respond to mussel presence; it may not be reasonable to expect the recovery of a species to be affected by the presence of an engineer it usually precedes. In this case, targeting engineers that are early or mid-successional species (e.g fucoid or perennial red algae) may be a more effective approach. This is true in forest restoration strategies where restoring mid-successional shrubs prior to planting tree species has been more successful than direct planting of tree species (Gómez-Aparicio 2009).

It is clear the use of ecosystem engineers in restoration will not simply be a matter of "if you build it, they will come". Instead, engineers are a part of a complex set of interactions that are context dependent. Therefore, as we saw in this study, the positive effects of engineers will benefit some areas and some restoration goals but not all. While ecologists have largely focused on identifying where ecosystem engineers are important, it will be equally important for future work to identify where they are not, in order to maximize limited restoration resources.

Figure 1.1: Transplant treatment types: (left) transplant 1 with 100 mussels in one patch, (right) transplant 3 with 100 mussels in three patches.

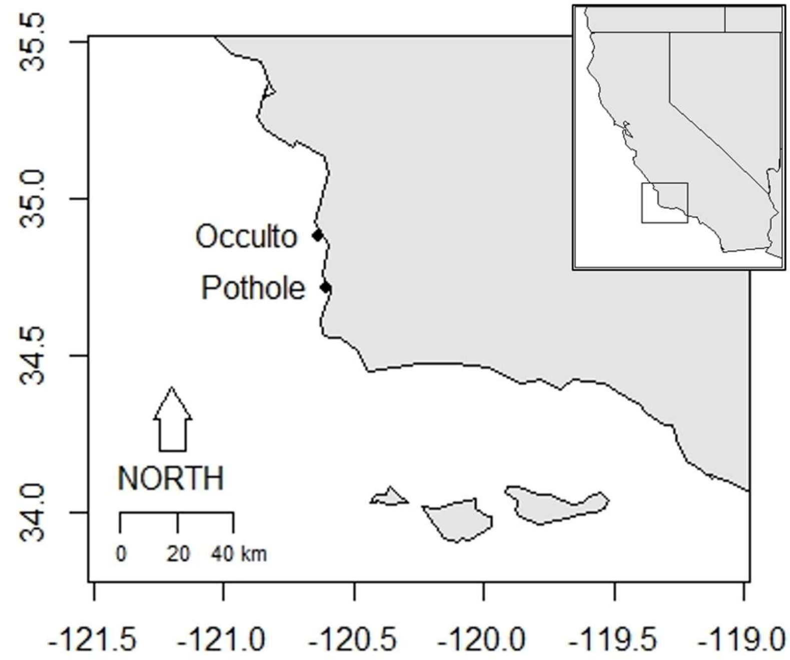


Figure 1.2: Site locations along Vandenberg Air Force Base coastline.

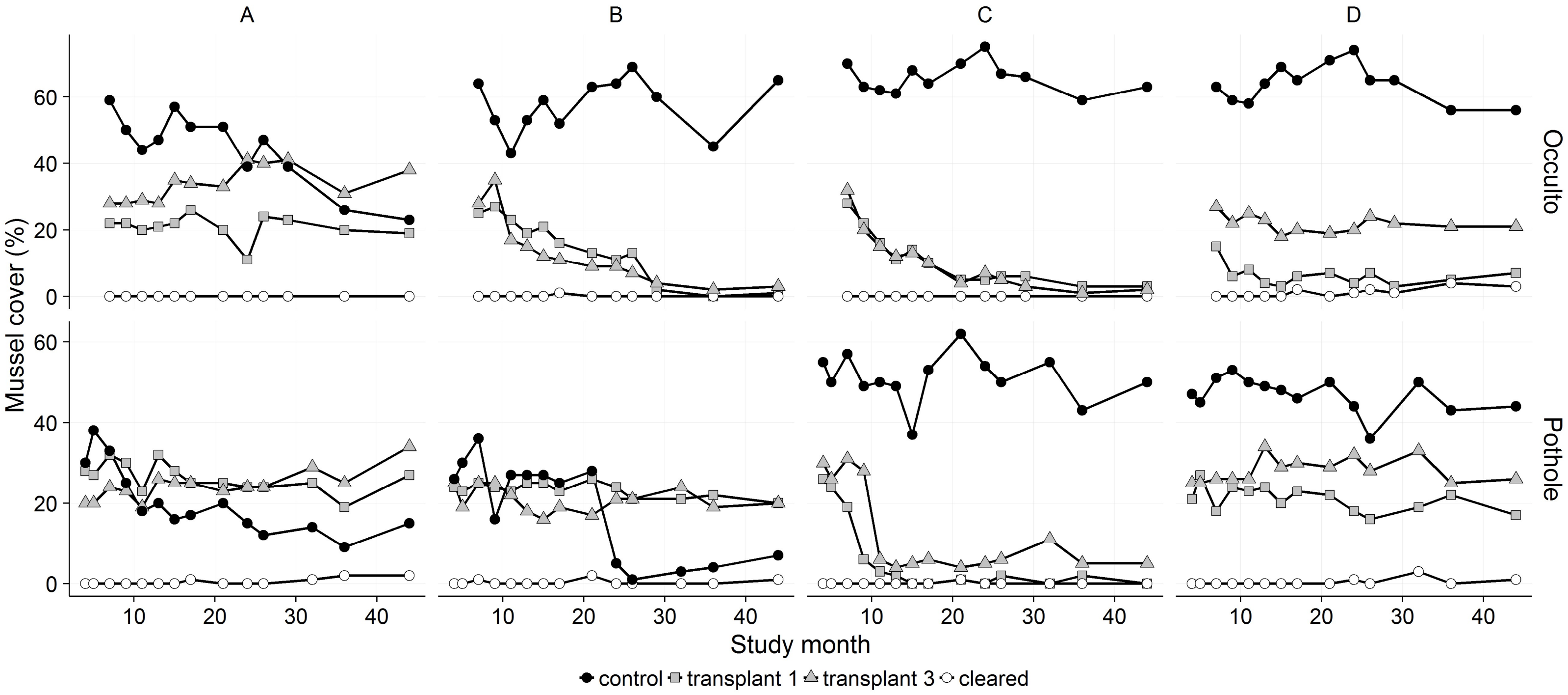


Figure 1.3: Percent mussel cover measured in each treatment plot and control plot over the study period at Occulto (upper row) and Pothole (lower row).

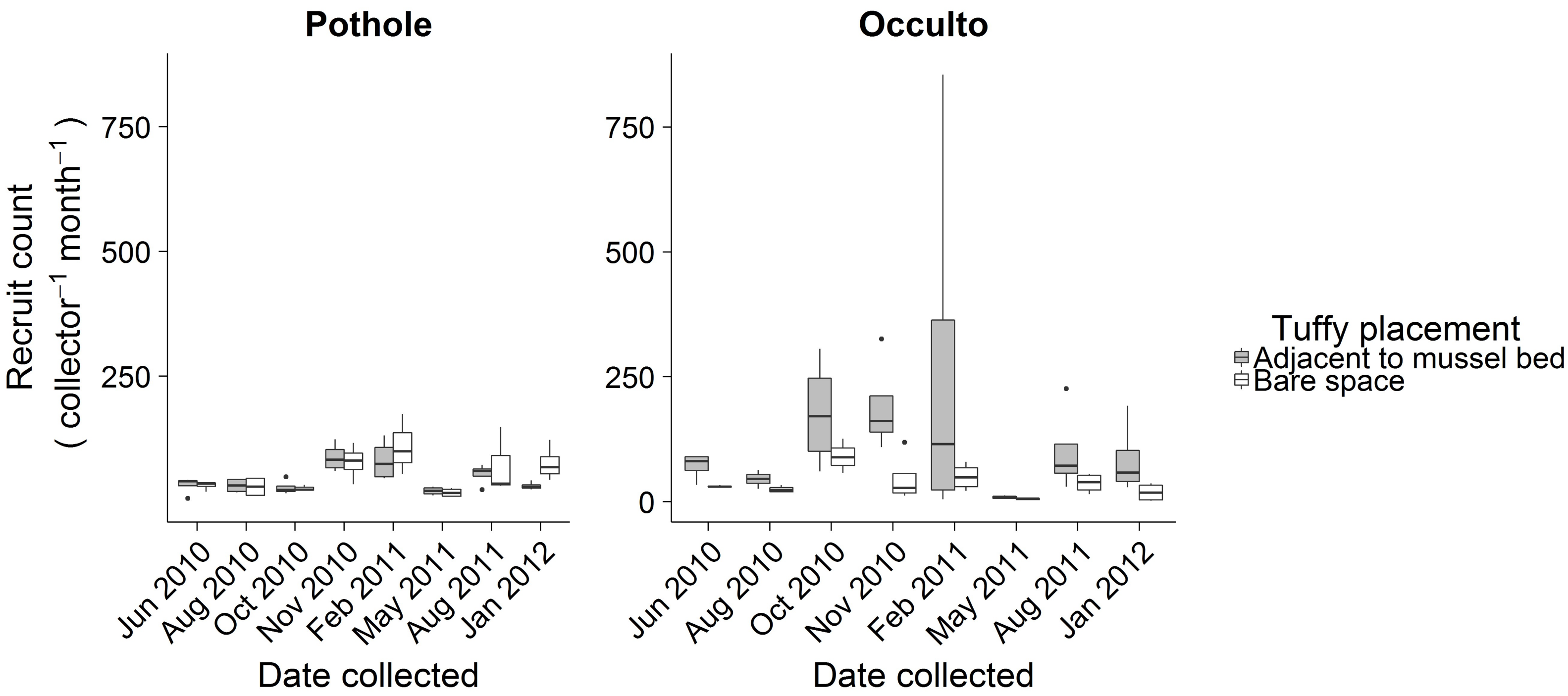


Figure 1.4: Mussel recruit count per collector per month at Occulto (left) and Pothole (right). Box and whisker plots show the mean count (horizontal line inside box), interquartile range (box), range (bars), and outliers (dots). Gray boxes represent tuffy collectors placed adjacent to mussel beds, white boxes represent tuffy collectors placed in bare spaces between mussel beds.

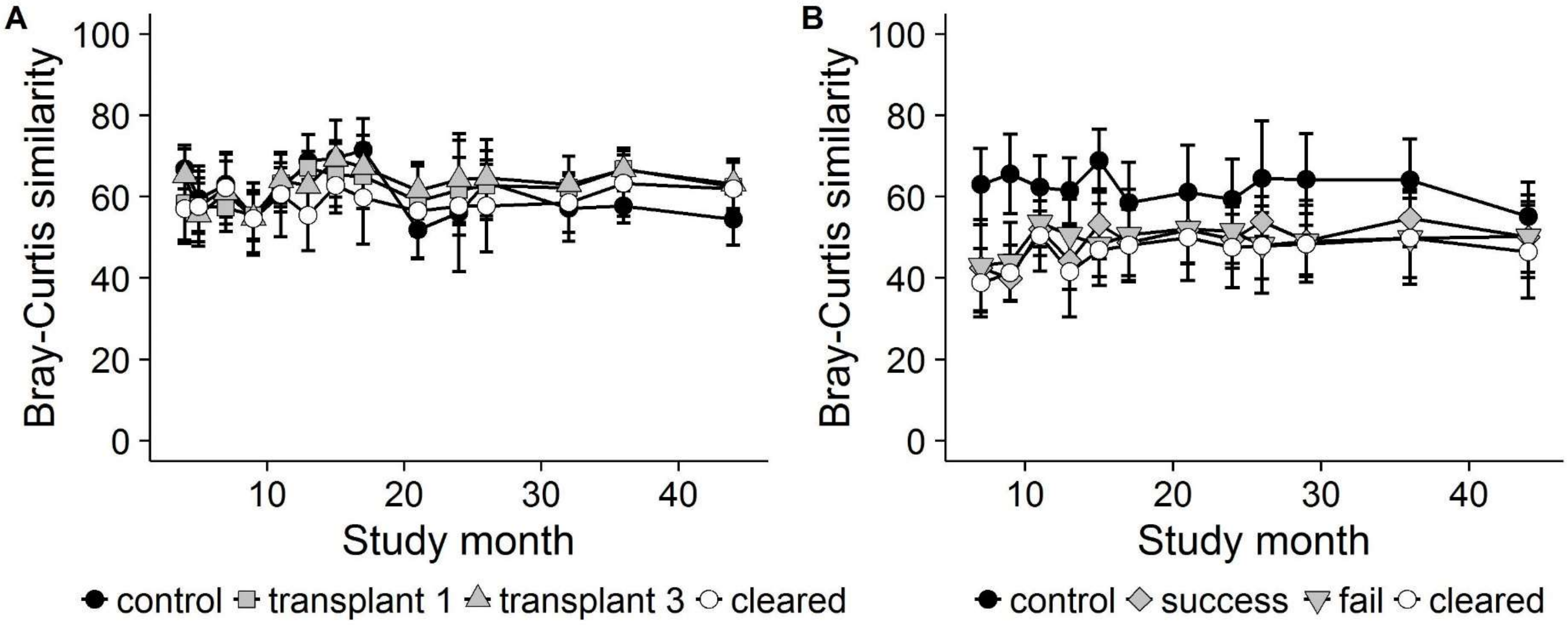


Figure 1.5: Mean (+/- SD) Bray-Curtis similarity for **(a)** cleared and transplant plots to each control plot and of the control plots to each other at Pothole. These data exclude plots with major predation events **(b)** for cleared plots, successful transplant plots, and failed transplant plots to each control plot and of the control plots to each other at Occulto. All mussel points have been removed from the data and represent only the invertebrate and algal community.

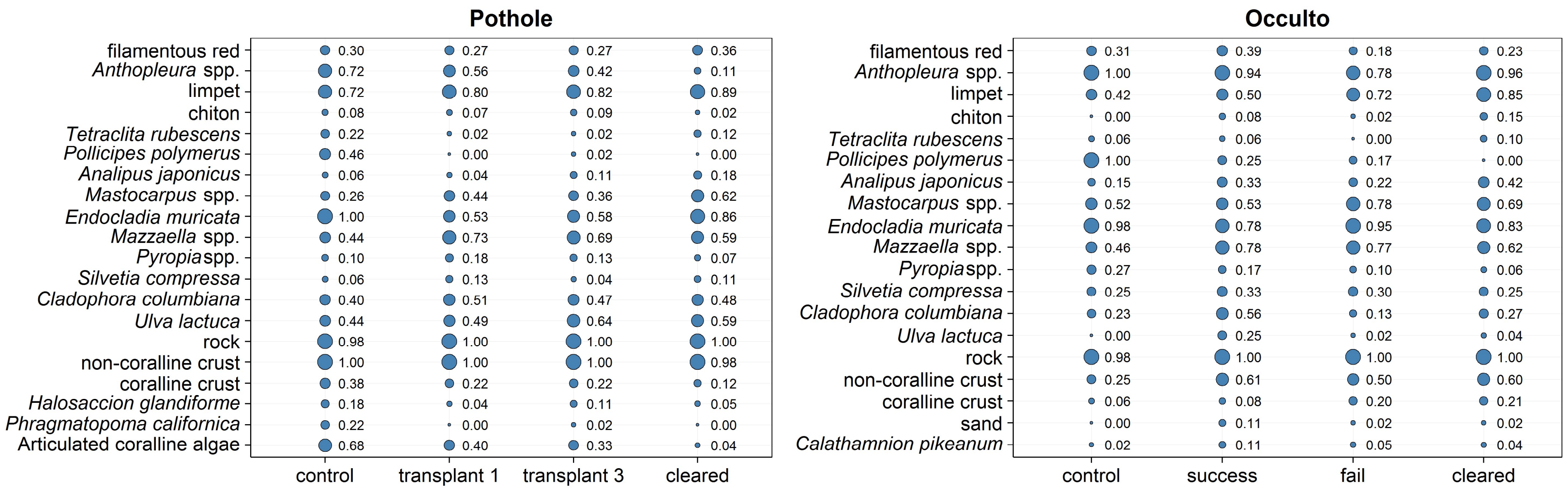


Figure 1.6: Bubble plot showing the frequency of species/substrate presence in each plot type (control, transplant 1, transplant 3, and cleared) for both sites throughout the study period. Large bubbles/values represent species/substrates that were observed nearly every time a plot type was sampled. Small bubbles/values represent species/substrates that were rarely observed. Patterns in species presence that support our hypothesis (i.e. that mussel transplants would benefit species/community recovery) were seen for *Anthopleura* spp., coralline crust, and articulated coralline algae at Pothole and *Pollicipes polymerus*, *Analipus japonicas*, and *Pyropia* spp. at Occulto. Overall patterns that support our hypothesis are rare and many of the patterns in species presence contradict our hypothesis.

Chapter 2

Stress, ontogeny, and movement determine the relative importance of facilitation for juvenile mussels

Abstract

An increasing appreciation for the role of positive species interactions in natural communities has led to a rapidly growing area of ecological research. A number of ecological factors have been shown to influence the importance of positive interactions (i.e. facilitation) in nature, including environmental stress and ontogenetic effects, and many more are likely to emerge as facilitation research expands to new ecosystems and taxa. In this study, I used a combination of field surveys and experiments to explore the roles of stress, ontogeny, and organismal movement in determining the importance of mussel (*Mytilus californianus)* recruit facilitation in central California. Results indicate that interactions between mussel recruits (shell length < 20 mm) and habitat ameliorating neighbors shift from neutral to positive from the low to high mussel zone. I also observed ontogenetic shifts in recruit survival and growth in the upper mussel zone that suggest mussel recruits migrate from algal substrate to adult mussel beds. This type of habitat shift where an organism moves sequentially from one facilitator to another may be common in nature and presents an exciting new area for research.

Introduction

The importance and prevalence of positive species interactions (i.e. facilitation) in ecological communities has been well established; however, identifying the factors that regulate these interactions in order to achieve a predictive understanding of where and when facilitation drives community dynamics remains an active area of research. A key paradigm that has emerged from this work is the stress gradient hypothesis (SGH) (Bertness and Callaway 1994), which predicts that the relative importance of positive species interactions increases with increasing environmental stress. Empirical tests over the past two decades have resulted in a large body of evidence to support the generality of the SGH and the relationship between abiotic/biotic stress and facilitation (He et al. 2013). But researchers have also identified a number of other factors, including ontogenetic effects, and species-specific responses to stress (Brooker et al. 2008, Maestre et al. 2009, He et al. 2013), that mediate the magnitude and outcome of positive species interactions. For example, juveniles are expected to more often benefit from facilitation due to their increased susceptibility to environmental stress (Callaway and Walker 1997, Miriti 2006). Evidence from plant communities suggest these interactions often shift from facilitation to competition throughout ontogeny (Schiffers and Tielborger 2006, Miriti 2006). For this reason, researchers recommend future facilitation studies use a multi-factorial approach that considers ecological factors, like life history and species traits, along with environmental stress (He et al. 2013).

As facilitation research moves forward, it should also be considered that studies of positive interactions have primarily focused on plant and sessile invertebrate communities. New research will need to be aware of and incorporate factors that may not have been relevant to previous work. For example, the effects of organismal mobility and facilitation have been largely ignored (but see Grof-Tisza et al. 2014) and may have important ecological consequences. Organisms that are capable of movement may be able to avoid negative interactions by moving sequentially from one facilitator to another, particularly during juvenile stages.

In this study, I use juvenile mussels (*Mytilus californianus*) in rocky intertidal habitats to explore the combined role of stress, ontogeny, and organismal movement in determining the importance of positive interactions. *M. californianus* is an important foundation species along rocky shores of the west coast of North America, forming dense beds that support a diverse array of algal and invertebrate species on and within the mussel bed matrix (Suchanek 1992, Lohse 1993a). Mussel recruits are considered poor settlers of bare rock and have long been thought to require the presence of habitat ameliorating species (e.g. conspecific adults, turf algae, or barnacles) (reviewed by Seed and Suchanek 1992) . Because stress is such a salient feature of the rocky intertidal it is reasonable to predict that interactions between mussel recruits and neighboring species (i.e. species that mussel recruits either directly attach to or settle underneath) may vary across a stress gradient. There is also evidence to suggest these interactions may shift throughout ontogeny.

Ontogenetic changes in mussel recruit sensitivity to stressors like predation (Dayton 1971) and heat/desiccation stress (Jenewein and Gosselin 2013) are well documented. It has even been suggested that these changes in sensitivity may result in shifts in habitat usage, where small recruits initially settle into filamentous algae and then later move to adult mussel beds (reviewed by Seed and Suchanek 1992). But surprisingly little attention has been given to these potential species interactions since they were first described and there are no direct measurements of these interactions to evaluate these hypotheses.

Here I examine facilitation of mussel recruits (< 20 mm shell length) by using and building upon the robust conceptual understanding of positive species interactions that has developed over the last two decades. I used a multi-step approach to address my research questions. I first conducted a field survey to determine if recruit associations varied predictably across tidal stress gradients and if positive associations were present that might indicate potential facilitator species. I then used that information to conduct a field experiment to (1) further evaluate the variability of recruit facilitation by directly measuring survival across the mussel zone and (2) to evaluate the role of ontogenetic effects and movement by measuring survival and growth of mussel recruits in different size ranges with two potential facilitator species.

Methods

Study sites

This study was conducted at four rocky intertidal sites along the Santa Cruz County coastline: Terrace Point, Davenport Landing, Scott Creek, and Greyhound Rock (for site map see Appendix A.2.1). The mussel zone at each site has a distinct upper and lower boundary containing monolayered beds of *M. californianus*. These sites experience mussel recruitment throughout the year with periodic pulses typically in the winter and spring months (Hart unpublished data).

Surveying recruit associations across tidal stress gradients

To examine recruit associations with available settlement substrate across a tidal stress gradient, I conducted field surveys at all four rocky intertidal sites between Dec. 2013 and Jan. 2014. At each site, I ran two 30 m transects parallel to the shoreline along the upper and lower portion of the mussel zone. Each transect was placed so that it followed the contour of the mussel zone and was within 0.5 m of either the upper or lower limit of the mussel band.

I first characterized the composition of available substrate for mussel settlement by sampling every 0.25 m along each transect and recording the substrate observed as if a mussel recruit were settled at each point, noting both the primary substrate for mussel attachment and any overlying algal canopy. I then made observations of recruits (shell length < 20 mm) and their associated substrate for comparison. Recruits are cryptic and patchily distributed making non-biased, independent observations difficult. To address this I made observations by placing a

50 cm x 50 cm quadrat at every meter on either side of the transect tape. In each quadrat, I made two random observations by dropping an object into the plot and searching in a circular fashion until the first recruit was encountered. If no recruits were observed in a plot, I continued to the next meter mark. Using this method it was possible to make up to 120 independent and random observations of recruits across a 30 m x 1 m swath of intertidal mussel zone. For each recruit observed, I recorded the primary substrate (i.e. the substrate to which the byssal threads were physically attached) and secondary substrate (i.e. any overlying algal canopy). For this study, I did not make observations of mussel recruits in adult mussel beds as it would require destructive sampling methods and instead focused on non-mussel substrates.

Species/habitat composition varied considerably across the mussel zone and between sites. This presented a challenge to comparing recruit associations. To address this, I categorized the specific substrates observed into four broad categories: (1) exposed hard or crustose substrate -- bare rock, acorn barnacles, the tube-forming worm *Phragmatopoma californica*, and non-coralline and coralline crusts (2) hard or crustose substrates under algal canopy (3) algal substrate, which included any observation where recruits were attached directly to the thallus of a fleshy or coralline alga and (4) other substrate types – including rock pools and attachment sites on the aggregating anemone *Anthopleura elegantissima*. Using these categories, I compared observations of recruit substrates with available substrates along the upper and lower transects at all four sites. I used a goodness of fit test to determine if the frequency of recruit observations with a given substrate was different than expected based on substrate availability. All analyses were completed using SYSTAT 13 (version 13.1).

Since other *Mytilus* species occur along open coasts as recruits and do not survive to adulthood (Johnson and Geller 2006) and cannot be morphologically distinguished from *M. californianus* until >10 mm (Suchanek 1978), I confirmed the identity of a subsample of mussel recruits using genetic analysis techniques (detailed methods Appendix A.2.2). I genetically identified 40 recruits of which 100% were assigned to *M. californianus;* therefore, it seems unlikely that other *Mytilus* species influenced the patterns observed in this study.

Identifying specific substrate associations

To identify potential mussel recruit facilitators, I used data collected during the field survey and calculated a standardized percent difference for each specific substrate using the formula: $\frac{\%R-\%A}{\%R+\%A}$,where %R is the number of recruits observed with a given substrate out of the total recruit observations and %A is the percent availability of a given substrate along a transect. The resulting values range from -1 to 1, where positive values indicate positive associations (i.e. recruits where found more often with a substrate than expected) and negative values indicate negative associations (i.e. recruits were found less often with a substrate than expected). This analysis is not able to evaluate associations with rare species, so I eliminated substrates with less than three observations total along a transect.

Measuring recruit survival across the tidal stress gradient

To evaluate how interactions between mussel recruits and the species they associate with vary across the tidal stress gradients, I used a non-traditional approach. This was because habitat composition varied between the upper and lower mussel zone making it difficult to conduct a traditional neighbor-removal experiment where direct measures of survival with and without neighbor species are used to compare the benefits of species interactions across stress gradients. As an alternative, I tested the inverse hypothesis – that placement at random points carries a higher survival cost in the upper zone when compared to the lower zone. To do this, I conducted a tethering experiment at Terrace Point during October 2014. This site was selected for its proximity to Long Marine Lab, which reduced stress on tethered mussels by minimizing transport time to and from the lab. Mussel recruits (5-15 mm shell length) were collected at Terrace Point and tethered in the lab by gluing a small piece of fishing line to the mussel valve. These mussels were then returned to the field and attached to the substrate in a way that allowed the mussel's ventral side to face downward in order to facilitate byssal attachment (detailed methods in Appendix A.2.3). The tethering approach allowed me to track individual survival and growth over time without the possibility of movement via byssal crawling.

To measure recruit survival across the tidal stress gradient, I placed 50 recruits – 25 small (5-10 mm shell length) and 25 large (11-15 mm shell length) – at random points along two 20 m permanent transects parallel to shore in the upper and lower mussel zone. All recruits were placed within a meter of the transect tape. The exact location of the recruit along each transect and the distance from the transect was selected using a random number table and then recorded so tethered recruits could be relocated. I relocated all tethered recruits within 24-48 hours of being deployed to track survival and ensure byssal attachment. Over two-thirds of surviving recruits had produced byssal thread attachments by 48 hours, the majority of those that had not were on bare rock substrate, which suggests the lack of byssal attachment was due to the unsuitable nature of this substrate type rather than an artifact of the tethering process. I located tethered recruits again at two weeks and one month to track their fate. I estimated survival for each treatment group based on the number alive at one month divided by the number that were successfully tracked (tethers that went missing during the experiment (< 10%) were removed from the total count). Differences in recruit survival between the upper and lower transects was evaluated using a chi-square contingency test.

Evaluating the role of ontogenetic effects

To compare survival and growth of mussel recruits with and without neighbor species and explore the effect of recruit size and movement on these interactions, I conducted a second tethering experiment in October 2014. Recruits were tethered in the same manner as the previous experiment but were placed only along the upper transect because the earlier field survey identified this as the area where positive associations were important. To do this, 40 recruits – 20 small (5-15 mm) and 20 large (11-15 mm) – were tethered with each of three different substrate types: two potential facilitator species (adult *M. californianus* and the alga *Mastocarpus* spp.) and bare rock. Placement with the two facilitator species allowed tethered juveniles to attach within the adult mussel bed matrix or directly to or under the canopy of *Mastocarpus* spp. The bare rock areas used in this study were not experimental clearings, however, given the ephemeral nature of bare space in *M. californianus* beds, I concluded the natural bare areas selected for tethering were sufficiently random and any benefits to creating independent clearings were outweighed by the habitat destruction this would require.

Prior to tethering, I measured each recruit shell in three dimensions (shell length, height, and width) to +/- 0.02 mm using digital calipers. At the end of the study, I collected all survivors and re-measured shell length, height and width. I calculated recruit growth rates as the percent change in shell volume using the formula for an ellipsoid. Then I evaluated the effect of recruit size and substrate type on recruit growth rates using an analysis of variance (ANOVA). Since only three individuals survived the rock treatment, I only included recruits on *Mastocarpus* and mussel bed in the growth analysis. I also estimated survival for each treatment group based on the number of recruits alive at one month divided by the number that were deployed and successfully tracked. I then used a normal approximation test to determine the effects of recruit size and substrate type on recruit survival.

Results

Recruit associations across the tidal stress gradient

Field surveys revealed that the strength of recruit associations with available substrates varied significantly across the mussel zone at all four study sites (Fig 1a). Along the upper transect, recruits (< 20 mm) were observed with substrates at significantly different frequencies than expected based on substrate availability (Fig. 2.1a; all sites $P < 0.005$). Across sites, recruits along the upper transect had negative associations with exposed substrates. For example, at Terrace Point, 60% of available substrate was exposed but less than 10% of recruits were observed on this substrate type. Recruits along the upper transect had positive associations with algal substrate and canopies, particularly at Scott Creek where 60% of recruit observations were with this substrate type despite making up only 10% of available substrate.

In contrast, there were no strong positive or negative associations with available substrates for recruits along the lower transect (Fig. 2.1a; all sites $P > 0.1$). This was true across all sites despite considerable variation in the composition of available substrate, even at Scott Creek where ~ 40% of available substrate in the low zone was exposed.

Specific substrate associations

Standardized percent difference values identified several specific substrate types driving positive and negative associations in the upper portion of the mussel zone (Fig. 2.1b). Negative associations with exposed substrates were driven by bare rock, non-coralline crust, and acorn barnacle substrate. Positive associations with algal substrates were due to strong associations with *Mastocarpus*, articulated coralline algae, fucoid algae (both direct attachment to the holdfast and canopies), *Cryptosiphonia woodii*, and combinations of these algal substrates. Recruits at Terrace Point had strong positive associations with hard substrates (rock, coralline crust, acorn barnacles) under fucoid and other algal canopies, although many of these same associations were negative at other sites. The only strong negative algal association was with *Endocladia muricata* at Terrace Point, although there was a positive association with this alga under fucoid canopies at Scott Creek. At Davenport Landing, a positive association was observed with the aggregating anemone, *Anthopleura elegantissma,* which may have been due to its abundance in bare space.

Recruit survival across the tidal stress gradient

Survival of tethered recruits (5-15 mm) placed at random points along the lower transect was three times as high as recruits along the upper transect (% survival upper = 8%, % survival lower = 30%; chi-square = 6.479, df = 1, P = 0.011).

Role of ontogenetic effects

Overall, mussel survival on bare rock was poor (and survival was significantly higher for recruits tethered with a facilitator species (i.e. adult mussel bed and *Mastocarpus)* (proportion surviving on rock = 0.103, proportion surviving with facilitator= 0.397, Z = 3.261, *P* = 0.001) (Fig. 2.2a). However, there were size-dependent responses to these facilitator species (Fig. 2.2). Small recruits (5-10 mm) had significantly higher survival rates with *Mastocarpus* than with adult mussel bed (proportion surviving with *Mastocarpus* = 0.400, proportion surviving with adult mussel bed = 0.158; Z = 1.724, *P* = 0.042), while large recruits (11-15 mm) had similar survival rates with either adult mussel beds or *Mastocarpus* (proportion surviving with *Mastocarpus* = 0.500, proportion surviving with adult mussel bed = 0.526; Z = 0.164, *P* = 0.435) (Fig. 2.2a).

Growth rates of recruits tethered with *Mastocarpus* and adult mussel bed were also size dependent (*F* = 4.941, *P* = 0.015, df = 1). Growth rates where highest in *Mastocarpus* when recruits were small and highest in adult mussel beds when recruits were large (Fig. 2.2b).

Discussion

Patterns in mussel recruit associations (Fig. 2.1a) and direct measures of survival across the tidal stress gradient suggest recruit interactions with neighbor species shift from neutral to positive with increasing tidal height. This pattern is consistent with the predictions of the SGH and its significance across four different sites, despite differences in geomorphology, wave exposure, and habitat composition make alternative explanations seem unlikely. For example, the absence of strong positive associations in the low mussel zone could be attributed to higher algal cover, which might mask the presence of associations by creating a uniform level of habitat ameliorating conditions. But if this were true, the opposite of the observed pattern should have emerged at Scott Creek, where the low mussel zone was mostly exposed and the upper mussel zone was algal dominated (Fig. 2.1a).

Many of the strong positive recruit associations I observed were with fucoid algae (*Fucus gardneri*, *Silvetia compressa*, and *Pelvetiopsis limitata*) (Fig 2.1b). This is contrary to previous work that found whiplash generated by the large fronds of fucoid species reduced invertebrate recruitment (Leonard 1999). Observations of recruits with fucoid algae in this study suggest they may be able to find refuge from whiplash either by attaching near or on the holdfast of rockweeds or by attaching to another alga underneath a fucoid canopy. Past studies have shown mussel recruits preferentially settle with filamentous substrata and turf algae (reviewed by Seed and Suchanek 1992), but these results indicate associations with turf and filamentous algae were most often neutral and in some cases negative (e.g. *E. muricata* at Terrace Point) . This may be due in part to mussel species differences, since this study focused on *M. californianus* and previous work focused primarily on *M. edulis* and *M. trossolus*. There may also be key differences in environmental conditions between central California and past study regions (mainly in the Pacific Northwest) that favor different facilitator species. For example, I often observed patches of filamentous/turf algae in the upper mussel zone that were dry at low tide suggesting this substrate may not provide refuge from desiccation and heat stress in this region.

The characteristics of species identified as facilitators and the role of tidal height in this study suggest variation in the strength of recruit-algal interactions is driven by heat and/or desiccation stress. This interpretation is consistent with recent findings that desiccation, in particular, is a limiting stressor for juvenile mytilids and algal tufts and fucoid algae are capable of creating conditions that alleviate this stress (Jenewein and Gosselin 2013). This is also consistent with intertidal studies that have found heat/desiccation stress to be the driving mechanism for facilitation (Hay 1981, Lively and Raimondi 1987, Silliman et al. 2011). There was no evidence that predation influenced patterns in recruit associations across the mussel zone. This was surprising given that the lower limit of the mussel zone is typically characterized by heavy consumer pressure (Paine 1974). These results may reflect differences in the distribution of adult vs. juvenile mussel predators, namely, juvenile mussel predators may be more evenly distributed across the mussel zone and/or utilize the same habitats as mussel recruits.

While these patterns are similar to terrestrial plant-plant interactions, they may arise through an entirely different mechanism. Patterns revealing positive interactions between plants arise following differential post-settlement mortality (i.e. seeds settle randomly and then only survive with a habitat ameliorating neighbor).

Patterns of recruit facilitation can result from two additional mechanisms: preferential settlement of larvae using a settlement cue and/or post-settlement movement. These mechanisms are not mutually exclusive and all three likely occur to some degree; however, existing literature suggests settlement cues may be particularly important. Studies have shown that *M. californianus* larvae avoid some surfaces and preferentially settle on others (Petersen 1984b). In this study, survival of recruits at random points in the upper and lower zone indicate there is a significantly higher cost to not using a settlement cue in the upper mussel zone. Selective forces may therefore support cues that enable settlement with facilitator species in the upper mussel zone. In this way, post-settlement positive interactions may affect larval behavior and have evolutionary consequences for recruiting marine organisms.

Results from this study are similar to those in plant communities that found ontogenetic variability in the importance of positive interactions (Schiffers and Tielborger 2006, Miriti 2006). I found as mussel recruits increased in size, their survival and growth in response to different facilitators changed. The mechanism responsible for these shifts was not resolved in this study but past research presents several potential hypotheses. For example, differences in recruit survival between *Mastocarpus* and adult mussel beds may be due to an ontogenetic shift in recruit susceptibility to predation. Past studies have shown decreases in the susceptibility of *M. californianus* recruits to predators as they increase in size (Dayton 1971). Mussel beds harbor a host of recruit predators (including crabs, whelks, and seastars), therefore, recruit survival may be lower in this habitat until recruits reach a size refuge. Growth rates with different facilitators may reflect similar ontogenetic shifts in either tolerance to desiccation stress or wave pressure or may be explained by differences in access to food among facilitators.

Ontogenetic shifts in survival and growth provide a basis for the hypothesis that mussel recruits migrate from algae to mussel beds, although further investigation will be necessary to resolve the debate over how, when and if this actually occurs in nature (reviewed by Seed and Suchanek 1992). It is clear from this study that the ability to move results in drastically different outcomes for recruit-algal interactions. Movement from algae to mussel beds may mitigate antagonistic interactions through sequential facilitation; whereas, the inability to move, as found for the mussel *Perna perna* (Erlandsson et al. 2011), may result in algal substrates acting as a recruitment sink. This contrast highlights the under-explored role of organismal movement which may enable habitat amelioration and ontogenetic variation in stress sensitivity to interact in ways that drive patterns in habitat usage and species distribution, not only for mobile organisms but also for sessile organisms that can alter location through growth (e.g. plants with rhizomatous growth). Greater consideration of organismal movement in facilitation studies may therefore present new ways to understand how positive interactions affect community dynamics.

Figures

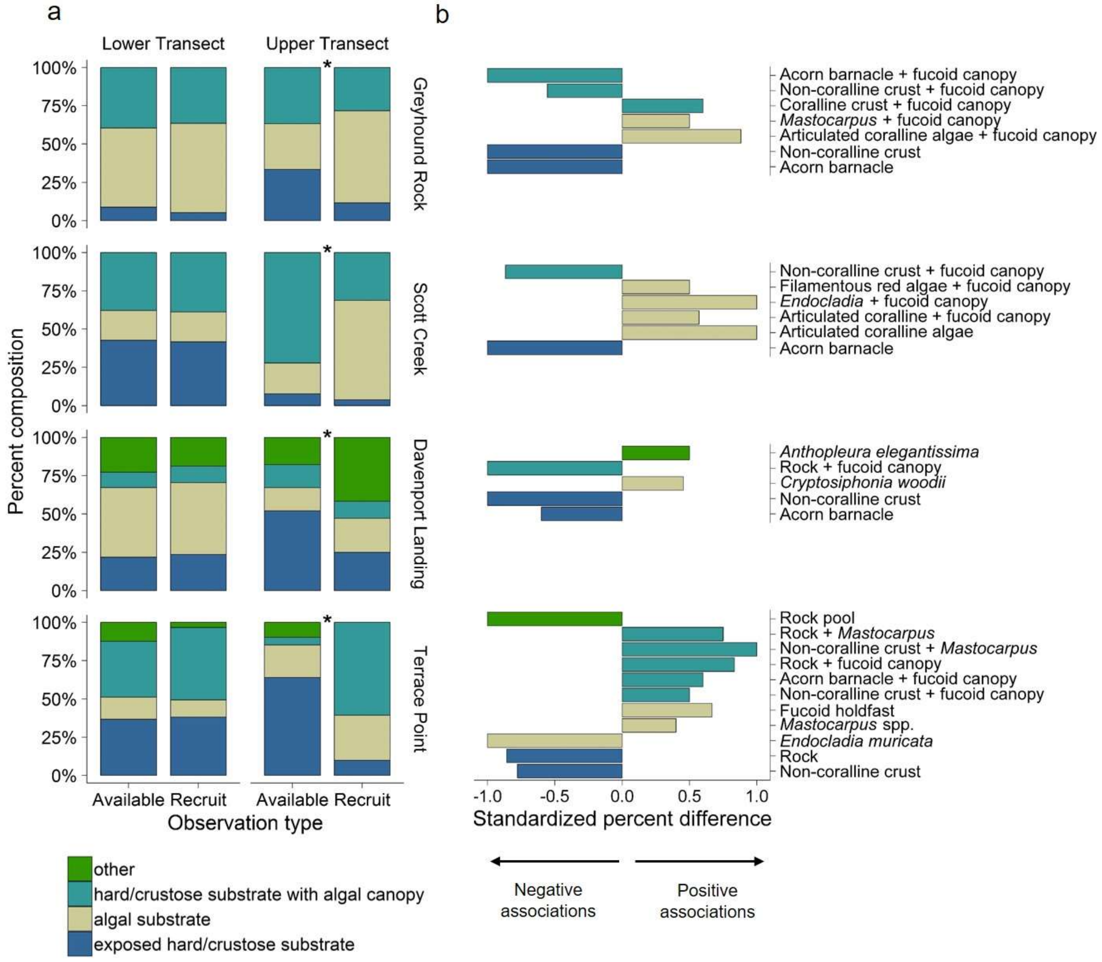


Figure 2.1: Patterns in mussel recruit associations across the tidal stress gradient and with specific substrate types (a) Available substrate composition compared to recruit substrate composition along the upper and lower transects at all four study sites. Substrates are grouped into four broad categories. Asterisk denotes statistically significant differences between available and recruit substrate composition. Recruits along the upper transect had strong positive and negative associations with available substrate (Greyhound Rock: chi-square = 12.172, df = 2, $P = 0.002$; Scott Creek 32.542, df = 2, $P \ll 0.001$; Davenport Landing: 15.828, df = 3, $P = 0.001$; Terrace Point 59.283, df = 3, $P \ll 0.001$). Along the lower transect there were no associations observed (Greyhound Rock 1.607, df = 2, $P = 0.448$; Scott Creek 0.065, df = 2, $P = 0.968$; Davenport Landing 5.553, df = 3, $P = 0.907$; Terrace Point 5.313, df = 3, $P = 0.150$) **(b)** Strong positive and negative recruit associations (> 0.4 or <-0.4 standardized percent difference) with specific substrates along the upper transects for each site in Fig 1a.

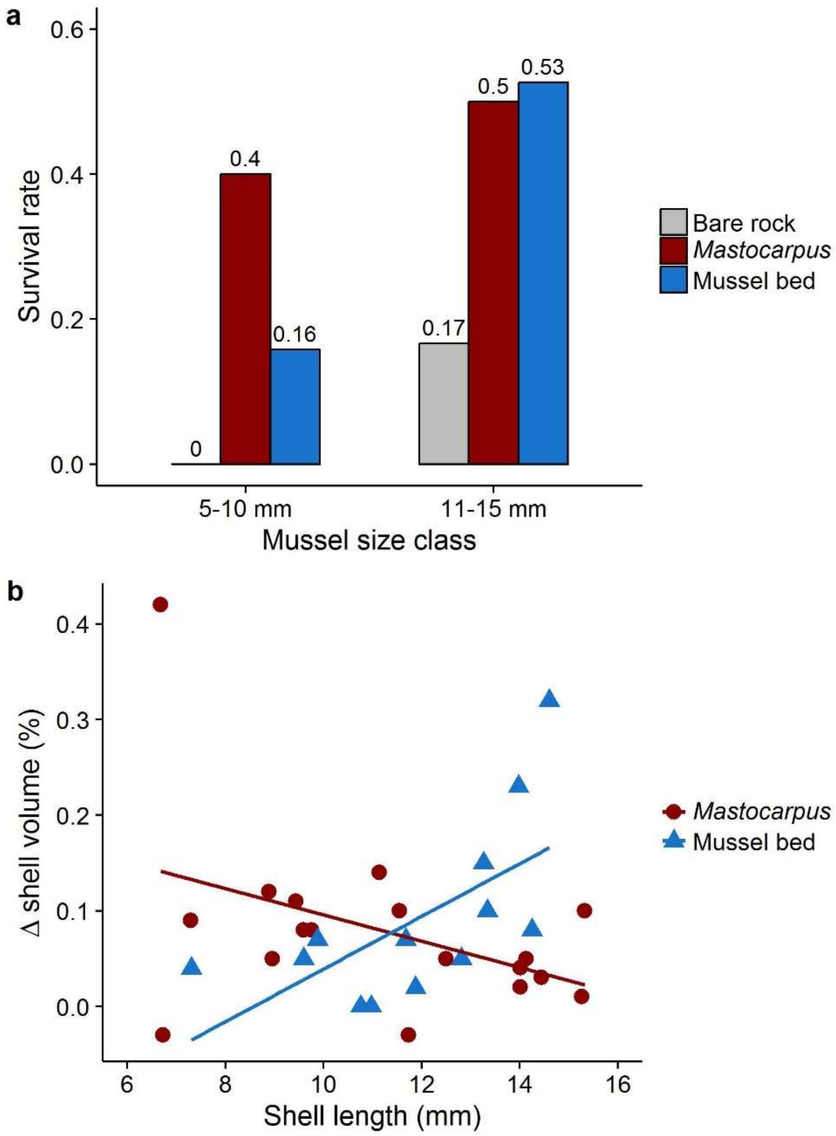


Figure 2.2: Tethered mussel survival and growth (a) Percent survival of two size classes of mussel recruits (small: 5-10 mm, large: 11-15 mm) when tethered with three different substrates (bare rock, *Mastocarpus* spp. and adult mussel bed) **(b)** Percent change in shell volume vs. initial shell length (mm) for mussel recruits tethered with two facilitator species (*Mastocarpus* spp. and adult mussel bed)

Chapter 3

Improving compensatory restoration in marine habitats: an evaluation of natural resource damage assessments for California’s rocky intertidal

Abstract

Compensatory restoration (i.e. restoration used as a mitigation strategy to compensate for natural resource loss) is becoming an important way to address adverse human impacts on marine habitats. The effectiveness of restoration in this context is determined by both the strength of the policy framework and the science that guides and informs the mitigation process. Here I evaluate the mitigation policy and science guiding compensatory restoration planning following oil spills using rocky intertidal habitats as a case study. I begin with a brief overview of the Natural Resource Damage Assessment (NRDA) process, which guides restoration planning following oil spills in the United States. To identify areas where there are opportunities to advance this process, I review six NRDA cases in California where rocky shorelines were oiled. These cases show that considerable advances in the tools and approaches to injury assessment have occurred over the past two decades; however, there are still only a limited number of restoration projects proposed and selected to address these injuries. I discuss the growing body of research on rocky

intertidal restoration that can inform future NRDA projects, and how NRDA projects can contribute to future research development if they are designed as long-term experiments and include regular project monitoring. I also show that without considerably more data to evaluate the feasibility and compensatory value of rocky intertidal restoration approaches, the NRDA process may unwittingly select ineffective restoration approaches to address rocky intertidal injuries. This suggests a synergistic effort to develop, evaluate, and broaden mitigation approaches will benefit compensatory restoration efforts in marine habitats.

Introduction

In the face of increasing impacts from human activity, environmental mitigation and restoration have become a necessary part of managing natural resources. Recognizing this, mitigation has become an increasing priority in the United States and includes a broad array of measures that aim to avoid, minimize and compensate for damage to natural resources (80 (2015) FR 68743). One approach to achieving these objectives involves recovering from and compensating for resource loss using restoration.

There are two types of restoration activities that occur as part of mitigation measures (Fig. 3.1). These two approaches differ in the way restoration targets and projects are evaluated (English et al. 2009). Primary restoration involves recovering injured resources with the goal of returning those resources to a baseline state.

Compensatory restoration, on the other hand, attempts to compensate the public for the loss of resources due to an injury, with the goal of recovering a resource value equivalent to the resources lost. Achieving these goals, therefore, requires a different set of metrics, with compensatory restoration relying, in part, on the economic valuation of biological parameters as a basis for the type and amount of mitigation (English et al. 2009).

Restoration measures also occur in two different legal contexts. The first addresses authorized impacts, which are usually related to development projects, and falls under the policy framework created by legislation like the National Environmental Policy Act (NEPA), the Clean Water Act (CWA), and the Endangered Species Act (ESA). The second is the Natural Resource Damage Assessment (NRDA) process, which addresses unauthorized impacts, usually accidental spills or chemical releases, and falls under the Comprehensive Environmental Response, Compensation and Liability Act (CERCLA) and the Oil Pollution Act (OPA).

These legal processes rely heavily on scientific input to assess injury, develop and implement restoration projects, and evaluate project effectiveness. For example, advances in seedling production and planting techniques have greatly improved the ability to conduct successful forest restoration (Oliet and Jacobs 2012). Likewise, the ability to assess the hydrogeomorphic and vegetation features of natural wetlands has enabled scientists to identify the appropriate design characteristics for restored sites (Brooks and Gebo 2013). Strengthening the connection between mitigation policy and science, therefore, improves our ability to protect and restore natural resources from harmful human activities.

When advances in policy and science fall out of step, barriers emerge that affect the success of mitigation efforts. For example, mitigation policies for unauthorized environmental impacts are only effective at holding responsible parties accountable for natural resource injuries when baseline data and ecological characterizations are available to measure the extent of natural resource loss. Likewise, advances in restoration science can only aid mitigation efforts when there is a strong policy framework to implement it. This was evident following the Deepwater Horizon oil spill in the Gulf of Mexico when existing mitigation policy and science were not prepared to accommodate subsurface impacts of a deep water oil well blowout (Peterson et al. 2012). To continue advancing mitigation efforts, it is necessary to periodically evaluate the status of policy and science relating to environmental problems and identify key challenges and areas for improvement.

Here I examine the mitigation policy and science guiding compensatory restoration planning following unauthorized impacts in marine habitats. In particular, I focus on oil spill impacts, one of the most conspicuous cases for restoration in this context. Oil spills affect a number of ecologically valuable marine habitats, particularly those along the coast. This case study reviews how restoration is used to compensate for oil spill impacts on one of the most common coastal habitats: the rocky intertidal. Rocky intertidal habitats have considerable ecological value and provide a rich environment for education, research, and recreation. These habitats are affected by a number of anthropogenic threats, oil spills being one of the most visible (Thompson et al. 2002).

This paper begins with a brief overview of the NRDA legal process. Then I review NRDA cases in California where rocky intertidal habitats were impacted by oil spills. I conclude by discussing areas where there are opportunities to advance restoration science and mitigation policy to address anthropogenic impacts on marine habitats.

Compensatory restoration under NRDA

The NRDA process is initiated following an oil spill when evidence indicates injuries to natural resources have occurred, the spill response alone is not expected to fully address injuries, and feasible restoration actions exist to address potential injuries (15 CFR § 990.42). The overall goal of this process is to "make the environment and public whole" through restoration, rehabilitation, replacement, or acquisition of natural resources and services equivalent to those injured (15 CFR § 990.10). There are four core steps that occur once a NRDA is initiated: (1) assess the injury (2) select the restoration action (3) hold the responsible party accountable (4) restore the environment (Natural Resource Damage Assessment, www.darrp.noaa.gov). A trustee coudncil made up of relevant federal, state and/or tribal partners is formed to oversee each step of this process (15 CFR § 990.11).

Injury assessment in NRDA is a complex process that requires establishing a baseline condition, determining causality, and measuring injury (Barnthouse and Stahl 2002). When compensatory restoration options are being considered, this process also involves determining the scale of compensatory restoration necessary to offset natural resource losses. There are a number of methods available for quantifying natural resource service loss and scaling compensatory restoration action; however, Habitat Equivalency Analysis (HEA) (NOAA 2000) has quickly become the most commonly used in NRDA, since its introduction in 1997 (Dunford et al. 2004).

Once the injury assessment has quantified natural resource loss for wildlife, habitat, and/or human use, the trustees must select a restoration alternative to recover or compensate for those specific injuries. During this restoration planning phase, trustees consider natural recovery along with primary and compensatory restoration alternatives (15 CFR § 990.53). These alternatives are then evaluated using a set of selection criteria developed by trustees using OPA regulations (15 CFR § 990.54) and additional spill-specific considerations. At a minimum trustees consider:

i. The cost to carry out the alternative;
ii. The extent to which each alternative is expected to meet the trustees' goals and objectives in returning the injured natural resources and services to baseline and/or compensating for interim losses;

iii. The likelihood of success of each alternative;

iv. The extent to which each alternative will prevent future injury as a result of the incident, and avoid collateral injury as a result of implementing the alternative;

v. The extent to which each alternative benefits more than one natural resource and/or service; and

vi. The effect of each alternative on public health and safety

Additional considerations include, how closely the project addresses injured resources (i.e. project nexus), timeliness, and feasibility. These considerations are particularly relevant for compensatory restoration projects; projects that have a clear connection to the resource or service injured, meaning they will restore resources of the same type and quality and comparable value are strongly preferred (DOI 2007). However, if trustees determine feasible compensatory actions of the same type and quality and comparable value do not exist, trustees can identify actions that provide natural resources and services of comparable type and quality as those provided by the injured natural resources (15 CFR § 990.53c). Projects selected for compensatory restoration are usually "in-kind" (i.e. replace similar resources near injured areas) but more novel approaches that are able to quantitatively demonstrate a benefit to resources of the injured type, for example preventative measures that help to avoid future resource loss, are beginning to gain consideration (Chapman and Julius 2005).

Final project selection occurs after a mandated period of public comment on draft restoration plans (15 CFR § 990.5(c)). Projects are then initiated once restoration planning has been finalized and a settlement has been reached with the responsible party.

NRDA restoration planning for California's rocky intertidal

To explore how rocky intertidal habitat injuries have been addressed in the NRDA restoration planning process, I examined NRDA cases in California (www.wildlife.ca.gov/OSPR/NRDA) where oil was documented on rocky shorelines (six cases summarized in Table 3.1). Thorough review of the Final Restoration Plan and Environmental Assessment for each case, along with associated documents, allowed me to identify advances and continued challenges in addressing three key steps in the NRDA process: assessing the injury, selection the restoration action, and restoring the environment.

Assess the injury

In two of the NRDA cases reviewed, there was no injury assessment for rocky intertidal habitats, despite shoreline oiling. This is common when oil impacts are too light to quantify but can be complicated by other injury assessment challenges including, when not enough resources exist to get an on the ground assessment of shoreline habitats, when not enough previous data exist to establish a baseline state for the habitat, or when oiling effects cannot be distinguished from background variability.

The ability to deal with such challenges and obtain detailed injury assessments increased markedly from early to recent cases. Early spill reports had only a coarse description of injury to shorelines, if any at all. For example, the final report for the 1998 Command oil spill (Command Oil Spill Trustees 2004) describes oiling along 24 km of shoreline and injury to rocky intertidal habitats as being one of the primary impacts of the spill. However, the report includes no additional quantitative or qualitative injury assessment. This is in stark contrast to the more recent injury assessment for the 2007 *Cosco Busan* oil spill, which included a detailed report (Raimondi et al. 2009) with pre- and post-spill field data describing rocky intertidal species assemblages in the affected areas. This level of detail reflects the increasing amount of information and tools available to assess injury to rocky intertidal habitats over the last two decades. For example, long-term monitoring programs by the Multi-Agency Rocky Intertidal Network (MARINe) and the development of *Go-Kits,* used to rapidly assess habitat quality prior to an oil spill reaching shore (Ambrose and Diaz 2008), now allow trustees to more readily attribute post-spill habitat changes to oil and seek compensation for spill effects.

Selection the restoration action

In all of the NRDA cases examined here, primary restoration immediately following an oil spill injury was not considered since most rocky intertidal resources were assumed to recover naturally in a reasonable time frame. Restoration efforts that were considered were used to compensate for the interim loss of intertidal resources.

During the restoration planning phase, trustees rely on receiving viable restoration project proposals to address natural resource injuries. These projects are then evaluated using the selection criteria described above. Across all six NRDA cases I examined, there were considerably fewer proposals for restoration projects targeting habitat resources when compared to projects targeting human use resources or specific taxa, like birds or fish (Fig. 3.2). Further, while the number of projects considered for compensatory restoration of other natural resources, like birds, wetlands, and human use, appear to be increasing over time, the number of projects considered for rocky intertidal habitats have not (Fig. 3.3). Project proposals, therefore, seem to be a limiting factor in the restoration planning process.

The few projects that have been proposed to address rocky intertidal injuries (summarized in Table 3.2) include active restoration by targeting habitat-forming foundation species, like fucoid algae (i.e rockweeds) and mussels, and using educational outreach efforts to restore sites by reducing negative human impacts. Very little peer-reviewed literature was used to support the selection or feasibility of these projects (Table 3.2), likely because so little was available when the majority of these spills occured. However, final restoration plans alluded to successful past projects suggesting some restoration work has not been published (SS Cape Mohican Trustee Council 2002, Torch/Platform Irene Trustee Council 2007).

Restore the environment

Reports monitoring the success of ongoing and completed rocky intertidal restoration projects were difficult to find, although this may be because final reporting for many projects is still in progress (Table 3.2). The reports that are available (e.g. press releases) include details on project implementation but very little data on progress towards achieving restoration goals. OPA regulations require restoration projects include a monitoring plan to evaluate project effectiveness (15 CFR § 990.55); however, it is unclear if these plans were ever implemented in these cases. The importance of evaluating project successes and failures will likely become more important as trustees rely more on past results for restoration planning and implementation (e.g. the Dubai Star oil spill restoration plans will be based on the results of Cosco Busan restoration projects).

Opportunities to advance compensatory restoration

The NRDA cases examined here show considerable advances have been made in rocky intertidal injury assessment over the past two decades. However, they also show there are few compensatory restoration projects proposed for rocky intertidal injuries, the majority of projects selected are for traditional “in-kind” restoration, and evaluation of the compensatory benefits of these projects is murky at best. In short, we have improved our ability to assess the debit (i.e injury) side of the equation but remain limited in our ability to address the credit (i.e compensatory restoration) side of the equation. Thus, there is considerable opportunity for researchers, practitioners and decision-makers to work together to advance restoration science and NRDA policy to better address future injuries.

Restoration science for rocky intertidal habitats is in its infancy. Historically, active restoration of rocky shorelines following a human disturbance has been seen as unnecessary, the expectation being that propagules from outside the system would quickly replenish most populations (Hawkins et al. 1999). But evidence that human impacts are having widespread negative effects on rocky intertidal communities (Thompson et al. 2002) has increased interest in intervention strategies and there are now a growing number of studies evaluating rocky intertidal restoration techniques (Table 3.3).

These studies provide valuable information for future compensatory restoration projects, including pitfalls to avoid and promising design strategies. For example, Whitaker et al. 2010 found rockweed (*Silvetia compressa*) transplant survival was enhanced by artificial canopies and placement on vertical rather than horizontal surfaces and recent work in China suggests inoculating artificial pools constructed in situ could be a successful approach to establishing rockweed recruits without the ongoing presence of fertile adults (Yu et al. 2012). A study on mussel transplantation demonstrated ways to avoid transport of harmful algae species (Hégaret et al. 2008).

And promising new evidence from a ten year study in southern California suggests education and outreach programs can decrease harmful human behaviors in rocky intertidal habitats and result in positive species responses (Lucas and Smith 2016). However, much of this work has focused on the technical details of project success and are only beginning to produce the evidence needed for NRDA to accurately estimate the compensatory value of these restoration activities.

Considerably more research will be needed to fully evaluate the feasibility and benefits of using these restoration approaches for NRDA projects and it remains to be seen if any of these strategies will be cost-effective and feasible at the scales necessary to address oil spill impacts. Some of the more pressing research questions that can be addressed by future studies are outlined in Table 3.4. This research is necessary to improve NDRA project selection and scaling and to ensure the NRDA process maximizes benefits to society.

Future NRDA efforts can address some of these research questions if NRDA projects are approached and evaluated as long-term experiments. Research is not an explicit goal of the NRDA process but, as one of the few contexts where active rocky intertidal restoration occurs, it will be a necessary component for generating more feasible restoration alternatives. As part of this effort, NRDA restoration projects should incorporate more frequent and comprehensive monitoring in project designs to evaluate restoration performance and increase the availability of these findings to the public, NRDA practitioners, and the broader scientific community. This may require additional resources but will benefit future NRDA restoration planning and rocky intertidal restoration science as a whole.

Most of the projects that have been selected for compensatory restoration in rocky intertidal habitats involve actively restoring target foundation species (e.g. rockweeds, mussels, or oysters). These projects are deemed favorable because they represent a close nexus to injured resource and it is relatively easy to equate the resource/services gained from this type of restoration to the resource/services lost due to an injury, a necessary component for scaling compensatory actions in NRDA. However, establishing these species in rocky intertidal environments remains a significant hurdle. For example, even the most successful rockweed transplant approach experienced nearly 50% mortality rates (Whitaker et al. 2010). Additionally, donor stock for affected rocky intertidal species are likely to come from extant wild populations since large-scale cultivation methods do not currently exist; hence restoration may come at the expense of a natural donor population. Even in marine systems where restoration approaches are relatively successful at establishing target foundation species, like in wetlands, mitigation projects are often criticized because restored sites do not fully mimic natural systems (Brooks and Gebo 2013).

For these reason, it would be prudent to consider other restoration alternatives. However, remaining options, within the traditional scope of NRDA compensatory mitigation, focus on manipulating physical habitat characteristics (e.g.

altering hydrology and topography in wetland restoration). This is problematic in rocky intertidal habitats where geological and hydrodynamic factors are difficult or impossible to manipulate (Ambrose 2007). Further, rocky intertidal habitats are restricted to a narrow interface between land and sea, which is not easily expanded (Ambrose 2007).

The remaining restoration approaches are more novel and less direct and include approaches that minimize anthropogenic stressors to allow passive recovery or enhance interconnected resources that benefit rocky intertidal habitats. However, while many of these options are promising, quantitatively scaling the amount of restoration required to offset resource injuries, is problematic for many of these more novel approaches (NOAA 1997, Chapman and Julius 2005). For example, while research suggests rocky intertidal resources respond positively to reducing impacts of human visitation using education and outreach programs (Lucas and Smith 2016), not enough detailed data currently exist to develop a common metric to equate these project benefits with resource loss (e.g. what amount of resource loss is prevented by educational signage?) In the absence of this, these projects remain less preferable in an NRDA context. Other projects that aim to improve water quality, reduce pollution, or minimize the effects of future oil pollution (Chapman and Julius 2005) are also challenging in an NRDA context because it is difficult for these projects to demonstrate a relationship to injured rocky intertidal resources (DOI 2007).

The problem created by these issues is that the NRDA project selection process will continue to favor traditional (i.e. in-kind) restoration actions for rocky intertidal injuries, even when they are ineffective, unless there is (1) data to evaluate the relative feasibility, likelihood of success, and compensatory value of novel alternative strategies and (2) support from trustees to select these alternatives. If this problem persists, ineffective restoration actions could become further entrenched as social and legal consensus builds around and favors the past approaches (Levrel et al. 2012). Solving this problem does not require a major policy change (Sutton-Grier et al. 2014), as the language in NRDA statutory mandates does not prohibit consideration of novel restoration approaches, as long as a reasonable relationship to injured resources can be established (15 CFR § 990.53c, Chapman and Julius 2005, DOI 2007). However, greater synergy among researchers, practitioners (i.e. individuals and agencies that conduct NRDA restoration), and trustees will be necessary to continue to develop and accurately assess options for compensatory restoration in rocky intertidal habitats.

These same issues are relevant in other marine habitats and with the continued occurrence of unauthorized impacts, like oil spills, and a growing number of authorized impacts requiring compensatory restoration of marine environments (e.g. desalination plants), it must be considered whether a broader approach to mitigation in these environments would provide a greater and more compensatory benefit to society. It is certainly understandable that relaxing requirements for project nexus is controversial and probably inappropriate in some instances (e.g. human use resource compensation); but where it is necessitated by the ecological constraints of natural systems and justified by net compensatory benefits, it is the logical approach for achieving overall mitigation goals.

Table 3.1: Summary of NRDA oil spill cases affecting rocky shorelines in California

Spill Name	*Spill Date*	*Settlement Date*	*Final RP/EA Published*	*Project Start Date*	*Total Spill Amount (gal)*	*Acres of Rocky Intertidal Oiled*	*Injury Assessed?*	*No. of Projects Proposed*	*No. of Projects Selected*	*Total settlement ($)*	*Allocation for Rocky Intertidal Projects ($)*
Refugio	May 2015				100,000						
Dubai Star	October 2009	April 2012	na	TBD	400	35	Y	1	1	$850,000	$44,000
Cosco Busan	November 2007	January 2012	February 2012	June 2013	53,569	384.3	Y	3	2	$30,000,000	$1,200,000
Command	September 1998	September 1999	June 2004	na	3,000	nd	N	0	0	$4,000,000	$0
Platform Irene/Torch	September 1997	January 2002	October 2007	June 2009	6,846	85	Y	4	2	$1,900,000	$241,150
Cape Mohican	October 1996	September 1998	March 2002	June 2005	40,000	516	Y	1	1	$3,625,000	$487,000
Avila I	August 1992	March 1996	June 1999	na	24,200	5	N	0	0	$1,400,000	$0

Table 3.2: Summary of projects selected to address injury to rocky intertidal habitats

Spill	*Project Name*	*Final Classification*	*Reason, if not selected*	*Project Goal*	*Literature Cited?*	*Performance Monitoring?*	*Budget*
Dubai Star 2009	Rockweed restoration	Highly preferred*		Transplant rockweed into areas with low abundance to enhance existing rocky intertidal habitat	na	TBD	$44,000
Cosco Busan 2007	Native oyster restoration	Preferred		Provide suitable natural hard substrate to enhance oyster larvae settlement and recruitment as a means to compensate for lost services to natural rock and rip rap intertidal habitats.	Y	project ongoing	$600,000
	Rockweed restoration	Preferred		Increase vegetative cover of a key mid-high intertidal alga in areas that were directly impacted by oil spill.	Y	project ongoing	$600,000
	Albany Bulb rocky shoreline restoration	Not selected	Timing and Feasibility	Improvements to the South Albany Neck to create and enhance rocky intertidal habitat and stabilize an eroding shoreline and thereby limit sedimentation and degradation of sensitive habitats.	na	na	na
Cape Mohican 1998	Protection of Duxbury Reef through education	Highly preferred		Avoid further injury to and facilitate the natural recovery of intertidal rocky habitat at the DRMR through environmental education and stewardship.	none cited	limited	$360,000
Torch 1997	Mussel Bed Restoration	Highly preferred		Accelerate natural recovery of mussel beds by seeding barren areas with adult mussels.	none cited	Y	$104,650
	Rocky Intertidal Habitat Protection Program	Highly preferred		Provide local community outreach and education regarding the sensitivities of rocky intertidal habitats and reduce the impact of human disturbance on tidepools.	none cited	limited	$136,500
	Black Abalone Restoration	Moderately preferred	Feasibility	Black Abalone artificial culturing and out-planting of disease-resistant black abalone	none cited	na	na
	Reduced Take of Intertidal Species: Enforcement and Education	Least preferred	Redundancy	Use education and enforcement measures to reduce take of intertidal species.	none cited	na	na

* pending results of *Cosco Busan* restoration projects

Table 3.3: Selected papers that support or provide guidance for rocky intertidal restoration strategies

Author	**Topic of paper**	**Relevant finding(s)**
Rockweed restoration		
Yu et al. 2012	Establishing *Sargassum thunbergii* in intertidal beds using germling seeding and habitat creation	• Description of technique used in China that successfully established a reproductive population of *S. thunbergii* using artificial cement pools constructed on a rocky intertidal platform and inoculated with fucoid germlings released from fertile thalli at low tide
Whitaker et al. 2010	Investigation of techniques and abiotic/biotic factors that affect restoration of *Silvetia compressa*	• Juvenile transplant survival was enhanced by the presence of an artificial canopy, unaffected by site or herbivore presence • Larger thalli had higher survival • Survival was higher on vertical vs. horizontal surfaces • Transplanting reproductive adult thalli resulted in subsequent recruitment
Bellgrove et al. 2010	Potential for fucoid algal restoration to be impeded by competition with coralline turfs	• Conceptual framework for evaluating the likelihood of fucoid restoration success • Coralline turfs competitively exclude fucoid alga *Hormosira banksii*
Speidel et al. 2001	Recovery of *Fucus gardneri* after varying levels of experimental removals	• *Fucus* is robust in the face of canopy reducing disturbance but complete removal delays recovery time • Recovery may be facilitated by the presence of only a few surviving individuals
Stekoll and Deysher 1996	Recolonization and restoration of *Fucus gardnerii* following Exxon Valdez	• Coconut fiber mats facilitated settlement and growth with juvenile *Fucus gardneri* reaching 2 cm in length in one year • Presence of mats alone was enough to result in recruitment of young thalli but required nearby reproductive adults • Inoculating mats with *Fucus* zygotes did not increase density of young thalli
Mussel bed restoration		
Hégaret et al. 2008	Potential transport of harmful algae via transplants	• Bivalve mollusk transplants can be vectors for the transport of harmful algae • A holding period in clean water or emersion may mitigate this risk
Carls et al. 2004	Restoration of oiled mussel beds following Exxon Valdez	• Manual removal and replacement of mussels reduced oil contamination in sediments and did not negatively impact mussel density • Hydrocarbon concentrations did not decrease in mussel tissues
Navarrete and Menge 1996	Experimental tests of interaction strength between *Mytilus* and its predators	• Description of method for successful mussel transplantation
Restoration through education and reducing effects of human visitation		
Lucas and Smith 2016	Alterations in human visitation patterns and behavior following increased management in an Orange County, CA MPA	• Increased management (signage, interpretative programs, enforcement) correlated with reduction in detrimental collecting and fishing behaviors • Size increase in *Lottia gigantea* population possibly due to reduced live collection

Table 3.3 continued

Garcia and Smith 2013	Factors influencing human visitation to rocky intertidal	• Popularity of site for educational field trips was strongest determinant of visitation level • Sites more difficult to access (increased physical exertion) have decreased visitation rates • Presence of non-tidepooling attractions influences visitation
Smith et al. 2008	Impacts of human visitation on California mussel beds inside and outside marine reserves	• Areas with higher visitation had significantly lower mussel populations • No consistent pattern in mussel populations inside and outside no-take marine reserves- suggests regulations are ineffective
Smith and Murray 2005	Experimental tests of the effects of trampling and bait collection on *M. californianus* beds	• Even low levels of trampling and bait collection resulted in significantly lower mussel cover, mass, and density
Murray et al. 1999	Effects of human visitation and collecting on rocky intertidal in Southern CA marine reserves	• Collecting not deterred by marine reserve signage • Most commonly collected items were mussels, snails, limpets, urchins, and octopuses • More gaps and less mussel cover at sites frequented by recreational fishers
Other		
Chapman 2012	Restoring boulder fields by creating new habitat with quarried stone	• Sessile assemblage developed slowly, mobile assemblage colonized quickly and included specialist and generalist species • Colonization of mobile invertebrates occurred due to movement of adults into new habitat not new larval propagules • Higher degree of variability between boulders than between sites
Bull et al. 2004	Evaluation of surfgrass restoration techniques	• Out of three techniques, transplanted sprigs (short lengths of rhizome containing a few shoots) had the greatest overall increase in aerial coverage per unit effort, suggesting that this method may be the most effective approach for restoring *Phyllospadix torreyi*

Table 3.4: Potential research questions that may be tested by future rocky intertidal restoration projects, organized by restoration strategy

Restoration theme	Research question
Rockweed restoration	Are transplants unaffected by grazing pressure once thalli reach a size refuge?
	What microscale features of substrata affect fucoid transplant success?
	Does grouping of transplant thalli reduce stress and increase survival?
	What species interactions facilitate and exclude fucoid propagules?
	What is the optimal age/size structure of thalli for population persistence?
Mussel bed restoration	Under what recruitment conditions, if any, do transplants speed up recovery of mussel bed cover?
	How does transplant arrangement (patch size, bed depth, cover, mussel size composition) affect transplantation success?
	Can artificial substrata be used to facilitate mussel bed recovery?
	What are the species/community benefits of mussel bed restoration?
Restoration through education/reducing effects of human visitation	What are the effects of individual management efforts (e.g. signs, brochures, managers, enforcement, outreach, educator/docent program) on human behavior?
	What effort or combination of efforts is most effective at reducing human impacts?
	For onsite educator/docent programs, what is the optimal visitor to educator ratio?
	What are species/community benefits of programs?

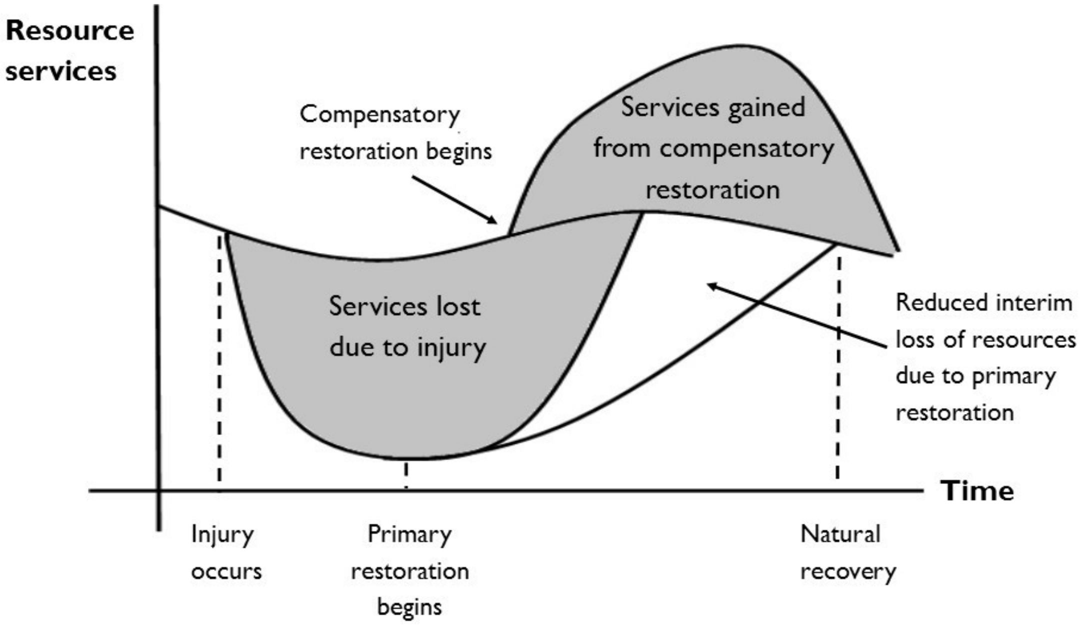


Figure 3.1: Conceptual diagram of the relationship between injured resources and primary and compensatory restoration activity.

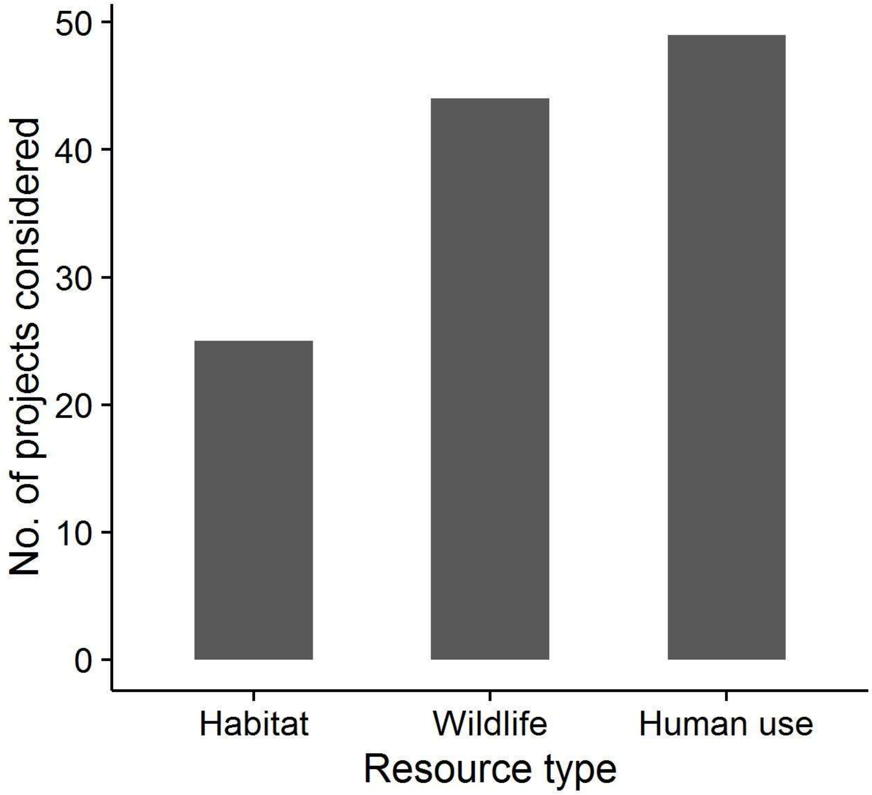


Figure 3.2: Total number of restoration projects considered for each resource type (habitat, wildlife, and human use) in NRDA cases with rocky intertidal injuries.

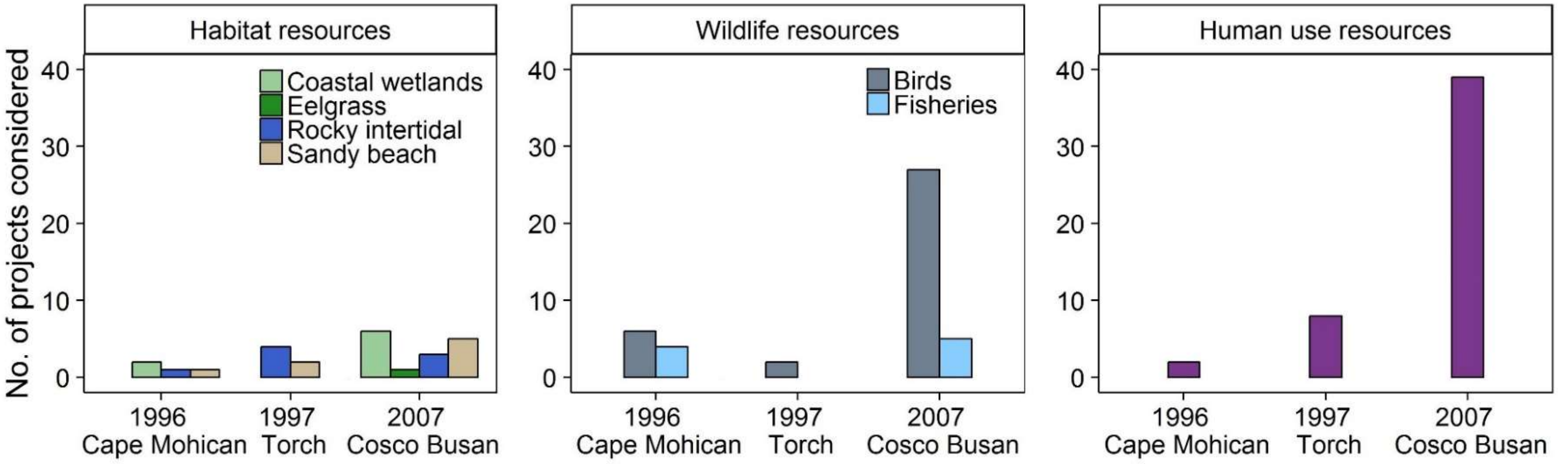


Figure 3.3: Number of restoration projects considered for specific habitat, wildlife, and human use resources for three NRDA oil spill cases where rocky intertidal restoration projects were considered (Cape Mohican, Torch/Platform Irene, and Cosco Busan). Cases are ordered by spill date.

Synthesis

Overview

The goal that initially motivated this work was to explore whether effective restoration strategies could be developed for rocky intertidal habitats. With this in mind, I began my dissertation work with what seemed like the most direct and practical approach to achieving this goal: field test a restoration method. However, it quickly became apparent that to fully understand how to make restoration more "effective", I would need to dive deeper into the ecology and policy that informs and motivates rocky intertidal restoration work. To do this, I specifically addressed (1) the benefits of using the mussel engineer *Mytilus californianus* to restore rocky intertidal habitats, (2) the role of stress, ontogeny, and organismal movement in determining the importance of species interactions that facilitate mussel recruits and (3) the science and policy used to plan, select, and evaluate compensatory restoration projects for rocky intertidal habitats following oil spills in the United States.

Key insights for rocky intertidal ecology and restoration

My results provide several insights for the understanding and management of rocky intertidal habitats. The results from **Chapter 1** show mussel transplants may only have limited restoration benefits; in this study, transplants increased mussel presence and attracted mussel recruits but did not result in any additional mussel bed expansion beyond what was originally transplanted, and did not appear to have any effect on the recovery of the invertebrate and algal community that typically settles on and around mussel beds. These results indicate that the benefits of mussel transplants will be determined by recruitment dynamics and potentially a number of other factors including the type/severity of environmental stress and mussel characteristics (size, depth, patchiness) that influence bed complexity. However, the results of this study also highlight the extremely slow recovery rates of mussel beds in the central/southern California region where the study took place – experimentally cleared areas with no intervention (i.e. no mussel transplants) gained zero mussel cover during the entire four year study period. This suggests that without some type of intervention, these regions will experience prolonged loss of mussel bed cover following human disturbance events.

In this regard, I believe there are two areas that should be explored to improve future mussel bed restoration approaches. First, it appears, in hindsight, the mussel transplant approach may be able to net more restoration benefits by creating larger mussel transplant patches. This is because many of the positive effects of mussels (i.e. wave attenuation) result from the effects of mussel aggregations rather than the effects of individual mussels. This may also help to minimize the loss of transplants over time and increase the likelihood that an intact mussel bed is present when recruitment pulses occur, even if those pulses are few and far between.

However, even if the mussel transplant approach can be improved, there still remain significant challenges to making mussel transplantation feasible and cost-effective for large-scale restoration applications. In particular, this strategy requires collecting mussels from a donor population, which, at large-scales, would result in significant negative population and community-level consequences. For this reason, I believe alternative mussel bed restoration approaches, which do not require individuals from donor populations, should also be explored.

One specific approach that has the potential to be successful involves leveraging positive species interactions to facilitate mussel recruitment. My results from **Chapter 2** provide support and guidance for this approach and indicate that positive interactions are most important for mussel recruitment in the upper extent of the mussel zone, where heat and desiccation stress are high. These results also demonstrate that the habitat forming species that facilitate recruits have a broader range of morphologies than previously appreciated and include rockweeds, and coralline algae along with turf and filamentous algal species. Finally, these results show recruit interactions with habitat forming species shift during ontogeny suggesting juvenile mussels may require multiple facilitators to maximize survival and growth. This information could be useful in developing restoration strategies that utilize natural or artificial mussel recruit facilitators to recover mussel beds.

In thinking about rocky intertidal restoration, it is important to recognize the demand for restoration strategies, particularly in the United States, stems mostly from the need to compensate for the interim loss of natural resources that result from oil spills injuries. Thus, rocky intertidal restoration projects occur most often in the context of the Natural Resource Damage Assessment (NRDA) legal process. My review of NRDA cases in **Chapter 3**, shows that compensatory restoration options for rocky intertidal habitats are currently limited by (1) a lack of restoration science to determine the relative feasibility and compensatory value of different approaches and (2) traditional policy norms that favor actions that directly replace resources near injured areas. Based on this findings, I suggest greater synergy between researchers, practitioners, and decision-makers is needed to expand on the existing evidence used to support and select restoration projects in rocky intertidal habitats.

Future directions

The results of these chapters also provide several general insights for ecology, restoration science, and natural resource management that I hope will motivate future research. First, this work suggests ecosystem engineers are not important everywhere and determining whether they will benefit restoration approaches depends on the specific restoration goal and a variety of environmental and biological factors that ecologists currently do not understand well. This work also indicates that efforts to identify ideal target species for restoring ecological communities will benefit from considering their role in successional dynamics and that early successional species may provide the most benefits to restoration projects.

This approach is used in tropical forest restoration (Gómez-Aparicio 2009) but may be a general rule that applies to all ecosystems and should be incorporated into restoration practice.

This work also makes important contributions towards the study of positive species interactions and extends previous hypotheses developed and tested primarily in plant communities to animals (i.e. mussels) capable of small-scale movement. The main results of this work provide evidence that supports the existing paradigm regarding the role of environmental stress in determining the importance of these interactions; specifically, that positive interactions (i.e. facilitation) increase with increasing abiotic/biotic stress. These results also provide evidence to support recent work in terrestrial systems that indicates species interactions can shift from positive to negative (or vice versa) across life-stages. Interestingly, by focusing on an organism that is capable of small-scale movement within its environment, these results also raise the possibility that mobility enables facilitation to drive habitat shifts and species distribution patterns in nature. There are numerous studies of ontogenetic niche shifts (i.e. changes in niche breadth and/or position during the life of an individual) in the ecological literature, but very few have examined the role of facilitation in driving these shifts, instead focusing on the role of bottom-up factors (Grof-Tisza et al. 2014). It may be that considerable evidence already exists for the role of facilitation in driving habitat shifts in mobile organisms, but it has yet to be examined from this perspective.

Finally this work shows marine systems pose unique challenges for compensatory restoration. Traditional mitigation approaches, like habitat creation or modification used in wetland mitigation, are often not feasible in marine habitats, which have hydrological and geological characteristics that are difficult to manipulate. And direct species restoration efforts often don't work or are not feasible given the ecological constraints of these systems. Therefore, novel approaches to mitigation will need to be explored by scientists and supported by policymakers to maximize the compensatory benefits of marine habitat restoration for society.

Appendices

A.1.1: Detailed epibiotic community composition results and individual species abundance over the study period

As noted in the text, we saw significant differences in plot community composition based on plot type at both Pothole (R = 0.781 , *P* < 0.001) and Occulto (R = 0.831, *P* < 0.001).

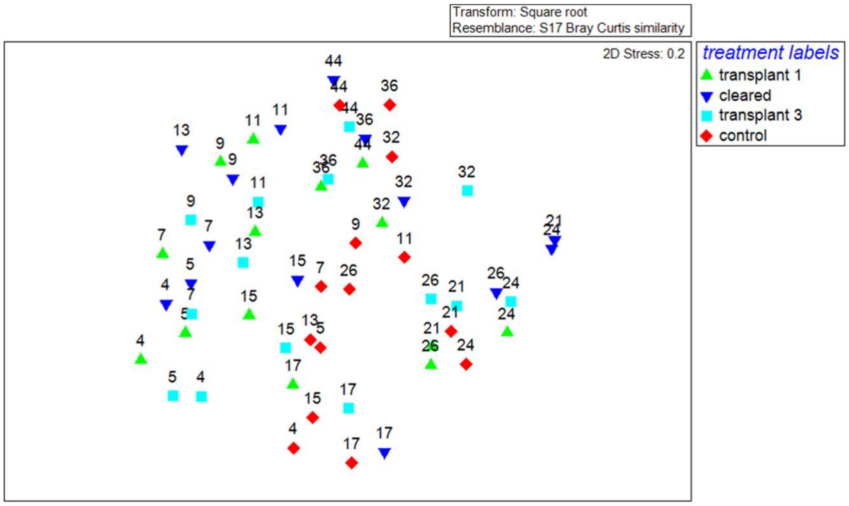


Fig. S1: MDS plot of plot community similarity by plot type (i.e. transplant 1, transplant 3, cleared, control) at Pothole (numbers indicate study month).

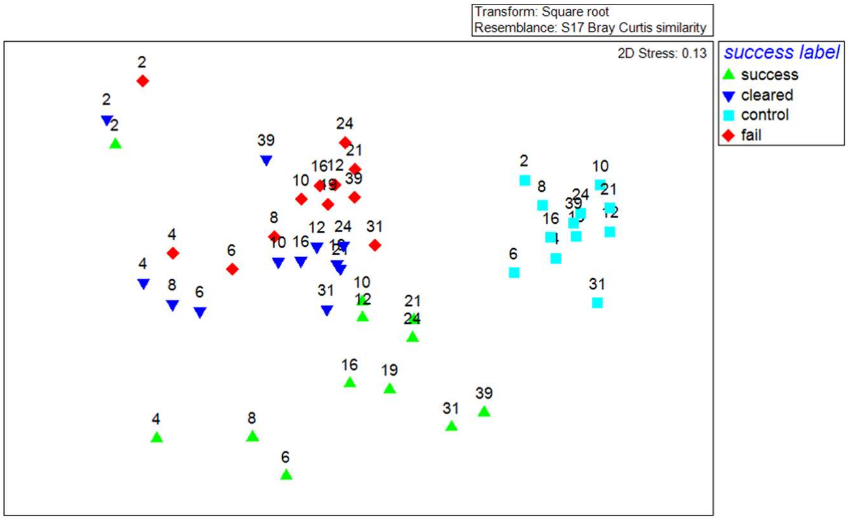


Fig. S2: MDS plot of plot community similarity by plot type (i.e. transplant 1, transplant 3, cleared, control) at Occulto (numbers indicate study month)

Yet, changes in the similarity of treatment plot communities to control communities over the study period show mussel transplants did not accelerate or alter the recovery trajectory towards a control state (Fig. 1.6).

We were then interested in whether there were patterns in individual species presence or abundance, which may not have been detected in the community composition analyses, that would indicate mussel transplants benefitted community recovery,. As reported in the text we did not see any consistent patterns in species presence to support this hypothesis. We found the same result when we examined patterns in individual species abundance (see below). With the possible exception of rock substrate abundance in plots at Occulto, the mean abundance of species/substrates in transplant plots appeared to be the same in value and behavior to the mean abundance of species/substrates in cleared plots:

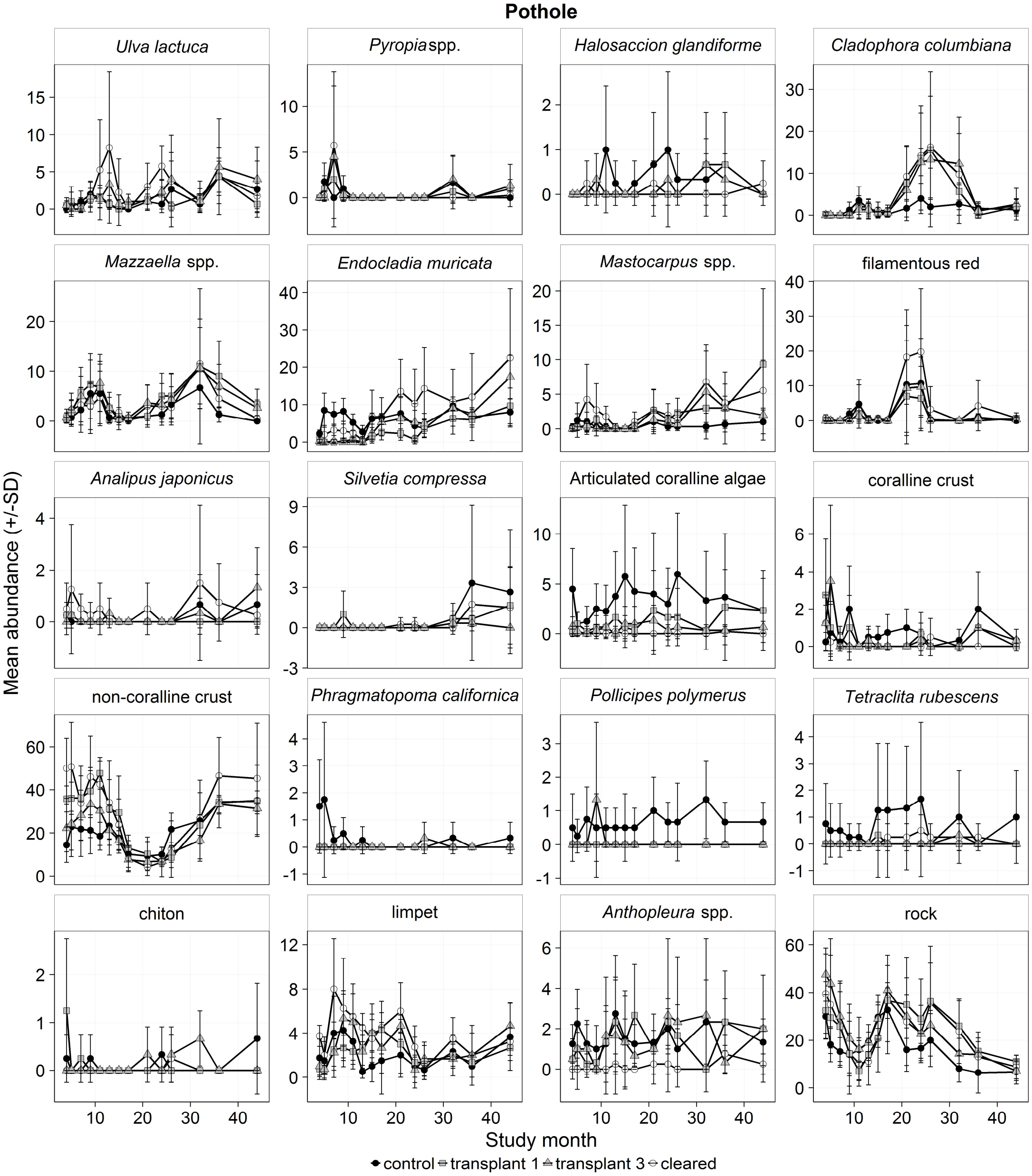


Fig. S3: Mean abundance (+/- SD) for each species observed in control, cleared, and transplant plots over the study period at Pothole.

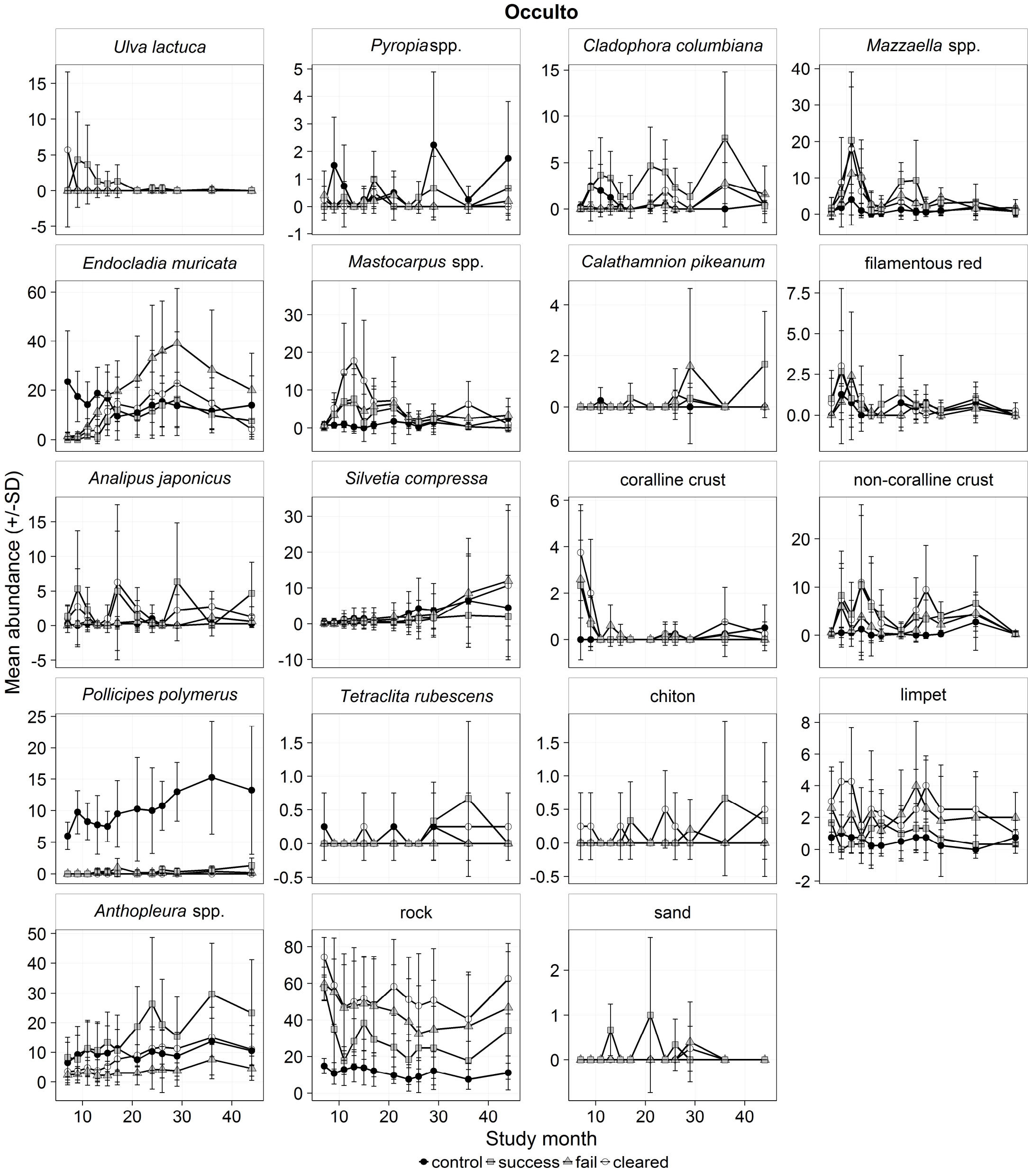
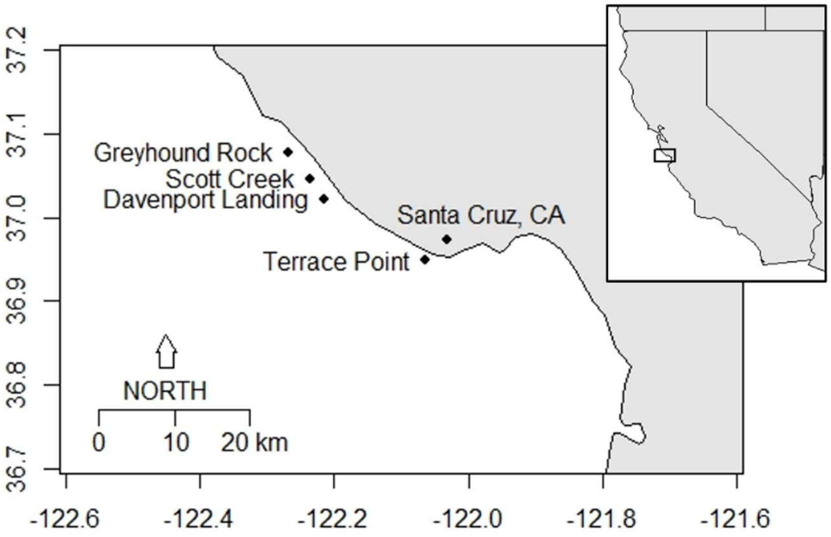


Fig. S4: Mean abundance (+/- SD) for each species observed in control, cleared, and transplant plots over the study period at Occulto.

A.2.1: Recruit survey study site map



A.2.2: Mussel genetic analysis methods

I used genetic analysis to identify a sample of mussel recruits collected at Greyhound Rock in April 2014. Recruits (< 10 mm) were collected along an upper and lower mussel zone transect using the sampling protocol used to survey recruit associations in this study. Greyhound Rock was selected based on previous recruitment data (Hart, unpublished) that indicated it was most likely to have other mytilid recruits. The collected mussel recruits were stored in ethanol in individual vials at -20 ºC until processed.

DNA extractions were conducted using a QIAGEN DNeasy Blood and Tissue kit. Prior to extraction, I removed mussel recruits from ethanol and allowed them to dry. For mussels > 5 mm, I extracted gill tissue from each shell. Mussels < 5 mm were too small to remove only gill tissue, therefore, I removed all tissue to use for DNA extraction. I followed the standard extraction procedure provided by QIAGEN but with a single elution step of 200 µL AE buffer.

I used a multiplex PCR method to distinguish between the three potential *Mytilus* species found in the central California area (*M. californianus, M. galloprovincialis,* and *M. trossolus*) (K. Mesa unpublished). This method uses four 12S mtDNA primers within a single reaction: a conserved forward primer (12sF34 5′GGGATCCTGGGTGTTAAAGG) and three unique reverse primers that amplify fragments of different base pair length:

12sR366 (*M. trossulus*, 366 bp) 5′TTTGTCTACTTAGTTGAGCTACCTTTT

12sR300 (*M. californianus*, 300 bp) 5'TATCCCAGGCTGACCTTAG

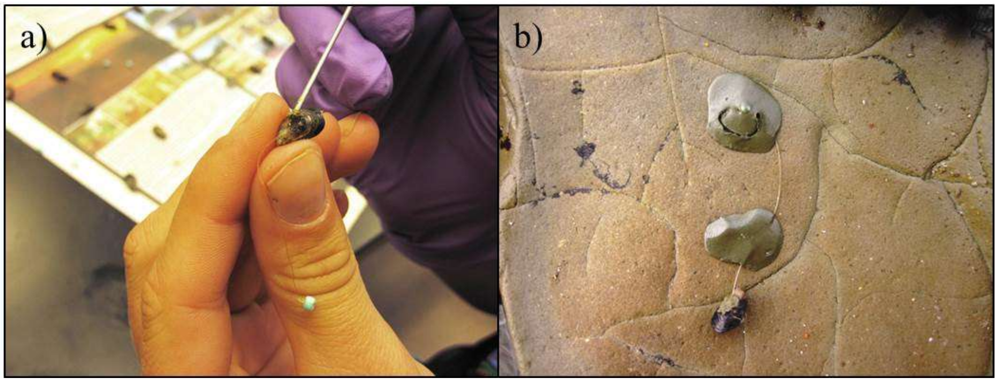
12sR231 (*M. galloprovincialis*, 231 bp) 5'AATAAACCCCTTCTACTAGCTGCAT

Each species is then easily identified by a differently sized band when visualized on a gel with adult controls.

Since this procedure was not optimized for large sample sizes, I created a small batch of PCR mixture for each set of 10 samples. This mixture was composed of 5 μL of each of the four 5 μM primer dilutions, 10 μL of 10 x Thermopol buffer (NEB), 10 μL of 2 mM dNTP, 1 μL 50 mM $MgCl_2$, 2 μL Tween 20, 0.8 μL Taq polymerase (NEB), and 46.2 μL of nanopure water.

For each 10 μL PCR reaction, I added 1 μL of sample DNA to each PCR tube (Applied Biosystems, .2 ml with cap) followed by 9 μL of PCR mix and allowed samples to sit for 10 minutes at room temperature before placing them in the PCR machine. The PCR program was 95 ºC for 3 mins [94 ºC for 30 secs, 64 ºC for 30 secs, 72 ºC for 20 secs] x 40 cycles, 72 ºC for 1 min. PCR products were separated by 2% agarose gel electrophoresis stained with ethidium bromide run for 30 mins at 120V. Individual mussel samples were then positively IDed using a 100bp ladder and comparisons to control samples of known *M. californianus, M. trossolus,* and *M. galloprovincialis.*

A.2.3 Detailed mussel tethering methods



I collected mussel recruits at Terrace Point during an afternoon low tide and placed them overnight in a water table with continuously flowing seawater. The following day I removed recruits from the water table and placed them in a small tub in preparation for tethering. Prior to tethering, the shell of each individual recruit was dried using a paper towel, and measured in three dimensions (shell length, height, and width) to +/- 0.02 mm using digital calipers. Individual recruit measurements were recorded and matched to a unique ID #. Then I glued a piece of 20 gauge monofilament fishing line (~50 mm long) to the center of the mussel valve using Loctite® Ultra Gel Control Super Glue. Each piece of fishing line was attached at the opposite end to a small bead (used to facilitate attachment in the field) and labeled with the recruit's unique ID # on a small piece of labelling tape. Once the super glue had dried (1-2 hours) it was covered with a small dab of marine epoxy using a metal probe as an applicator (Fig a).

Throughout the tethering process individual recruits remained exposed to air for no more than 3-5 hours and care was taken to ensure adhesives did not glue the mussel valves shut. After the marine epoxy was no longer tacky, I placed tethered recruits back into the seawater table overnight. I deployed the tethered recruits in the field during the following day's low tide (48 hours after collection). I used a 31 day pill organizer with holes drilled into the individual pill compartments to organize and separate the uniquely identified mussels in the water table and to facilitate transport and deployment in the field. Using this method ~60% of tethered recruits survived and attached to substrate during the first 48 hours and ~15% -28% survived the study period for growth analysis. While there were likely some negative effects of the tethering process on survival and growth I assumed they affected treatment groups equally and did not skew the overall patterns observed in this study.

Bibliography

Ambrose, R. F. 2007. Habitat restoration. Pages 260–263 *in* M. W. Denny and S. D. Gaines, editors. Encyclopedia of tidepools and rocky shores. Univ of California Press.

Ambrose, R. F., and N. Diaz. 2008. Pre-spill assessments of coastal habitat resources. California Department of Fish and Game Office of Spill Prevention and Response.

Ambrose, R. F., and J. R. Smith. 2005. Restoring rocky intertidal habitats in Santa Monica Bay. Santa Monica Bay Restoration Commission:1–116.

Angelini, C., and B. R. Silliman. 2012. Patch size-dependent community recovery after massive disturbance. Ecology 93:101–110.

Barnthouse, L. W., and R. G. Stahl. 2002. Quantifying natural resource injuries and ecological service reductions: Challenges and opportunities. Environmental Management 30:1–12.

Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis*-L (Mollusca). Journal of Animal Ecology 33:513–523.

Beck, M. W. 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Marine Ecology Progress Series 169:165–178.

Benedetti-Cecchi, L., F. Pannacciulli, F. Bulleri, P. Moschella, L. Airoldi, G. Relini, and F. Cinelli. 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Marine Ecology Progress Series 214:137–150.

Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. Trends in Ecology & Evolution 9:191–193.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976.

Borthagaray, A. I., and A. Carranza. 2007. Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. Acta Oecologica 31:243–250.

Bradshaw, A. D. 1983. The reconstruction of ecosystems. Journal of Applied Ecology 20:1–17.

Briggs, S. V. 2006. Integrating policy and science in natural resources: Why so difficult? Ecological Management and Restoration 7:37–39.

Broitman, B. R., C. A. Blanchette, B. A. Menge, J. Lubchenco, C. Krenz, M. Foley, P. T. Raimondi, D. P. Lohse, and S. D. Gaines. 2008. Spatial and temporal patterns of invertebrate recruitment along the West Coast of the United States. Ecological Monographs 78:403–421.

Brooker, R. W., F. T. Maestre, R. M. Callaway, C. J. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. I. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard, and R. Michalet. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96:18–34.

Brooks, R. P., and N. A. Gebo. 2013. Wetlands Restoration and Mitigation. Pages 421–440 Mid-Atlantic Freshwater Wetlands: Advances in Wetlands Science, Management, Policy, and Practice.

Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–218 Marine Community Ecology.

Burbidge, A. H., M. Maron, M. F. Clarke, J. Baker, D. L. Oliver, and G. Ford. 2011. Linking science and practice in ecological research and management: How can we do it better? Ecological Management and Restoration 12:54–60.

Byers, J. E., K. Cuddington, C. G. Jones, T. S. Talley, A. Hastings, J. G. Lambrinos, J. A. Crooks, and W. G. Wilson. 2006. Using ecosystem engineers to restore ecological systems. Trends in ecology & evolution 21:493–500.

Callaway, R. M., and Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78:1958–1965.

Carrington, E., G. M. Moeser, S. B. Thompson, L. C. Coutts, and C. A. Craig. 2008. Mussel attachment on rocky shores: the effect of flow on byssus production. Integrative and comparative biology 48:801–7.

Chapman, D. J., and B. E. Julius. 2005. The use of preventative projects as compensatory restoration. Journal of Coastal Research SI:120–131.

Choi, Y. D. 2004. Theories for ecological restoration in changing environment: toward “futuristic”restoration. Ecological Research 19:75–81.

Command Oil Spill Trustees. 2004. Command Oil Spill Final Restoration Plan and Environmental Assessment. Prepared by: United States Fish and Wildlife Service National Oceanic and Atmospheric Administration California Department of Fish and Game California Department of Parks and Recreation California State Lands Commission.

Commito, J. A., and B. R. Rusignuolo. 2000. Structural complexity in mussel beds: The fractal geometry of surface topography. Journal of Experimental Marine Biology and Ecology 255:133–152.

Conway-Cranos, L. 2012. Geographic variation in resilience: an experimental evaluation of four rocky intertidal assemblages. Marine Ecology Progress Series 457:67–83.

Cosco Busan Oil Spill Trustees. 2012. Cosco Busan Oil Spill Final Damage Assessment and Restoration Plan/Environmental Assessment. Prepared by California Department of Fish and Game, California State Lands Commission, National Oceanic and Atmospheric Administration, United States Fish and Wildlife Service, National Park Service, Bureau of Land Management.

Crain, C. M., and M. D. Bertness. 2006. Ecosystem engineering across environmental gradients: Implications for conservation and management. BioScience 56:211–218.

Dayton, P. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–389.

DOI. 2007. The Final Report of the U.S. Department of the Interior Natural Resource Damage Assessment and Restoration Federal Advisory Committee.

Dunford, R. W., T. C. Ginn, and W. H. Desvousges. 2004. The use of habitat equivalency analysis in natural resource damage assessments. Ecological Economics 48:49–70.

English, E., C. Peterson, and C. Voss. 2009. Ecology and economics of compensatory restoration. Report, NOAA Coastal Response Research Center.

Erlandsson, J., C. D. McQuaid, and S. Stanczak. 2011. Recruit/algal interaction prevents recovery of overexploited mussel beds: Indirect evidence that post-settlement mortality structures mussel populations. Estuarine, Coastal and Shelf Science 92:132–139.

Estes, J., N. Smith, and J. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology 59:822–833.

Fonseca, M., D. Meyer, and M. Hall. 1996. Development of planted seagrass beds in Tampa Bay, Florida, USA. II. Faunal components. Marine Ecology Progress Series 132:141–156.

Gómez-Aparicio, L. 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology 97:1202–1214.

Gómez-Aparicio, L., and R. Zamora. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14:1128–1138.

Grof-Tisza, P., M. Holyoak, E. H. Antell, and R. Karban. 2014. Predation and associational refuge drive ontogenetic niche shifts in an arctiid caterpillar. Ecology 96:80–89.

Gutiérrez, J. L., C. G. Jones, D. L. Strayer, and O. O. Iribarne. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:79–90.

Halpern, B. S., B. R. Silliman, J. D. Olden, J. F. Bruno, and M. D. Bertness. 2007. Incorporating positive interactions in aquatic restoration and conservation. Frontiers in Ecology and the Environment 5:153–160.

Hastings, A., J. E. Byers, J. a Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. Ecology Letters 10:153–64.

Hawkins, S. J., J. R. Allen, and S. Bray. 1999. Restoration of temperate marine and coastal ecosystems: nudging nature. Aquatic Conservation: Marine and Freshwater Ecosystems 9:23–46.

Hay, M. E. 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 62:739–750.

He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. Ecology Letters 16:695–706.

Healey, D., and K. A. Hovel. 2004. Seagrass bed patchiness: Effects on epifaunal communities in San Diego Bay, USA. Journal of Experimental Marine Biology and Ecology 313:155–174.

Heck, K., and R. Orth. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay: Decapod Crustacea. Estuaries and Coasts 3:289–295.

Hégaret, H., S. Shumway, G. Wikfors, S. Pate, and J. Burkholder. 2008. Potential transport of harmful algae via relocation of bivalve molluscs. Marine Ecology Progress Series 361:169–179.

Jenewein, B., and L. Gosselin. 2013. Ontogenetic shift in stress tolerance thresholds of *Mytilus trossulus*: effects of desiccation and heat on juvenile mortality. Marine Ecology Progress Series 481:147–159.

Johnson, S. B., and J. B. Geller. 2006. Larval settlement can explain the adult distribution of *Mytilus californianus* Conrad but not of *M. galloprovincialis* Lamarck or *M. trossulus* Gould in Moss Landing, central California: Evidence from genetic identification of spat. Journal of Experimental Marine Biology and Ecology 328:136–145.

Jones, C. G., J. L. Gutiérrez, J. E. Byers, J. A. Crooks, J. G. Lambrinos, and T. S. Talley. 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119:1862–1869.

Jones, C. G., and J. H. Lawton. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as Ecosystem Engineers. Oikos 69:373.

van Katwijk, M. M., A. Thorhaug, N. Marbà, R. J. Orth, C. M. Duarte, G. A. Kendrick, I. H. J. Althuizen, E. Balestri, G. Bernard, M. L. Cambridge, A. Cunha, C. Durance, W. Giesen, Q. Han, S. Hosokawa, W. Kiswara, T. Komatsu, C. Lardicci, K.-S. Lee, A. Meinesz, M. Nakaoka, K. R. O'Brien, E. I. Paling, C. Pickerell, A. M. A. Ransijn, and J. J. Verduin. 2016. Global analysis of seagrass restoration: the importance of large-scale planting. Journal of Applied Ecology 53:567–578.

Kinnetic Laboratories Inc. 1992. Study of the rocky intertidal communities of Central and Northern California. Report to the Minerals Management Service OCS

Study MMS 91-0089.

van de Koppel, J., J. C. Gascoigne, G. Theraulaz, M. Rietkerk, W. M. Mooij, and P. M. J. Herman. 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. Science 322:739–42.

Leonard, G. H. 1999. Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. Marine Ecology Progress Series 178:241–249.

Levrel, H., S. Pioch, and R. Spieler. 2012. Compensatory mitigation in marine ecosystems: Which indicators for assessing the "no net loss" goal of ecosystem services and ecological functions? Marine Policy 36:1202–1210.

Lively, C. M., and P. T. Raimondi. 1987. Desiccation, Predation, and Mussel-Barnacle Interactions in the Northern Gulf of California. Oecologia 74:304–309.

Lohse, D. P. 1993a. The importance of secondary substratum in a rocky intertidal community. Journal of Experimental Marine Biology and Ecology 166:1–17.

Lohse, D. P. 1993b. The effects of substratum type on the population dynamics of three common intertidal animals. Journal of Experimental Marine Biology and Ecology 173:133–154.

Lucas, B. J., and J. R. Smith. 2016. Alterations in human visitation patterns and behaviors in southern California rocky intertidal ecosystems over two-decades following increased management efforts. Ocean & Coastal Management 121:128–140.

Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology 97:199–205.

Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765.

Menge, B. A., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. P. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. Ecological Monographs 74:663–684.

Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973–979.

Murray, S., T. Denis, J. Kido, and J. Smith. 1999. Human visitation and the frequency and potential effects of collecting on rocky intertidal populations in southern California marine reserves. California Cooperative Oceanic Fisheries Investigations Reports 40:100–106.

Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. Ecological Monographs 66:409–429.

NOAA. 1997. Scaling Compensatory Restoration Actions. Guidance Document for Natural Resource Damage Assessment under the Oil Pollution Act of 1990. Silver Spring, MD.

NOAA. 2000. Habitat Equivalency Analysis: An Overview. National Oceanic and Atmospheric Administration, Washington, DC.

Okamura, B. 1986. Group living and the effects of spatial position in aggregations of *Mytilus edulis*. Oecologia 69:341–347.

Oliet, J. A., and D. F. Jacobs. 2012. Restoring forests: Advances in techniques and theory. New Forests 43:535–541.

Padilla, F. M., and F. I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. Frontiers in Ecology and the Environment 4:196–202.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120.

Paine, R. T., J. L. Ruesink, A. Sun, E. L. Soulanille, M. J. Wonham, C. D. G. Harley, D. R. Brumbaugh, and D. L. Secord. 1996. Trouble on oiled waters: lessons from the *Exxon Valdez* Oil Spill. Annual Review of Ecology and Systematics 27:197–235.

Palmer, M. a., R. F. Ambrose, and N. L. Poff. 1997. Ecological Theory and Community Restoration Ecology. Restoration Ecology 5:291–300.

Pennings, S. C., and M. D. Bertness. 2001. Salt Marsh Communities. Pages 289–316 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine Community Ecology.

Petersen, J. 1984a. Establishment of mussel beds: attachment behavior and distribution of recently settled mussels (*Mytilus californianus*). The Veliger 27:7–13.

Petersen, J. 1984b. Larval settlement behavior in competing species: *Mytilus californianus* Conrad and *M. edulis* L. Journal of experimental marine biology and ecology 82:147–159.

Peterson, C. H., S. S. Anderson, G. N. Cherr, R. F. Ambrose, S. Anghera, S. Bay, M. Blum, R. Condon, T. A. Dean, M. Graham, M. Guzy, S. Hampton, S. Joye, J. Lambrinos, B. Mate, D. Meffert, P. Sean, S. P. Powers, P. Somasundaran, R. B. Spies, C. M. Taylor, R. Tjeerdema, and E. E. Adams. 2012. A tale of two spills: novel science and policy implications of an emerging new oil spill model. BioScience 62:461–469.

Presidential Documents. 2015. Mitigating Impacts on Natural Resources from Development and Encouraging Related Private Investment. Federal Register: The Daily Journal of the United States Government 80:68743–68747.

Raimondi, P., D. Orr, C. Bell, M. George, S. Worden, R. Gaddam, L. Anderso, and D. Lohse. 2009. Determination of the extent and type of injury to rocky intertidal algae and animals one year after the initial spill (*Cosco Busan*): a report prepared for OSPR (California Fish and Game).

Schiffers, K., and K. Tielborger. 2006. Ontogenetic shifts in interactions among annual plants. Journal of Ecology 94:336–341.

Seed, R. 1976. Ecology. Pages 13–65 *in* B. Bayne, editor. Marine mussels: their ecology and physiology. Cambridge University Press, Cambridge, England.

Seed, R., and T. H. Suchanek. 1992. The mussel *Mytilus*: ecology, physiology, genetics and culture. Pages 87–170 Population and community ecology of *Mytilus*. Elsevier: New York.

Silliman, B. R., M. D. Bertness, A. H. Altieri, J. N. Griffin, M. C. Bazterrica, F. J. Hidalgo, C. M. Crain, and M. V Reyna. 2011. Whole-community facilitation regulates biodiversity on Patagonian rocky shores. PloS one 6:e24502.

Silliman, B. R., E. Schrack, Q. He, R. Cope, A. Santoni, T. van der Heide, R. Jacobi, M. Jacobi, and J. van de Koppel. 2015. Facilitation shifts paradigms and can amplify coastal restoration efforts. Proceedings of the National Academy of Sciences 112:14295–14300.

Smith, J. R., P. Fong, and R. F. Ambrose. 2008. The impacts of human visitation on mussel bed communities along the California coast: are regulatory marine reserves effective in protecting these communities? Environmental Management 41:599–612.

Smith, J. R., and S. N. Murray. 2005. The effects of experimental bait collection and trampling on a *Mytilus californianus* mussel bed in southern California. Marine Biology 147:699–706.

Snover, M. L., and J. A. Commito. 1998. The fractal geometry of *Mytilus edulis* L. spatial distribution in a soft-bottom system. Journal of Experimental Marine Biology and Ecology 223:53–64.

SS Cape Mohican Trustee Council. 2002. *SS Cape Mohican* Oil Spill Restoration Plan and Environmental Assessment. Prepared by California Department of Fish and Game, California Department of Parks and Recreation, National Park Service, United States Fish and Wildlife Services, National Oceanic and Atomospheric Administration.

Stachowicz, J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience 51:235–246.

Suchanek, T. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 31:105–120.

Suchanek, T. 1992. Extreme biodiversity in the marine environment: Mussel bed communities of *Mytilus californianus*. Northwest Environmental Journal 8:150–152.

Suchanek, T. 1993. Oil impacts on marine invertebrate populations and communities. American Zoologist 33:510.

Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. Trends in Ecology and Evolution 19:305–308.

Sutton-Grier, A. E., A. K. Moore, P. C. Wiley, and P. E. T. Edwards. 2014. Incorporating ecosystem services into the implementation of existing U.S. natural resource management regulations: Operationalizing carbon sequestration and storage. Marine Policy 43:246–253.

Thompson, R. C., T. P. Crowe, and S. J. Hawkins. 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environmental Conservation 29:168–191.

Tokeshi, M., and L. Romero. 1995. Filling a gap: Dynamics of space occupancy on a mussel-dominated subtropical rocky shore. Marine Ecology Progress Series 119:167–176.

Torch/Platform Irene Trustee Council. 2007. Torch/Platform Irene Oil Spill Final Restoration Plan and Environmental Assessment. Prepared by United States Fish and Wildlife Service, California Department of Fish and Game, United States Department of Air Force, Vandenberg Air Force Base, California State Lands Commission with Assistance from Santa Barbara County Planning and Develop.

Walker, L. R., J. Walker, and R. J. Hobbs. 2007. Linking restoration and ecological succession. Springer, New York.

Whitaker, S. G., J. R. Smith, and S. N. Murray. 2010. Reestablishment of the southern California rocky intertidal brown alga, *Silvetia compressa*: an experimental investigation of techniques and abiotic and biotic factors that affect restoration success. Restoration Ecology 18:18–26.

Wright, J., and C. Jones. 2004. Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. Ecology:2071–2081.

Wright, J., C. Jones, and A. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101.

Yu, Y. Q., Q. S. Zhang, Y. Z. Tang, S. B. Zhang, Z. C. Lu, S. H. Chu, and X. X. Tang. 2012. Establishment of intertidal seaweed beds of *Sargassum thunbergii* through habitat creation and germling seeding. Ecological Engineering 44:10–17.

Zedler, J. B., and S. Kercher. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. Annual Review of Environment and Resources 30:39–74.