Title: Functional redundancy buffers mobile invertebrates against the loss of foundation species on rocky shores

Running Title: Functional redundancy maintains diversity

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ABSTRACT

Foundation species are vital to the maintenance of biodiversity and ecosystem functioning in many systems. On rocky shores, rockweeds – large brown algae in the Order Fucales – have the potential to provide habitat and ameliorate stress for mobile invertebrates. To determine the relative role of two rockweeds (*Silvetia compressa* and *Pelvetiopsis* spp.) as foundation species at sites along a latitudinal gradient, we conducted observational surveys and then initiated a 12-month removal experiment. We found that richness and abundance of mobile invertebrates declined over time when rockweeds were removed, but only at the southernmost site. In contrast, at our other sites, there was no change in the richness and abundance of mobile invertebrates following rockweed removal. At the southern site, rockweeds played an important role in maintaining mobile invertebrate diversity. At our central and northern sites, rockweeds were less important in maintaining the diversity of mobile invertebrates. At these sites, alternative species – bladed and branching taxa in the genera *Mastocarpus*, *Mazzaella*, *Corallina*, and *Endocladia* – co-occur with rockweeds and can buffer the system against their loss. However, these alternative foundation species are rare to absent at the southern site, potentially due to greater physical stress. The loss of rockweed foundation species, which are declining at our southern site, can have cascading effects by causing local co-extinctions of associated species. This study highlights the importance of foundation species, especially in areas where their functional redundancy is low, and how the loss of foundation species can alter diversity, leading to potential changes in ecosystem functioning.

Key Words: Foundation Species, Rockweeds, Functional Redundancy, California

1. INTRODUCTION

Foundation species – dominant species that provide habitat for other organisms, creating community structure and enhancing stability (Dayton 1972, Bracken et al. 2007, Ellison 2019) – play integral roles in maintaining ecosystem functioning and biodiversity in a multitude of habitats. Foundation species modify the physical structure of ecosystems, influencing the diversity and abundance of associated species (Bertness et al. 1999, Bruno & Bertness 2001). These species can regulate the diversity of associated species by allowing additional species to survive in a location or by reducing the survivorship of competing species (Dayton 1971, Bertness et al. 1999, Lilley & Schiel 2006). The role and importance of a foundation species can vary across locations depending on environmental conditions, presence of other foundation species, and the attributes of the species themselves, including morphology, size, and chemical defenses (Angelini et al. 2015, McAfee et al. 2016, Wernberg et al. 2020).

Understanding how foundation species interact with other species and the effects of those interactions on community structure has been a long-standing goal of ecologists (Ellison 2019). Recognizing the importance of direct and indirect relationships between organisms – including foundation species and the organisms associated with them – is essential for predicting how ecosystems will respond to the threat of climate change. The loss of foundation species has resulted in corresponding rapid declines in biodiversity across habitats, making it increasingly important to understand how these changes will impact systems (Hawkins 1983, Jenkins et al. 1999, Ellison et al. 2005, Pocklington et al. 2018). Over the last several decades, researchers have highlighted the need to understand how species interactions, including those involving foundation species, may be modified by global climate change (Tylianakis et al. 2008). The complex nature of the interactions between foundation species and the species and ecosystems associated with them complicates predictions of community responses to global change (Ellison et al. 2005). For example, the decline of the American chestnut has led to not only changes in the communities directly associated with the chestnut but to changes in adjacent aquatic invertebrate communities (Vandermast et al. 2001). Furthermore, species responses to the loss of foundation species may depend on environmental context. For example, Moore et al. (2007) found that when *Fucus vesiculosus* was removed, the response of limpet species to the loss differed depending on whether the limpet species had a cold or warm water affinity.

Canopy-forming seaweeds provide well-known examples of stress amelioration by foundation species (Leonard 2000, Lilley & Schiel 2006). On southern California rocky shores, the rockweed *Silvetia compressa* shelters the chiton *Cyanoplax hartwegii*, and removal of the *Silvetia* canopy results in declines in *C. hartewegii* (Sapper & Murray 2003). Similarly, removal of the fucoid seaweed *Hormosira banksii* from the New Zealand rocky intertidal zone resulted in profound changes in community structure, including declines in understory algae (Lilley & Schiel 2006). Canopy-forming macroalgae can also have negative effects on other species, including preventing the recruitment of understory species by limiting light or by abrading recruits with their branches (Hawkins 1983, Kiirikki 1996, Jenkins 1999, Connell 2003, Jenkins et al. 2004), but, on average, foundation species tend to enhance the diversity and abundance of associated taxa (Jenkins et al. 1999, Bracken et al. 2007, Pocklington et al. 2018). Because of the roles that foundation species may play in ameliorating stress, understanding how communities are impacted by the loss of these important species can allow researchers to make better predictions about how systems will be altered by climate change. Given their roles in maintaining biodiversity and mitigating stress, foundation species may also be important targets for conservation (Bracken et al. 2007).

Many systems, including forests and coral reefs, are maintained by several foundation species operating concurrently, and an emerging body of research investigates how multiple foundation species affect communities and ecosystems (Altieri et al. 2007, Angelini et al. 2011, Thomsen et al. 2018). A system that is maintained by multiple, co-occurring foundation species may be characterized by a "faciltation cascade", where one foundation species enhances another. For example, Altieri et al. (2007) found that a primary foundation species, cordgrass, facilitated the settlement of a secondary foundation species, mussels, which further enhanced community structure on New Engand shores. Similarly, Bracken (2018) documented kelp – a known foundation species – growing on tubeworms, which provided a hard substratum in an otherwise unsuitable soft-sediment habitat. It is clear that multiple, co-occurring foundation species collectively structure many ecosysetms, but most research still focuses on a single, dominant species. We therefore focused on the roles of co-occurring foundational seaweed species on California rocky shores.

Furthermore, the interactions between species can vary across locations depending on the biotic and/or abiotic conditions associated with a site and across stress gradients. For example, the roles that foundation species play in structuring a community can change from facilitative to inhibitory depending on conditions. Leonard (2000) found that the interactions between the rockweed *Ascophyllum* and associated barnacle species in New England differed between northern and southern sites. *Ascophyllum* only played a facilitative role, enhancing barnacle survival, at more thermally stressful southern sites. At northern sites, predator abundances were higher under the algal canopy, and barnacle survival was reduced in the presence of *Ascophyllum* (Leonard 2000). Similarly, Hawkins (1983) found that the role of *Fucus* spp. differed depending on wave exposure. On moderately wave-exposed shorelines, *Fucus* abraded recruiting barnacles, reducing abundance (see also Jenkins et al. 1999). However, on sheltered shorelines, barnacle abundances were greater under the *Fucus* canopy. This research highlights the need to understand the context-dependency of the relationships between foundation and associated species.

Foundation species can also compete with one another for primary space and other resources, and both the sign (i.e., positive or negative), and the magnitudes of their effects can differ both among and within foundation species. For example, palo verde trees and saguaro cacti are two co-occurring foundation species in the Sonoran Desert. Palo verde trees provide shade and frost protection, ameliorating stress for small saguaros (Vandermeer 1980). However, the palo verde trees are subsequently out-competed by mature saguaros and are less effective at providing reseources for desert animal species (Turner et al 1966, Wolf & del Rio 2003). In coral reef systems, corals and seaweeds, both of which play foundational roles, often compete (Clements et al. 2020). For example, coral recruitment is reduced by the seaweed *Turbinaria* (Gleason 1996), but *Turbinaria* also enhances diversity and abundance of associated algal species (Bittick et al. 2010). The benefit of having multiple foundation species in a system appears to be context dependent. If one foundation species is lost, a community may remain more stable if another species is functionally redundant and can fulfill the same role in the associated communities.

Rockweed species – brown algae in the Order Fucales – can be found on rocky shores worldwide (Benedetti-Cecchi et al. 2001, Sapper & Murray 2003, Lilley & Schiel 2006). Multiple studies have demonstrated that rockweeds are declining, including some cases of local extinction (Benedetti-Cecchi et al. 2001, Gunnill 1980, Jenkins et al. 2008). Along the coast of California, USA, the mid- to upper-intertidal zone is dominated by rockweeds that form dense canopies, potentially providing habitat for a number of species. California rockweeds are also under threat and have been in decline over the past several decades (Whitaker et al. 2010). Declines in these dominant foundation species may have cascading effects on ecosystem functioning and stability (Crowe et al. 2013, Ellison 2019).

Here, we addressed how the roles of multiple rockweed species (*Silvetia compressa*, *Pelvetiopsis limitata*, and *Pelvetiopsis californica*) in structuring mobile invertebrate communities may change along a gradient in environmental conditions along the California coast. We hypothesized that rockweeds would ameliorate harsh physical conditions, increasing the abundance and richness of associated mobile invertebrate species. We also hypothesized that mobile invertebrate assemblages would be negatively impacted by the removal of rockweeds at all sites.

2. MATERIALS & METHODS

2.1. Study sites & species

We conducted surveys and experiments at three sites across ~700 km of the California rocky shoreline between June 2016 and July 2017 (Figure 1, Table 1). Sites included the University of California Bodega Marine Reserve (38.32° N, 123.07° W), the University of California Kenneth S. Norris Rancho Marino Natural Reserve (35.56° N, 121.08° W), and Corona del Mar State Beach (33.59° N, 117.87° W).

The geographic distribution of *Silvetia compressa* (J. Agardh) E.Serrão, T. O. Cho, S. M. Boo and Brawley is from Humboldt County, California, USA to Punta Baja, Baja California, Mexico (Silva 1990). *S. compressa* was present at all three of our study sites. The geographic distribution of *Pelvetiopsis limitata* (Setchell) N. L. Gardner is from Vancouver Island, British Columbia, Canada to San Luis Obispo County, California, USA (Abbott & Hollenberg 1976).

The geographic distribution of *Pelvetiopsis californica* (P. C. Silva) Neiva, Raimondi, G. A. Pearson and Serrão is from San Luis Obispo County, California, USA to Islas San Benito, Baja California, Mexico (Abbott & Hollenberg 1976). *S. compressa* grows to be 5-90 cm and *P. limitata* grows to be between 2-15 cm (Abbott & Hollenberg 1976, Figure 1). *P. californica* is between 10-50 cm in length, but at our site individuals were rarely larger than 20 cm (Abbott & Hollenberg 1976, Figure 1). Hereafter, *Pelvetiopsis* refers to *P. limitata* at Bodega Marine Reserve and Rancho Marino and to *P. californica* at Corona del Mar.

Intertidal distributions and physical characteristics of species and sites varied with location (Table 1). The water and air temperatures were measured using TidbiT® dataloggers (Onset Computer Corporation, Bourne, Massachusetts, USA) attached to the substratum outside of the rockweed canopy. Dataloggers were programmed to measure temperatures every 15 minutes. The maximum tide height of *Silvetia compressa* increased slightly at more northern locations. The minimum tide height of *S. compressa* was similar at Bodega Marine Reserve and Rancho Marino but much lower at Corona del Mar. The tidal distribution of *Pelvetiopsis limitata* was higher at Bodega Marine Reserve than Rancho Marino. Within the *Silvetia* zone, the average air and water temperature at each site increased with decreasing latitude.

2.2. Observational study

At our three study sites, we surveyed the rockweed zone (typically low to mid-high intertidal) for the abundance of rockweeds and their associated taxa. At each site, a 50 meter transect was laid parallel to the water line, and 10 vertical transects were randomly placed along the horizontal transect. Along each vertical transect, we surveyed five 0.25 m^2 evenly spaced quadrats within the zone of each species (N = 50 quadrats / per site). We counted the number of mobile invertebrates in each quadrat and quantified cover of sessile invertebrates and macroalgae. Species were identified to the lowest taxonomic level using field guides and taxonomic keys. Surveys were conducted prior to initiating experiments in June and July 2016.

2.3. Removal experiment

Based on the data from our observational study, we determined the center of each rockweed species' vertical distribution based on abundances, and we established N = 15 circular plots (25 cm diameter) at this central elevation for each species at each of our three study sites (Figure 1). Whereas the plot size was small, it was necessary in order to minimize disturbance in the reserves and State Beach where we conducted our work. We selected the center of the distribution to minimize impacts to the upper and lower edges of the populations, where abundances were lower. This was especially important given that two of our study locations were in marine protected areas. At each site, we applied treatments to each rockweed species independently of one another. At each site, we established and maintained N = 3 replicates of each of five treatments: (1) no rockweed (natural absence), (2) rockweed absent but mimic disturbance associated with removal, (3) rockweeds present, (4) rockweeds present and mimic disturbance, and (5) rockweeds removed (press removal). Prior to the application of treatments, all plots were surveyed for abundance of rockweed (cover) and mobile invertebrate species (individual counts). Plots where rockweeds were present had at least 80% cover of the target rockweed species prior to the application of the treatment. For mimicked disturbance treatments, we haphazardly scraped four one-cm-diameter areas (approximately the size of holdfast attachments). For the press removal treatment, we removed the entire thallus of the target rockweed species within the plots. We also trimmed the branches of adjacent rockweed thalli surrounding the removal plots to prevent impacts of canopy of plants attached outside of the plots. Plots were resurveyed every three months for one year. We removed all rockweed recruits that had grown in the plot on each survey date.

2.4. Data analysis

To determine if effective tide height influenced mobile species richness and abundance, we divided the quadrats into five zones (low, low-mid, mid, mid-high, high) based on surveyed tidal elevations. No rockweeds were present in the high zone, so this zone was omitted. For each site for each species, we used a two-way ANOVA to compare the main effect of tide height and rockweed presence on mobile invertebrate richness and abundance. We used a Shapiro-Wilk Test to test for the assumption of normality and Levene's Test to test for the assumption of the homogeneity of variances. These assumptions were not violated. Tukey post-hoc tests were used to compare the effects of rockweed species at each tide height. Rockweed species were analyzed separately, as they are vertically separated at each site. We used a repeated-measures ANOVA to compare removal and control plots over time at each site. We did not include procedural controls in these analyses because disturbance without rockweed removal did not alter invertebrate abundance or diversity. This was true when rockweeds were absent (natural absence vs. absence with disturbance; Repeated-measures ANOVA: Month x Treatment, *Pelvetiopsis*: abundance $p = 0.83$ richness: $p = 0.74$; *Silvetia*: abundance $p = 0.78$ richness: $p = 0.69$) and present (rockweeds present vs. present with disturbance; Repeated-measures ANOVA: Month x Treatment, *Pelvetiopsis*: abundance $p = 0.64$ richness: $p = 0.58$; *Silvetia*: abundance $p = 0.71$ richness: $p = 0.84$). Sites were analyzed separately, as different rockweed species were present at the different sites. Pair-wise post-hoc tests were done to compare treatments at each time point. Lastly, we compared the mobile invertebrate community pre-removal and 12 months post-removal using PERMANOVA and SIMPER analyses. For PERMANOVA analyses we used a Mauchly's Test to test for the assumption of sphericity and a Shapiro-Wilk Test to test for the assumption of normality. When the assumption of sphericity was violated we reported the Greenhouse-Geisser corrected p-values. Differences between treatments were visualized using principal coordinates analyses (PCoA; Borg & Groenen 2005) based on Bray-Curtis dissimilarity matrices. Analyses were conducted using R Core Team v 3.2.2 and R Studio v 1.1.453 ezANOVA and vegan packages (R Studio Team 2015).

3. RESULTS

3.1. Observational study

The average percent cover of *S. compressa* was highest in the low-mid zone of the intertidal at each site (Figure 1B, 1C, & 1D). *P. limitata* was present at the Bodega Marine Reserve and Rancho Marino sites. The average percent cover of *P. limitata* was similar in the mid and mid-high zones at each site, but the cover was much higher at Bodega Marine Reserve than at Rancho Marino Reserve (Figure 1B & 1C). The percent cover of *P. californica* was similar in the mid and mid-high zones at Corona del Mar (Figure 1D). *P. californica* was present at the Rancho Marino and Corona del Mar sites. At Rancho Marino, where *P. californica* is rare and patchy (L. Elsbery, *pers. obs.*), we only surveyed and established plots within the *P. limitata* zone.

Rockweed presence was generally associated with higher mobile invertebrate species richness and abundance across quadrats at all three sites. Mobile invertebrate richness was always higher where *Silvetia* was present in all three zones where this species of rockweed was found. With the exception of the mid-intertidal zone in the Bodega Marine Reserve, we observed a similar pattern for mobile invertebrate abundance in plots with and without *Silvetia*. At all sites, the presence of *Pelvetiopsis* was associated with higher mobile invertebrate richness and abundance in the highest zone where *Pelvetiopsis* was found.

The relationship between rockweeds and mobile invertebrate richness and abundance in the Bodega Marine Reserve depended on tide height (Richness: two-way ANOVA: tide height, $p = 0.06$; rockweed, $p = 0.05$; tide height x rockweed, $F = 16.72$, $p < 0.001$, Figure 2A; Abundance: two-way ANOVA: tide height, $p = 0.08$; rockweed, $p = 0.06$; tide height x rockweed, $F = 18.12$, $p < 0.001$; Figure 2B). The presence of *Silvetia* only increased mobile invertebrate species richness in the low zone ($p = 0.03$). *Pelvetiopsis* increased mobile species richness and abundance in the highest zone where *Pelvetiopsis* was present (Richness and Abundance: $p < 0.001$).

The relationship between rockweeds and mobile invertebrate richness and abundance at Rancho Marino depended on tide height (Richness: two-way ANOVA: tide height, $p = 0.08$; rockweed, $p = 0.04$; tide height x rockweed, $F = 11.22$, $p < 0.001$; Figure 2C; Abundance: two-way ANOVA: tide height, $p = 0.06$; rockweed, $p = 0.05$; tide height x rockweed, $F = 14.62$, $p = 0.03$; Figure 2D). Mobile species richness was significantly higher in low ($p < 0.001$) and mobile richness and abundance was higher in the low-mid plots (Richness: $p = 0.01$, Abundance: $p < 0.001$) where *Silvetia* was present and in mid-high plots when *Pelvetiopsis* was present (Richness: $p < 0.001$; Abundance: $p = 0.04$).

The relationship between rockweeds and mobile invertebrate richness at Corona del Mar depended on tide height (Richness: two-way ANOVA: tide height, $p = 0.03$; rockweed, $p = 0.03$; tide height x rockweed, $F = 13.45$, $p < 0.001$; Figure 2E; Abundance: two-way ANOVA: tide height, $p = 0.04$; rockweed, $p = 0.05$; tide height x rockweed, $F = 10.17$, $p < 0.001$; Figure 2F). Plots with rockweed species present had higher mobile invertebrate richness abundance than plots without rockweed; these differences were only significant for *Pelvetiopsis* in the highest zone (Richness: p = 0.03; Abundance: p = 0.02) and in the mid zone for *Silvetia* (p = 0.01).

At the mid-point of the tidal distribution of *Pelvetiopsis,* percent cover of seaweeds decreased from north to south (Table 2). At our northern and central sites, cover of branched (*Endocladia*) and bladed species (*Mastocarpus*) was higher than unoccupied "bare" space, but at Corona del Mar, bare rock and non-coralline crusts dominated the available space in the *Pelvetiopsis* zone. Similarly, at the mid-point of the distribution of *Silvetia*, seaweed cover was higher and bare space was lower at Bodega Marine Reserve and Rancho Marino than at Corona del Mar (Table 3). At our northern and central sites, cover of branched (*Endocladia* and *Corallina*) and bladed species (*Mastocarpus* and *Mazzaella*) was higher than bare rock cover, but at Corona del Mar, bare rock and non-coralline crusts dominated the available space (Table 3).

3.2. Removal experiment

The richness and abundance of mobile invertebrates were similar at Bodega Marine Reserve and Rancho Marino. The richness and abundance of mobile invertebrates was similar over time regardless of the presence or absence of *Pelvetiopsis* or *Silvetia* (Figures 3A-3D, 4A-4D; See Supplementary Tables 1-4 & 7-10).

For *Pelvetiopsis* plots at Corona del Mar, the effect of treatment on the richness of mobile invertebrates changed over time (Repeated-measures ANOVA: Month x Treatment p = 0.04, See Supplementary Table 5, Figure 3E). Initially, removal plots were to similar control plots, but over time removal plots became more similar to "no rockweed" plots. For *Pelvetiopsis* plots, the effect of treatment on the abundance of mobile invertebrates changed over time (Repeated-measures ANOVA: Month x Treatment, $p < 0.05$; Supplementary Table 6, Figure 3F). After nine months, the removal plots and "no rockweed" plots were significantly different from the control plots (control vs. removal, $p = 0.01$; control vs. “no rockweed”, $p = 0.02$), and this trend continued until the end of the experiment. Average mobile invertebrate richness and abundance were lowest at Corona del Mar compared to our other two sites.

For *Silvetia* plots at Corona del Mar, the effect of treatment on the richness of mobile invertebrates changed over time (Repeated-measures ANOVA: Month x Treatment, $p < 0.05$; Supplementary Table 11, Figure 4E). Initially, removal plots were similar to control plots, but over time removal plots became more similar to “no rockweed” plots. After nine months, the removal plots and “no rockweed” plots were significantly different from the control plots for mobile invertebrate richness (control vs. removal, $p = 0.01$; control vs. “no rockweed”, $p = 0.01$) and this trend continued until the end of the experiment. For *Silvetia* plots, the effect of treatment on the abundance of mobile invertebrates changed over time (Repeated-measures ANOVA: Month x Treatment, $p < 0.05$; See Supplementary Table 12, Figure 4F). After six months, the removal plots and “no rockweed” plots were significantly different from the control plots (control vs. removal $p = 0.02$; control vs. “no rockweed” $p = 0.03$) and this trend continued until the end of the experiment.

There was no difference in the community composition of plots in the *Pelvetiopsis* zone at the beginning and end of the experiment at Bodega Marine Reserve (PERMANOVA: $p = 0.74$, Figure 5A) or at Rancho Marino (PERMANOVA: $p = 0.64$, Figure 5C). At Corona del Mar, we observed significant differences between the initial and final mobile invertebrate communities when *Pelvetiopsis* was removed (PERMANOVA: $p < 0.001$, Figure 5E). A SIMPER analysis indicated that the species that contributed the most to the difference between communities were the limpets *Lottia scabra* and *Lottia austradigitalis* and the snail *Littorina* sp. Twelve months after *Pelvetiopsis* was removed, these species had all declined in abundance.

Similarly, there was no difference in the community composition of plots in the *Silvetia* zone at the beginning and end of the experiment at Bodega Marine Reserve (PERMANOVA: $p = 0.61$, Figure 5B) or at Rancho Marino (PERMANOVA: $p = 0.69$, Figure 5D). When *Silvetia* was removed from plots at Corona del Mar there was a significant difference in mobile invertebrate communities (PERMANOVA: $p < 0.05$, Figure 5F). The species that contributed the greatest differences between communities were the barnacle *Fissurella volcano,* the snail *Chlorostoma funebralis,* and the chiton *Cyanoplax hartwegii,* all of which declined in abundance over the 12-month experiment.

4. DISCUSSION

We found that the role of rockweeds as foundation species changed along a latitudinal gradient. Rockweeds at our central and northern sites played a less important role in structuring mobile invertebrate communities than rockweeds at our most southern site. At our southern site, removal of rockweeds appreciably decreased the richness and abundance of mobile invertebrate species in our plots (Figures 3E, 3F, 4E, & 4F). The differences in results between our observational study and removal experiment are likely associated with the locations of plots. Removal plots were only in the central part of tidal distribution, whereas observational plots were placed throughout the tidal distribution of the rockweeds allowing for different effects at the extreme ends of their distributions. Additionally, areas where rockweeds were naturally absent tended to be inhospitable to other organisms.

One potential factor underlying the latitudinal differences could be changes in air temperatures, which could alter the importance of these foundation species; average air and water temperatures increased by 7°C from north to south (see Table 1), but many of the invertebrate species remained the same. And whereas there is evidence for greater thermotolerance in southern populations (e.g., Gleason & Burton 2013), those differences cannot compensate for a 7ºC north-to-south temperature differential. In particular, the warmer air temperatures at our southern site may make rockweeds more important for stress amelioration. Changes in the importance of rockweeds as facilitators have been documented along the New England coast, where *Ascophyllum* only facilitates associated species at more thermally stressful southern locations (Leonard 2000).

Additionally, rockweeds may be functionally redundant at our northern and central sites, where a number of alternative seaweed species co-occur that could provide stress amelioration (Tables 2 & 3). Thomsen and South (2019) found that removal of the large (up to several meters in length) brown alga *Durvillaea* spp., also in the Fucales, allowed for alternative foundation species to colonize plots, altering the interactions among understory species. This is consistent with observations at Bodega Marine Reserve and Rancho Marino, where several species of bladed and branching seaweeds (e.g., *Mazzaella*, *Mastocarpus*, *Endocladia*, *Corallina*) co-occurred with our target rockweeds and seem to have compensated for their loss. However, at Corona del Mar there were few alternative seaweed species for mobile invertebrates to use as habitat when rockweeds were removed. Prior to establishing our treatments, a large proportion of plots at Corona del Mar contained bare rock or non-coralline crusts, which would force the mobile invertebrates to move outside the plots to find suitable habitat when rockweeds were removed (Tables 2 & 3). Lastly, we found that *Silvetia* and *Pelvetiopsis* play similar roles in their respective tidal zones at Corona del Mar. The pattern of decline following removal of these foundation species was similar in terms of both richness and abundance of mobile invertebrates. This indicates that in a thermally stressful environment these rockweeds are collectively and sequentially extending the range of many mobile invertebrates into higher tidal zones than would be possible if these rockweeds were not present.

Multiple other studies have investigated how the removal of fucoid species impacts grazer community dynamics (Speidel et al. 2001, Moore et al. 2007, Schiel & Lilley 2007, Crowe et al. 2013). Speidel et al. (2001) found that removal of *Fucus gardneri* in Washington did not change the mobile invertebrate community in their plots. Similarly, Schiel & Lilley (2007) removed *Hormosira banksii* from low intertidal plots in New Zealand and found no change in the mobile invertebrate community. Similar to these two studies, we found no change in the richness and abundance of mobile invertebrates at two of our three study sites. *F. gardneri* replaces *Silvetia* in the mid intertidal zone north of Humboldt County, California, therefore, the effect of these two rockweed species is consistent across a large geographic range when abiotic conditions are less thermally stressful.

As temperatures continue to increase as a result of climate change, biodiversity is under threat and is predicted to decline (IPBES 2016). An increase in temperatures can allow invasive species to colonize an area previously maintained by a native foundation species (Walther et al. 2009, Thomsen and South 2019). Rising temperatures are likely to alter trophic interactions. For example, Petchey et al. (1999) found that more diverse assemblages buffered communities against the effects of warming, allowing the community to maintain its structure and functioning. We found a decline in mobile invertebrate diversity at our most southern site, which is likely to cause changes in grazing patterns. Changes in grazing could lead to changes in both the micro- and macroalgal communities (Thompson et al. 2004, Thompson et al. 2005, O'Connor et al. 2015). Rockweeds are declining, especially in southern California, making it critical to understand their role in structuring communities, especially in the context of predicting the impacts of climate change (Thom & Widdowson 1978, Gunnill 1980, Whitaker et al. 2010). Maintaining diversity is essential to help mitigate the effects of climate change and maintain ecosystem function.

A shift in community composition, such as the one associated with the loss of foundation species, can lead to changes in ecosystem functioning (Sapper & Murray 2003, Koh et al. 2004a, Koh et al. 2004b, Thompson et al. 2004, Thompson et al. 2005, Moore et al. 2007, Ellison 2019). The local extinction of a foundation species can cause the local co-extinction of multiple other species that are associated with the foundation species, especially those with co-evolved relationships. Koh et al. (2004a) found that the relationship between local host extinctions and affiliated species among a variety of taxa was nearly one to one. For example, Koh et al. (2004b) found that the snout moth had gone locally extinct in Singapore because of the local extinction of the plant that supports its larval stage. Additionally, Moore et al. (2007) found that the removal of foundation species caused limpets with a cold-water affinity to disperse to alternative refugia. The loss of *S. compressa* from southern California rocky shores could similarly lead to the local co-extinction of *Cyanoplax*, which is virtually always found in association with *Silvetia* (Sapper & Murray 2003). Koh et al. (2004a) estimate that based on the current list of endangered species there are 6,300 species that are also at risk of local extinction because of their relationship with an endangered species. One of the major challenges with making generalizations about biodiversity loss in different systems is environmental heterogeneity and differences in the responses of species in different locations (Balvenera et al. 2006). Our study further demonstrates the importance of studying the drivers of species loss at multiple locations because of the variability in the response of communities.

ACKNOWLEDGMENTS

We thank the UC Natural Reserve System and the Orange County Marine Protected Area Council for access to field sites. We thank G. Bernatchez, R. J. Fales, and B. Nguyen for lab and field assistance and A. Carrillo for field assistance. C. Sorte and K. Mooney provided valuable feedback on this research and manuscript. This research was funded by a Mildred E. Mathias Graduate Student Research Grant (UC Natural Reserve System); a UC Irvine Data Science Fellowship; a UC Irvine OCEANS Initiative Graduate Fellowship; and a U.S. Department of Education Graduate Assistance in Areas of National Need Award to L.A.E.; and by the National Science Foundation (NSF-OCE 1736891 to M.E.S.B. and A. Martiny).

Permits -This research was completed with permission of the State of California Department of Fish and Wildlife Scientific Collecting Permit issued to L.A.E. (SC-1105) and the NOAA Greater Farallones and Monterey Bay National Marine Sanctuaries Research Permit awarded to L.A.E. (MULTI-2016-007).

Data Accessibility Statement - All data are available through the UC Natural Reserve System archives. This work was performed (in part) at sites in the University of California Natural Reserve System (Kenneth S. Norris Rancho Marino Reserve and Bodega Marine Reserve). Kenneth S. Norris Rancho Marino Reserve DOI:10.21973/N37943 and Bodega Marine Reserve DOI:10.21973/N32Q05

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Table1. Tidal distribution (m) of *Silvetia* and *Pelvetiopsis* at each site and average air and water temperature at each site. Temperatures were measured using TidBit temperature loggers placed within the rockweed zone.

	***Silvetia* tidal distribution (meters)**	***Pelvetiopsis* tidal distribution (meters)**	**Average (±SD) air temperature (°C)**	**Average (±SD) water temperature (°C)**
Bodega Marine Reserve	0.7-1.5	1.5-2.1	12.8 (±9.7)	10.1 (±2.7)
Rancho Marino	0.6-1.2	1.2-1.9	15.1 (±7.3)	13.6 (±2.1)
Corona del Mar	0.2-0.9	0.9-1.3	18.9 (±9.6)	17.4 (±3.7)

Table 2. Average percent cover (±SEM) of seaweeds in *Pelvetiopsis* zone plots prior to establishing experimental treatments at each site. NA = outside of geographic range of species.

	Cladophora	***Endocladia***	***Mastocarpus***	***P. hybrida***	***Ulva***	**Non-coralline crust**	**Bare Rock**
Bodega Marine Reserve	8.9 (±2.6)	15.7 (±4.8)	28.9 (±8.9)	NA	25.4 (±7.7)	2.9 (0.8)	41.8 (±17.3)
Rancho Marino	1.4 (±0.7)	12.3 (±3.1)	20.4 (±5.2)	7.9 (±2.3)	18.7 (±4.1)	5.6 (±2.4)	1.3(±0.4)
Corona del Mar	0	0	0	NA	10.5 (±2.9)	6.8 (±2.1)	82.7 (±12.5)

Table 3. Average percent cover (±SEM) of seaweeds in *Silvetia* zone plots prior to establishing experimental treatments at each site. NA = outside of geographic range of species.

	Corallina	***Endocladia***	***Fucus***	***Mastocarpus***	***Mazzaella***	**Non-coralline crust**	**Bare Rock**
Bodega Marine Reserve	0.0	13.4 (3.4)	0.0	20.3 (7.6)	45.8 (11.8)	2.3 (1.0)	18.2 (6.6)
Rancho Marino	3.0 (2.1)	26.5 (11.1)	3.4 (1.9)	34.9 (11.3)	16.8 (6.5)	4.5 (1.3)	10.9 (2.9)
Corona del Mar	12.6 (6.4)	3.4 (1.2)	NA	2.1 (0.9)	0.0	21.6 (8.3)	60.3 (13.1)

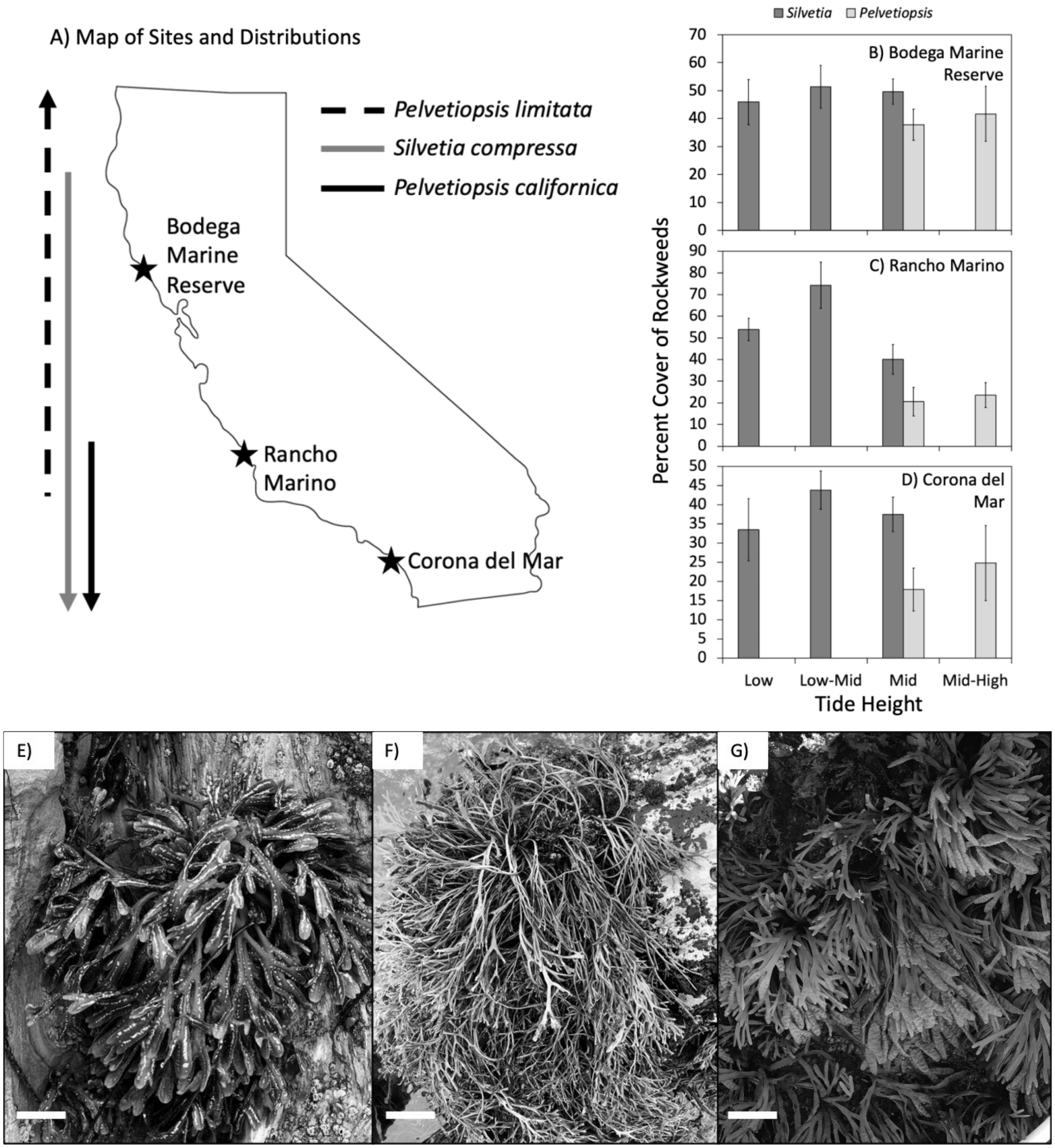

Figure 1. A) Location of study sites and the distribution within California of three rockweed species. Average rockweed percent cover (±SEM) by effective tide height in B) Bodega Marine Reserve, C) Rancho Marino, D) Corona del Mar. Pictures of typical individuals from study sites with 1 cm scale bars E) *Pelvetiopsis californica*, F) *Silvetia compressa*, G) *Pelvetiopsis limitata*.

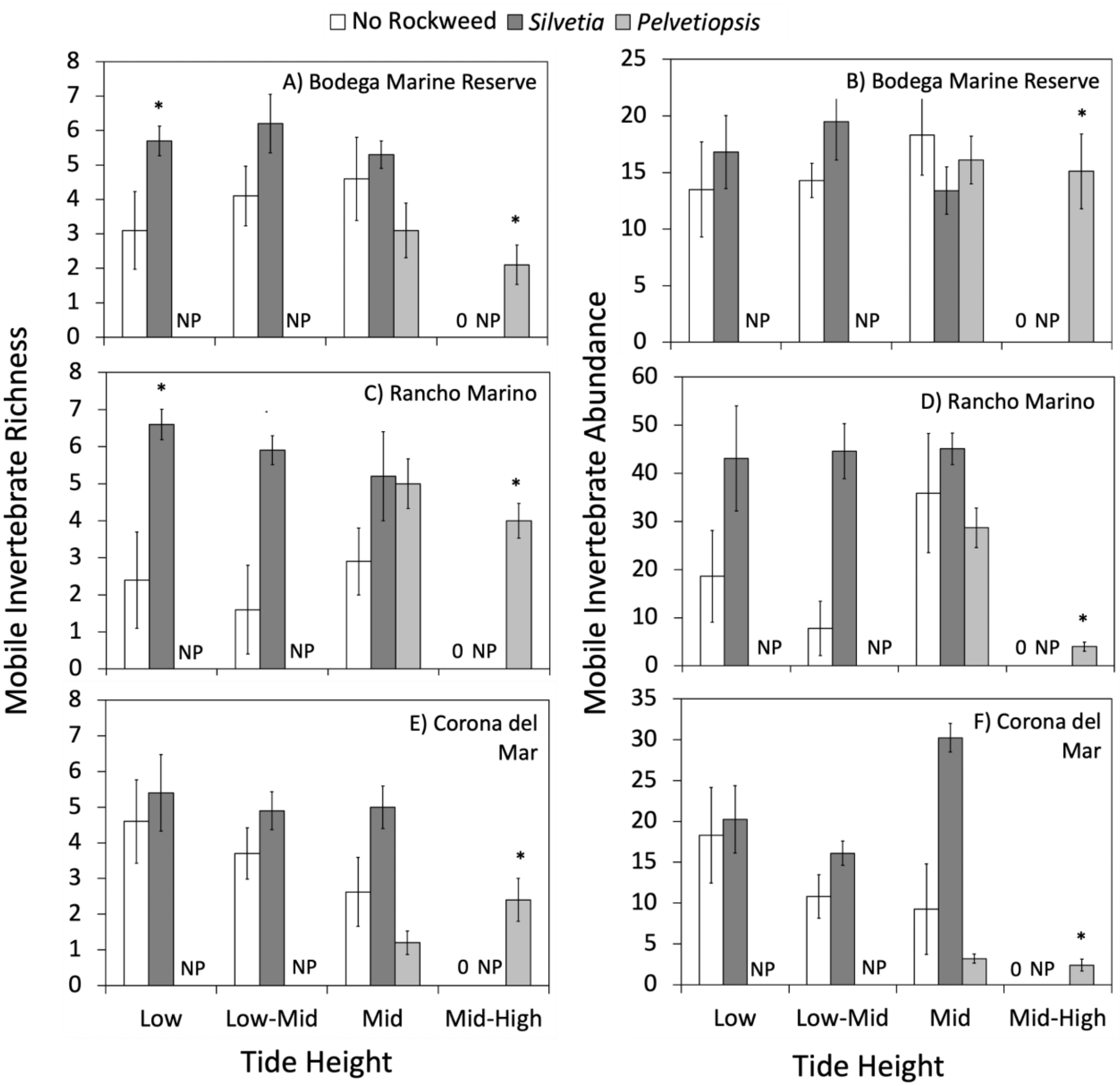

Figure 2. Average (±SEM) richness and abundance (individuals per 0.25 m^2) of mobile invertebrates in survey plots with and without *Silvetia* and *Pelvetiopsis*. A) Bodega Marine Reserve richness, B) Bodega Marine Reserve abundance, C) Rancho Marino richness, D) Rancho Marino abundance, E) Corona del Mar richness, F) Corona del Mar abundance. Note: NP indicates rockweed species not present, * indicates significant difference between plots ($p < 0.05$).

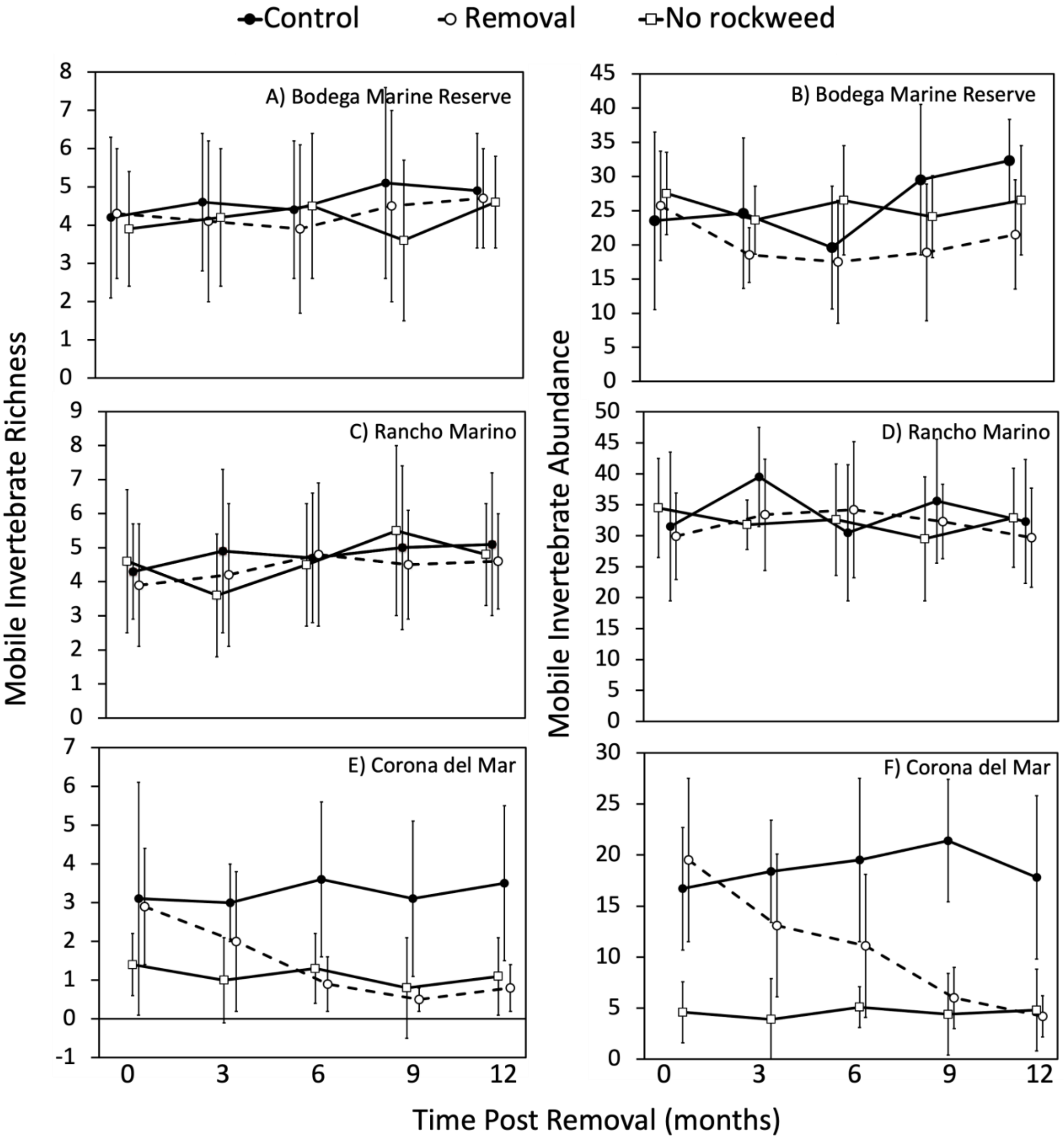

Figure 3. Average (±SEM) richness and abundance (individuals per 0.25 m^2) of mobile invertebrates in control and removal plots of *Pelvetiopsis*. A) Bodega Marine Reserve richness, B) Bodega Marine Reserve abundance, C) Rancho Marino richness, D) Rancho Marino, abundance, E) Corona del Mar richness, F) Corona del Mar abundance. Note: Points are offset to allow better visualization.

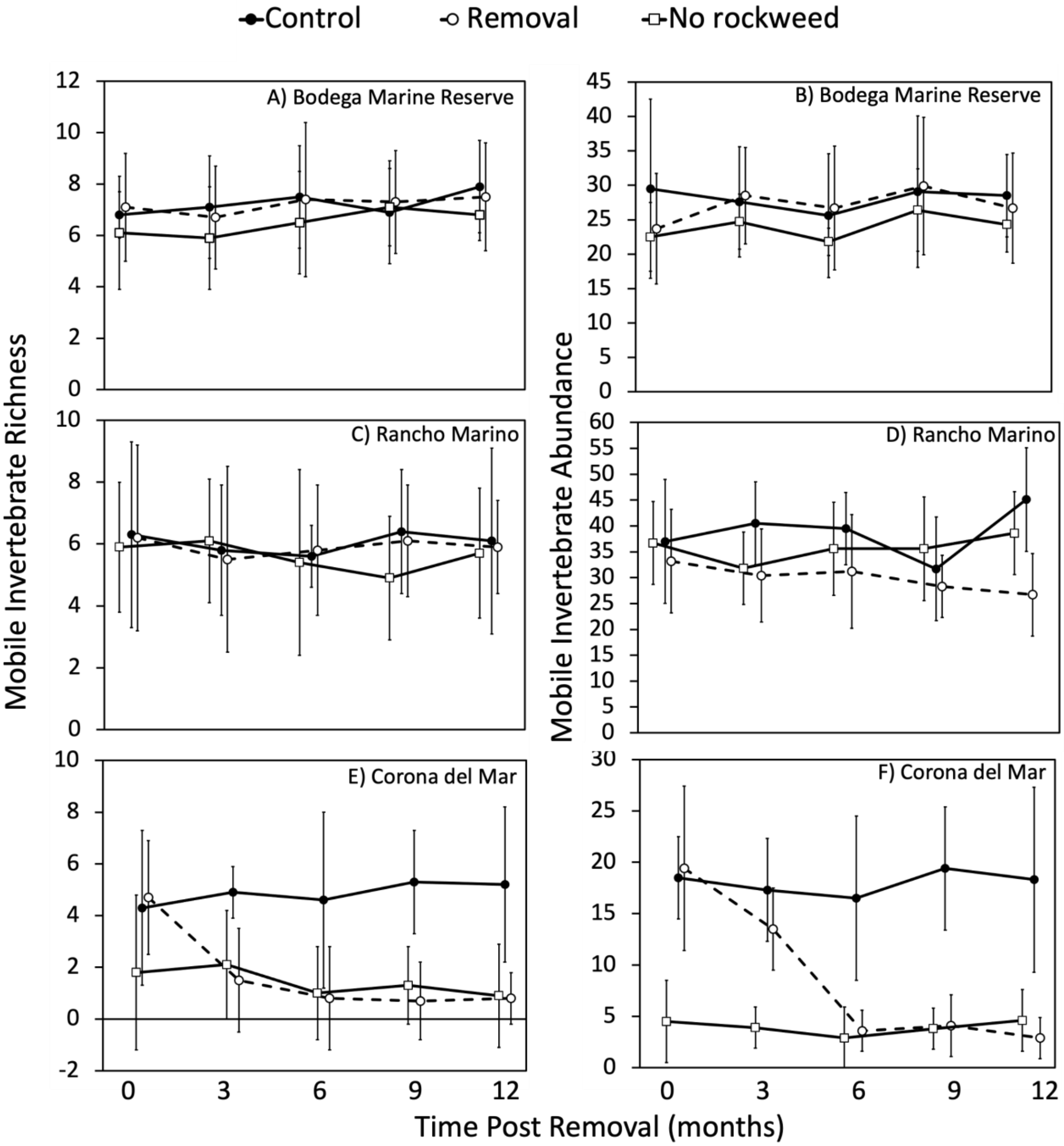

Figure 4. Average (±SEM) richness and abundance (individuals per 0.25 m^2) of mobile invertebrates in control and removal plots of *Silvetia*. A) Bodega Marine Reserve richness, B) Bodega Marine Reserve abundance, C) Rancho Marino richness, D) Rancho Marino abundance, E) Corona del Mar richness, F) Corona del Mar abundance. Note: Points are offset to allow better visualization.

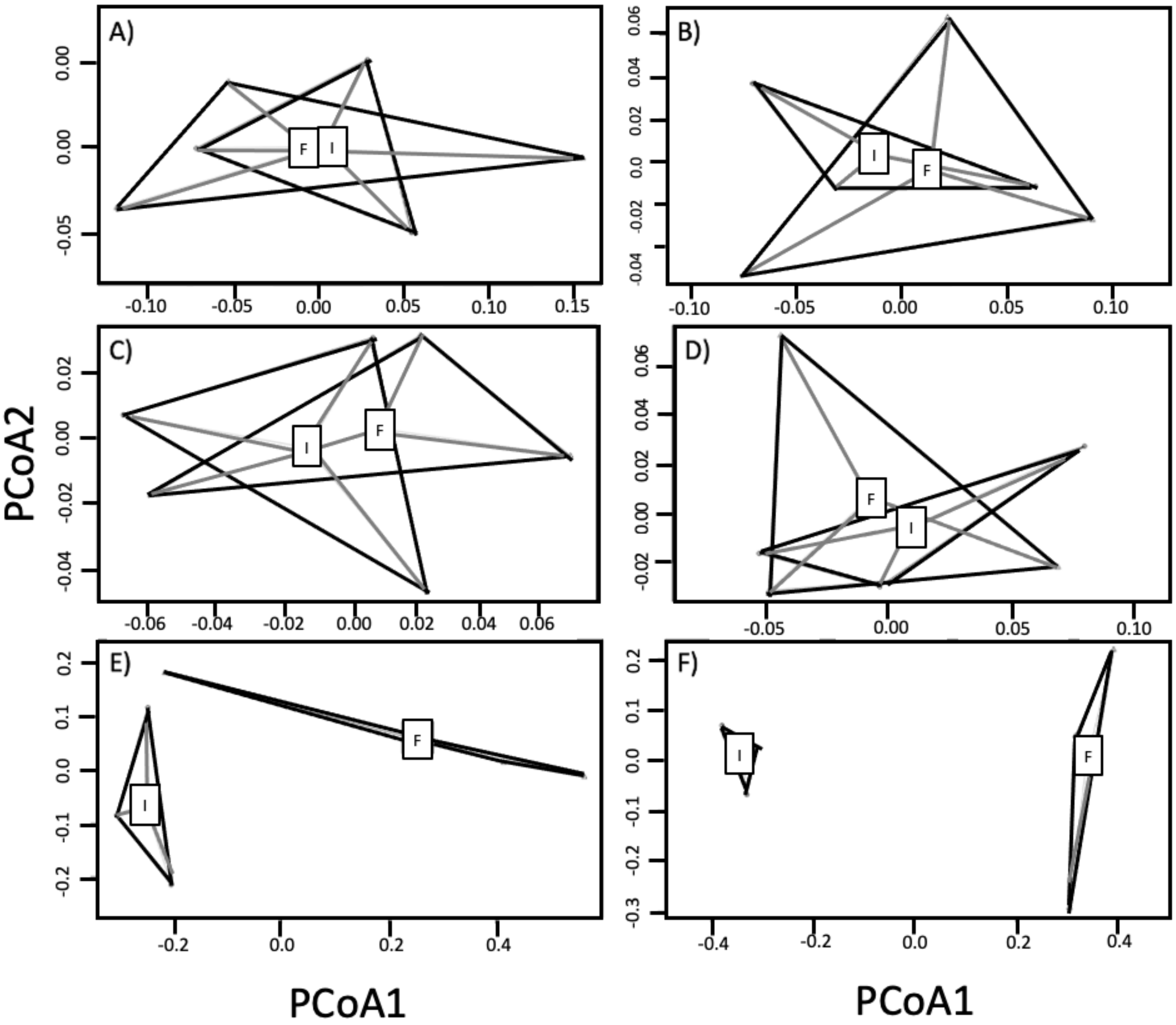

Figure 5. Principal coordinates analyses (PCoA) illustrating differences between the communities at each site before (I) and after removal (F) of A) *Pelvetiopsis* at Bodega Marine Reserve, B) *Silvetia* at Bodega Marine Reserve, C) *Pelvetiopsis* at Rancho Marino, D) *Silvetia* at Rancho Marino, E) *Pelvetiopsis* at Corona del Mar, F) *Silvetia* at Corona del Mar.