Spatial and Temporal Variation in Recruitment to Rocky Shores: Relationship to Recovery Rates of Intertidal Communities

Final Technical Summary

Final Study Report

U.S. Department of the Interior
MMS
Minerals Management Service
Pacific OCS Region

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FINAL TECHNICAL SUMMARY

STUDY TITLE: Spatial and Temporal Variation in Recruitment to Rocky Shores: Relationship to Recovery Rates of Intertidal Communities

REPORT TITLE: Spatial and Temporal Variation in Recruitment to Rocky Shores: Relationship to Recovery Rates of Intertidal Communities

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KEY WORDS: Recovery, succession, rocky intertidal, recruitment, *Chthamalus, Mytilus, Endocladia, Silvetia*

BACKGROUND: Community dynamics in the rocky intertidal may be governed to a large extent by the process of recovery after a disturbance, which may be variable across biogeographic regions or intertidal taxa. This study investigates the recovery process by performing experimental disturbances at three sites along the California coast in four different intertidal assemblages. Recruitment could be a key driver of recovery rates so we

measured the recruitment rate of each target species to see if recruitment is responsible for driving observed differences in recovery rate and trajectories.

OBJECTIVES: The goals of this study were, broadly, to determine which processes were most important in driving recovery rates in rocky intertidal assemblages and more specifically to address the following questions:
1. How do recovery dynamics change with biogeographic region?
2. Is recruitment rate a good predictor of recovery rate?
3. To what extent does disturbance magnitude (area) drive recovery processes at both the population and community level?
4. How do species with differing life history characteristics respond to disturbance?

DESCRIPTION: We made experimental clearings in an array of sizes at three sites along the California coast. Each site was chosen for its proximity to a long-term monitoring site and its location as north, near to or south of Point Conception, a major biogeographic barrier along the west coast of the United States. At each site, clearings were located in four different intertidal zones dominated by species with differing combinations of life history characteristics. The species chosen were *Mytilus californianus, Silvetia compressa, Endocladia muricata* and *Chthamalus dalli/fissus*. We also established control (unmanipulated) plots in each intertidal assemblage. We tracked the recovery of these clearings by assessing the percent cover of benthic invertebrates and algae in recovery and control plots over time. To determine the extent to which recruitment drives recovery rates, we measured recruitment onto natural and artificial substrata for each target species.

SIGNIFICANT CONCLUSIONS:
- Recovery rate as a function of initial disturbance size was distinctly different across sites and rocky intertidal assemblages such that for the *Chthamalus* assemblage, there was significantly negative relationship between initial disturbance size and recovery rate near Point Conception but no relationship at the sites north and south of Point Conception. For *Mytilus*, there was a significantly negative relationship between initial disturbance size and recovery rate at all three sites. For *Endocladia*, at Point Sierra Nevada (north of Point Conception), there was a negative relationship between initial disturbance size and recovery rate while at Stairs (near Point Conception), there was a positive relationship between initial disturbance size and recovery rate.
- Recruitment was highly variable across sites and assemblages and had a non-linear relationship with recovery rate.
- Community recovery was a strongly site-specific for all assemblages.

STUDY PRODUCTS:

Publications:
June 2006: Contribution to Cabrillo Beach Aquarium quarterly newsletter <u>Tidelines</u> "Disturbance and recovery of rocky seashores" Tish Conway-Cranos

Research Presentations:
March 2007: Pacific Ecology and Evolution Conference "Geographic variation in succession: Linking recovery rate, species interactions and recruitment" Tish Conway-Cranos

June 2006: International Temperate Reef Symposium: "Geographical variation in recovery of intertidal communities following a disturbance: Linking recruitment to recovery" Tish Conway-Cranos

November 2005: Western Society of Naturalists Conference "Geographical variation in recovery of intertidal communities following a disturbance: Linking recruitment to recovery" Tish Conway-Cranos

Posters:
March 2005: Monterey Bay National Marine Sanctuary Symposium "Geographical variation in recovery of rocky intertidal communities following a disturbance." Tish Conway-Cranos

FINAL STUDY REPORT

This project has become part of the PhD thesis of Tish Conway-Cranos, who has continued to monitor plots after the MMS funded portion of the project ended.

Introduction

The concept of ecological succession has intrigued ecologists since it was first studied by Cowles (1899).   In addition to providing insight into how communities develop over time, studies of succession have contributed to a deeper understanding of the ecological consequences of disturbance (e.g. Connell 1978; Dayton 1971) as well as the processes structuring natural communities in general (e.g. Odum 1969; Walker et al. 1986). Although there has been a great deal of work investigating succession and recovery processes in both terrestrial and marine systems, the circumstances governing both the likelihood and rate of ecological convergence remain poorly understood.

Propagule input: The importance of recruitment or propagule input to population dynamics is well established (e.g. Hanski 1999, Gaines and Roughgarden 1985), and studies of succession (e.g. Wood and del Moral 1987, Chapin et al. 1994) have indicated that arrival of new propagules may be one of the most important factors in determining successional dynamics. For species with open populations where input of propagules is decoupled from local production, recovery trajectories are likely to vary as a function of local recruitment patterns, whereas recovery trajectories of species with closed populations may vary as a function of local production rates. For this reason, species in the same geographic location with contrasting dispersal distances may respond very differently to the same magnitude of disturbance.

Disturbance area: Empirical work has shown that community processes and rates of recovery differ among disturbed patches of different sizes, often in non-intuitive ways (e.g. Hubbell et al. 1999, Bruna 2002, Levin and Paine 1974). In part, this is because the surrounding edge habitat may have strong and varying effects on new recruits. If organisms in intact edge habitat have a negative impact on incoming propagules or early life history stages, large disturbances may be expected to recover more quickly than small ones, since the center of such disturbances would represent a refuge from negative edge effects. In marine systems, negative effects could come in the form of algal whiplash (Jenkins et al. 1999, Cervin et al. 2004) or predation of larvae by adults (Young and Gotelli 1988). Conversely, surrounding biota may have a positive effect on recovering propagules through amelioration of physiological conditions (Shumway and Bertness 1994) or through gregarious settlement (Raimondi 1990; Michinton 1997). In such cases, smaller disturbances would be expected to exhibit faster recovery rate that large ones.

Longevity: Although the role of life history characteristics has long been recognized as important in determining the order of species replacement throughout succession (Littler and Littler 1981; Chapin et al. 1994; Walker et al. 1986), species with differing lifespans may also experience predictably different rates of recovery, yet this aspect of succession remains unresolved. For example, longer-lived species are likely to experience slower population

growth rates, which can result in slower population turnover and potentially slower recovery rates, whereas shorter-lived species are more likely to have faster population growth rates, faster population turnover and potentially more rapid recovery rates.

Biogeographic region: Despite agreement that geographic effects are likely to be important in determining the outcome of succession (e.g. Murray and Littler 1978; Dudgeon and Petraitis 2001; Foster et al. 2003), there have been relatively few succession studies that encompass more than one biogeographic region. Because geographic location may affect the relative importance of the abiotic and biotic factors that drive successional outcomes, conclusions drawn from one region may not hold true across larger spatial scales. We address this issue this by explicitly examining the relative importance of factors that drive recovery rates across multiple biogeographic regions.

Rocky intertidal: The rocky intertidal is characterized by assemblages or "zones" that are each numerically dominated by species whose life history characteristics differ significantly from one another, with dispersive phases that range from hours to weeks and lifespans that range from months to decades. Such differences may be important in determining a particular assemblage's recovery potential. We have chosen four species that are common in the rocky intertidal, occur in discrete zones and show different combinations of lifespan and dispersal potential (Table I). This orthogonal approach in choice of species will allow insight into the relative importance of lifespan and dispersal distance in determining the outcome of successional trajectories.

Table I. Life history characteristics of species assemblages.

	Long-dispersing	**Short-dispersing**
Long-lived	California mussel – *Mytilus californianus*	Fucoid rockweed - *Silvetia compressa*
Short-lived	Acorn barnacle - *Chthamalus dalli/fissus*	Red turf alga - *Endocladia muricata*

The California current: This study was conducted at intertidal sites on the Pacific Coast of the United States, spanning a major biogeographic boundary. Pt. Conception (Santa Barbara County, California) separates two biogeographic regions: The cooler (12˚C - 14˚C) Oregonian province to the north and the warmer (14˚C - 17˚C) Californian province to the south (Figure 1). This headland represents the boundary of many species' ranges (e.g. Murray and Littler 1978). The cooler Oregonian province is characterized by frequent seasonal upwelling (a process which delivers cool water and nutrients to shore) while the warmer Californian province experiences sporadic, weaker upwelling intensity (Hickey 1993). Variation in upwelling intensity is often correlated with variation in recruitment of species with planktonic propagules (e.g. Ebert and Russell 1988). In addition to contributing to faunal differences among marine biogeographic regions, water temperature affects processes that could change succession rates and outcomes such as development rates of larvae and growth rates of individuals. Oceanic currents themselves may also play a role in determining recruitment patterns. The equator-toward California current and the pole-ward Southern California

counter-current come together at Pt. Conception, potentially creating a region of offshore water movement near the point (Figure 1). The mussel *Mytilus californianus* and the acorn barnacle *Chthamalus fissus/dalli* both show a striking pattern of high recruitment both north and south of Pt. Conception but very low recruitment near the point itself (Raimondi et al. 1999), indicating that water movement may play a role in determining recruitment dynamics for species with planktonic larvae. Differences in abiotic (temperature, nutrients, currents) and biotic (recruitment) factors north, near to and south of Pt. Conception indicate that each of these three areas can be treated as a region likely to experience different recovery dynamics from one another. By taking this approach, we can directly assess the extent to which successional dynamics change as a function of biogegraphic region. Within the framework, we set out to answer the following questions:

I. How do recovery dynamics change with biogeographic region?

It is well established that many biological and ecological processes vary in intensity and relative importance in a site or region-specific manner (e.g. Connolly et al. 2001; McAuliffe 1988). To further understand and reliably predict successional rates and trajectories for intertidal species, it is necessary to obtain empirical recovery data from multiple biogoegraphic regions or oceanic regimes. Because of its proximity to Point Conception and susceptibility to offshore movement of dispersive propagules, we expected Stairs to exhibit slower recovery rates for the two long-dispersing species, *Chthamalus* and *Mytilus* when compared to recovery rates at Point Sierra Nevada and Point Fermin. Because recovery rates of short-dispersing species will likely be large determined by local production, we had no *a priori* prediction for a biogeographic pattern in the recovery rates of *Silvetia* and *Endocladia*.

II.   Is recruitment rate a good predictor of recovery rate?

In marine systems, input of propagules settling from a planktonic dispersive phase has been shown to be important in driving population (Caley et al 1996; Sutherland 1970; Gaines and Roughgarden 1985; Raimondi 1991) and community (Forde and Doak 2004) dynamics. Recruitment rate can also show strong spatial variation (Underwood et al. 1983; Caffey 1985; Connolly et al. 2001). The process of recovery could be driven primarily by larval input or by post-settlement processes. Understanding the extent to which recovery is determined by recruitment relative to other processes can aid in the prediction of recovery estimates

III. To what extent does disturbance magnitude (area) drive recovery processes?

Disturbance magnitude can have profound effects on recovery rate and trajectory (e.g. Sousa 1984). For *Chthamalus*, presence of adult conspecifics has been shown to increase settlement rate (Raimondi 1990) so large plots are expected to recover more slowly than small ones. For *Mytilus*, adults may slowly encroach from the edges and fill up gaps (Paine and Levin 1981) and recruits settle preferentially to adult byssal threads (Levin and Paine 1974). Both processes lead to the expectation that large disturbances will recover more slowly than small ones since large plots have a smaller edge-to-area ratio. *Endocladia* is a unique organism to study in this respect in that it reproduces both vegetatively and through spores, so a given disturbed patch could recover via recruitment of new individuals or through slow

encroachment from the edges. This creates an interesting tension between larger plot sizes, which often have lower grazer densities (Underwood et al. 1983; Sousa 1984; Farrell 1991) yet also have less potential for lateral encroachment relative to small plots due to the decreased edge-to-area ratio. Previous work on fucoid establishment suggests an optimum level of canopy cover for settlement with too much canopy resulting in dislodgement of recruits by adults (Cervin et al. 2004; Jenkins et al. 1999) and too little canopy resulting in mortality due to desiccation stress (Dudgeon and Petraitis 2001). Additionally, fucoid establishment has been positively associated with microhabitat refuges such as facilitator species such as *Endocladia* (Johnson and Brawley 1998) and rock crevices (Lubchenco 1983).

Materials and Methods

Site selection and sampling: We have selected three sites along the California coast at which to conduct this study; Point Sierra Nevada to the north of Point Conception, Stairs near Point Conception and Point Fermin to the south of Point Conception (Figure 1).
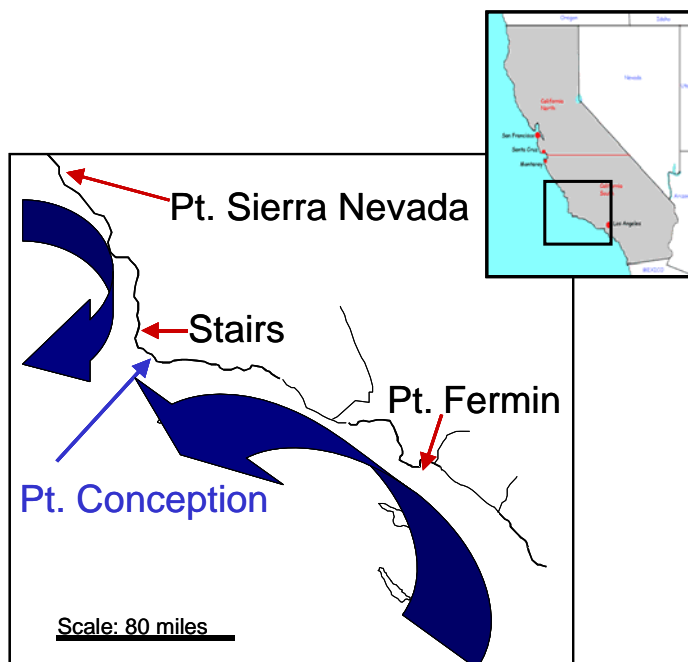

Figure 1. Simplified schematic of water movement patterns around Point Conception, California and location of field sites Point Sierra Nevada, Stairs and Point Fermin.

These sites encompass two major biogeographic regions yet have many of the same dominant benthic species. Each site is adjacent to long-term intertidal monitoring site conducted by the Multi-Agency Rocky Intertidal Network (MARINe). This was done intentionally so that recovery rates can be placed in the context of long-term species change.   In Fall 2003, we established 8 recovery plots of varying sizes ranging from 8 cm x 12 cm to 50 cm x 75 cm (Figure 2) and three control plots in each of the *Mytilus*, *Chthamalus*, *Endocladia* and *Silvetia* zones at three sites along the California coast (Figure 1). We denuded the substratum of all

visible biota and then burned each plot with a hand-held propane torch to remove microscopic propagules. Sampling consisted of placing a PVC frame with a uniform grid of monofilament line strung into it and noting the identity and location in the grid of species occupying the primary substratum and canopy (if present) under each intersection. All plots were marked with stainless screws in the corners to ensure consistency in the placement of the quadrat each sampling visit. All plots were sampled prior to clearing, then post-clearing in March 2004, June 2004, October 2004, February 2005, and June 2005.

Measuring recruitment: We determined relative recruitment rates onto artificial and natural substrata for all four taret species (*Mytilus*, *Chthamalus*, *Endocladia*, and *Silvetia*) at each of the three sites. From this information, we tested whether relative recovery rates across a broad spatial scale for a given dominant species can be predicted by recruitment rates. Because recruitment may be driven by substratum type (Raimondi 1988; Johnson and Brawley 1998), artificial recruitment substrata are used to explicitly compare recruitment dynamics across sites in a way that standardizes the amount of larval supply. We have put out collectors in each assemblage to provide a standardized settling environment for the dominant species. The recruitment collectors allowed us to compare the relative larval or spore availability among sites in a way that is not affected by the natural substratum at each site. Recruitment onto natural substrata was measured in all four assemblages except for *Mytilus*, where the only way to sample natural recruitment is by sampling destructively, which we are not doing. *Chthamalus* recruits were counted on bare rock and scraped off monthly (Figure 2A).

A *Chthamalus* recruitment onto artificial (Left) and natural (Right) substrata

B *Endocladia* recruitment onto natural (Left) and artificial (Right) substrata

C *Silvetia* recruitment onto natural (Left) and artificial (Right) substrata

D *Mytilus* recruitment onto artificial substratum

Figure 2. Recruitment collectors targeted towards each species.

For *Endocladia* and *Silvetia*, we have targeted areas within the assemblage where known facilitator species occur. We counted new *Endocladia* recruits in permanent 10 cm x 10 cm plots of barnacles adjacent to the collectors within the *Endocladia* zone (Figure 2B). For *Silvetia*, we counted new *Silvetia* recruits in permanent 10 cm x 10 cm patches of *Endocladia* adjacent to the collectors within the *Silvetia* zone (Figure 2C). Recruits are counted and removed monthly. To assess recruitment onto artificial (standardized across sites) substrata, *Chthamalus* recruitment was measured on PVC plates covered with Safety-walk grip tape (Figure 2A). *Endocladia* recruits were collected on barnacle mimics made from plaster casting material (Figure 2B). *Endocladia* mimics made from boat carpet and Safety-walk grip tape were used to collect Silvetia recruits (Figure 2C). Tuffy-brand dish scrubbers that mimic byssal threads (Menge 1991) were used to collect *Mytilus* recruits (Figure 2D). Each collector provides a benign settlement surface for the target organism, which will allow a standardized, relative estimate of propagule availability across sites. Each collecting method has been field-tested and works well. This combination of recruitment onto both artificial and natural substrata allowed us to measure recruitment under both standardized and natural conditions, which then permitted the assessment of site-specific differences in recruitment rate.

Measuring recovery: Recovery plots ranging from 8 cm x 12 cm to 50 cm x 75 cm in size (Figure 3) were established in Fall of 2003 in the *Mytilus*, *Chthamalus*, *Endocladia* and *Silvetia* zones at Point Sierra Nevada, Stairs and Point Fermin.
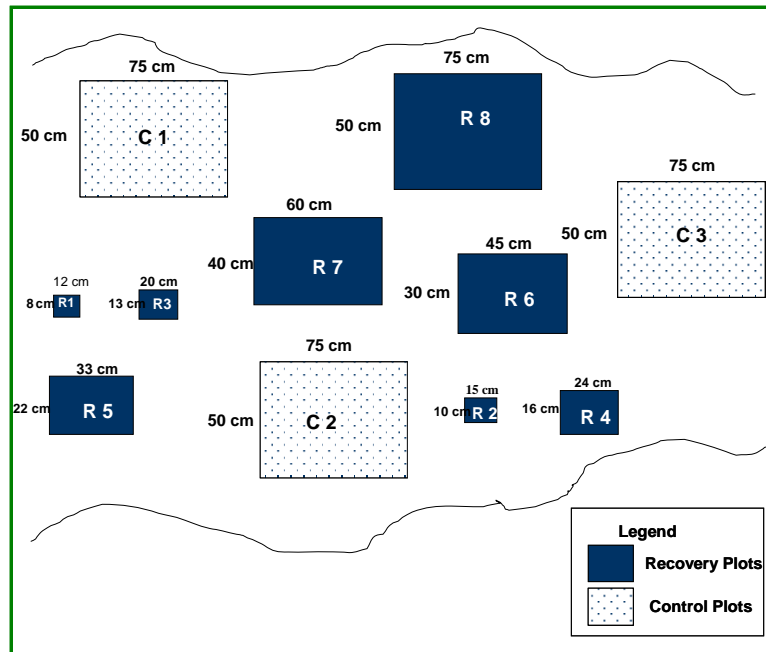

Figure 3. Schematic drawing of recovery (eight sizes ranging from 8 cm x 12 cm to 50 cm x 75 cm) and control plots (all 50 cm x 75 cm) in each assemblage (*Chthamalus*, *Endocladia*, *Silvetia* and *Mytilus*).

This gradient (rather than replicated tiers) of clearing sizes was chosen to allow taking a regression approach to understanding the effect of clearing size on the recovery rate. Each

clearing size was chosen to maintain a constant ratio between length and width (1:1.5) so that edge effects would scale in a similar manner. All recovery plots were sampled with 100 uniformly distributed points, except for the smallest three sizes, which were sampled with 50, 40 and 30 points, respectively. Control (uncleared) plots were the same size as the largest experimental plot (50 cm x 75 cm) and were sampled with 100 points.

Recovery analyses:

Population – level: Recovery rate of the target species for each plot at each site was calculated over time such that a slope (rate) was generated for each plot. For *Endocladia* and *Mytilus*, the first and last points in the recovery trajectory were used for this analysis. In all cases, the percent cover data were Arcsin-SquareRoot transformed prior to analysis and plot size (area) was log-transformed. To examine the relationship between recovery rate and disturbance area at each site, we either conducted a regression analysis of recovery rates as a function of disturbance area for a given site (*Chthamalus*) or conducted an Analysis of Covariance (ANCOVA) using disturbance area as the covariate (*Mytilus* and *Endocladia*). Recovery rates were not calculated for Silvetia since benthic percent cover is not a good indicator of biomass for this species. To assess the relationship between recovery rates of *Mytilus* and *Chthamalus* (both long-dispersing invertebrates) across all three sites, we conducted a two-away ANOVA. To calculate % recovery for each assemblage at each site, we divided the mean percent cover of each target species in recovery plots in June 2005 by the mean percent cover in control plots for the same date.

Community-level: Although experimental clearings were made in areas dominated by a particular species, each species is associated with a community other invertebrates and algae. Whether or not the suite of species that typically co-occur in each of the target intertidal zones show similar recovery dynamics is a key part of understanding recovery. Community-level analyses address the recovery trajectory of the entire assemblage. We have conducted a Multidimensional Scaling (MDS) analysis (Primer Software v.6) using recovery data from all four target assemblages from pre-clearing to June 2005. This method compares community composition across sites and disturbance sizes using a Bray-Curtis similarity index. We first examined community composition at all three sites prior to clearing and in June 2005. We then plotted the recovery trajectory of each individual plot over time. To assess the relative importance of initial disturbance area and geographic location in determining the shape of the community recovery trajectory, we conducted a Second-Stage MDS whereby community trajectories are formally compared using similarity matrices, resulting in an MDS plot where each point represents the recovery trajectory of a given disturbance plot at each site.

Results

Spatial variation in recruitment rate: *Chthamalus* recruitment to natural substrata was highest Point Fermin followed by Point Sierra Nevada and Stairs (Figure 4A). *Chthamalus* recruitment onto plates was much higher at Point Fermin than Point Sierra Nevada and Stairs (Figure 4B).
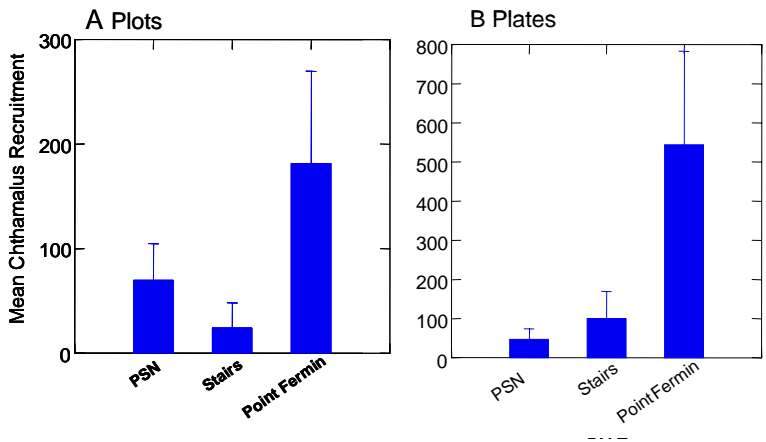
Figure 4. Monthly *Chthamalus* recruitment (mean ± SD) into 10 cm x 10 cm plots (A) and onto 10 cm x 10 cm PVC plates (B).

Endocladia recruitment to natural substrata was very similar at all three sites (Figure 5A) while Stairs experienced the highest recruitment onto plates (Figure 5B).
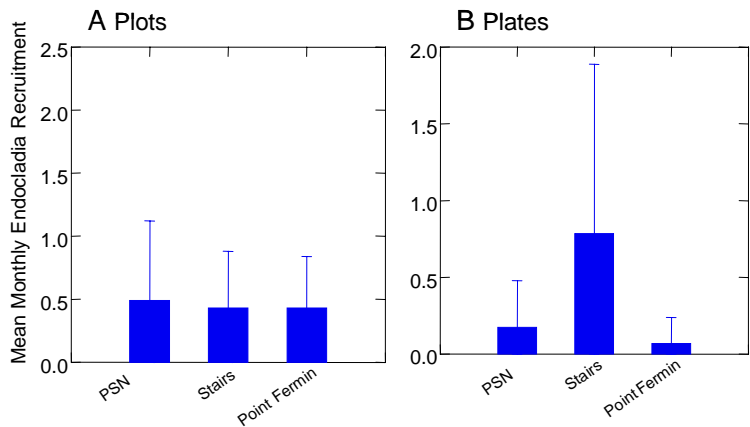

Figure 5. Monthly *Endocladia* recruitment (mean ± SD) into 10 cm x 10 cm plots (A) and onto 10 cm x 10 cm plaster barnacle mimics (B).

Fucoid recruitment to natural substrata was much higher at both Point Sierra Nevada and Stairs than at Point Fermin (Figure 6A). Recruitment to artificial substrata showed the same pattern (Figure 6B).
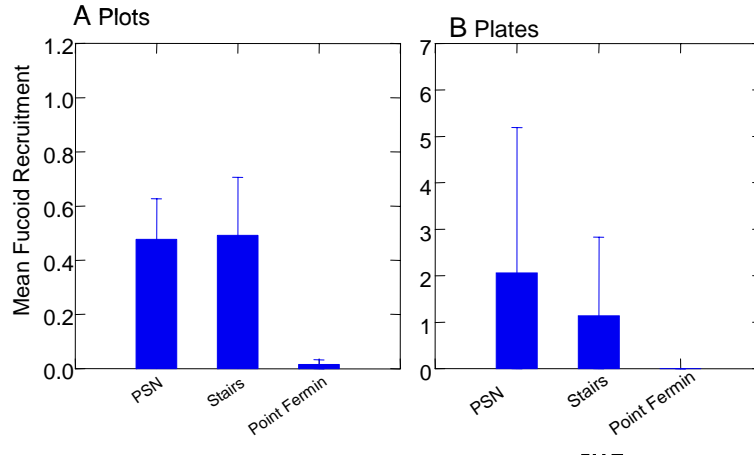
Figure 6. Monthly fucoid recruitment (mean ± SD) into 10 cm x 10 cm plots (A) and onto 10 cm x 10 cm *Endocladia*/rock mimics (B).

Temporal variation in recruitment: *Chthamalus* recruitment showed strong seasonal variability throughout the two years of data collection. At all three sites, there was a peak in December while at Point Fermin, there was a very high midsummer peak both years that was not experienced by the two other sites (Figure 7A). *Endocladia* recruitment was also highly variable, with highest recruitment all three sites in Fall (Figure 7B). *Silvetia* recruitment was also seasonal, with peaks in Spring and in Fall at Point Sierra Nevada and Stairs (Figure 7C).
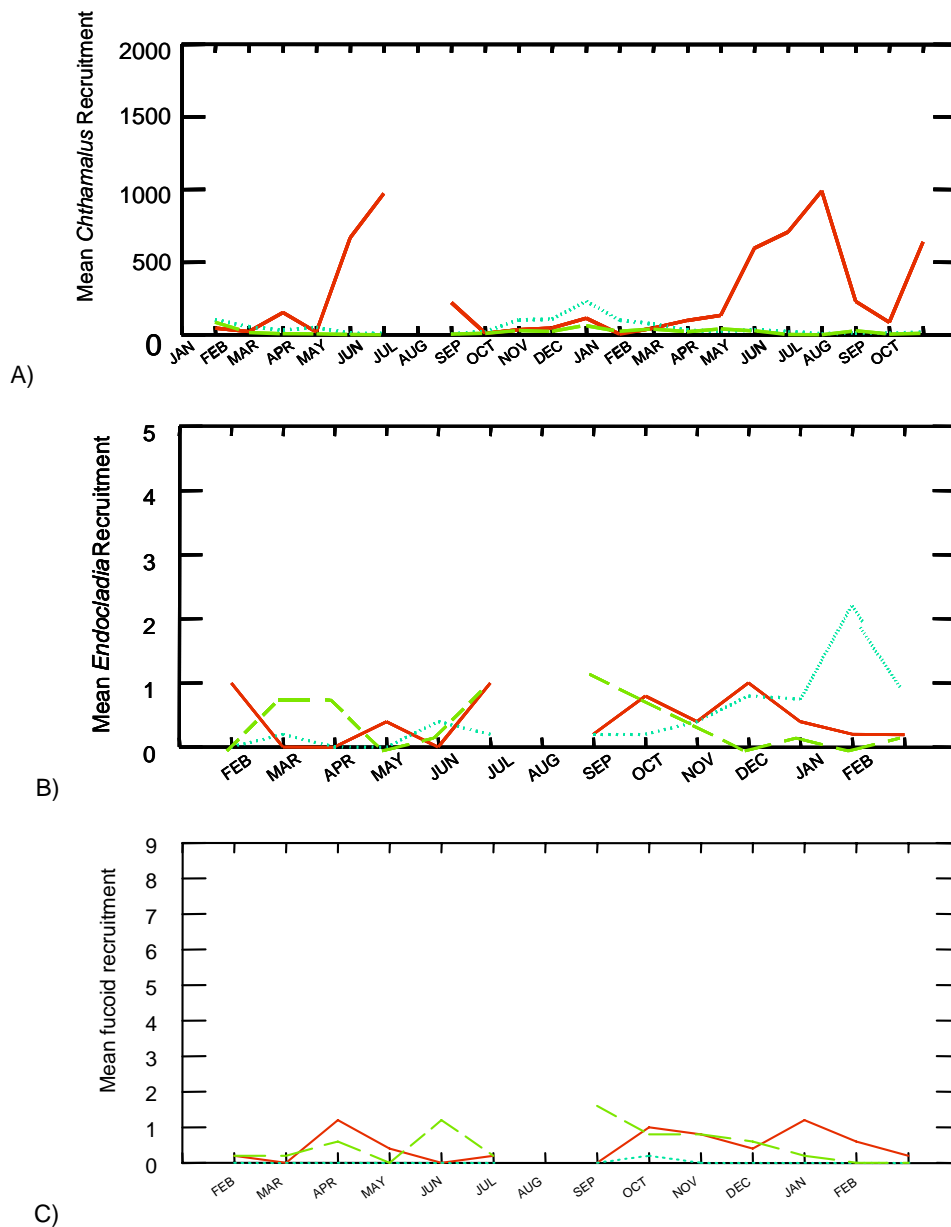
Figure 7. Temporal variation in Chthamalus (A), Endocladia (B), and fucoid (C) recruitment onto natural substrata at Point Fermin (solid lines), Point Sierra Nevada (dotted lines) and Stairs (dashed lines).

Recovery rates – population level response:
Chthamalus – Point Sierra Nevada and Point Fermin both showed more similarity to control plots (% Recovery) than did Stairs (Figure 8). This is the expected pattern if low recruitment due to oceanic currents is driving recovery.
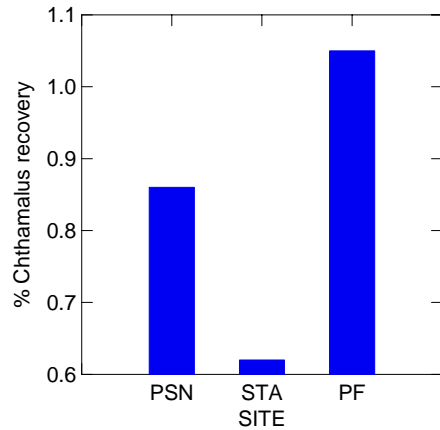
Figure 8. Mean % *Chthamalus* recovery (Mean Recovery/Mean Control) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) in June 2005.

Chthamalus showed strong recovery at nearly all plots at Point Sierra (Appendix A) by June 2005. Stairs *Chthamalus* plots showed a slower recovery rate, particularly in the larger plots (Appendix A). Point Fermin *Chthamalus* plots showed relatively rapid recovery (Appendix A). *Chthamalus* cover in control plots was fairly stable over time at Point Sierra Nevada and Stairs while showing a decrease followed by an increase at Point Fermin (Appendix B). Regression analysis of the recovery rates at all three site as a function of initial disturbance size revealed that at Point Sierra Nevada ($F_{1,5} = 0.0199$; $p = 0.893$) and at Point Fermin ($F_{1,5} = 0.0092$; $p = 0.927$), there was no relationship between recovery rate and disturbance area, but at Stairs ($F_{1,5} = 7.816$; $p = 0.0338$), larger plots had lower recovery rates than small plots (Figure 9).
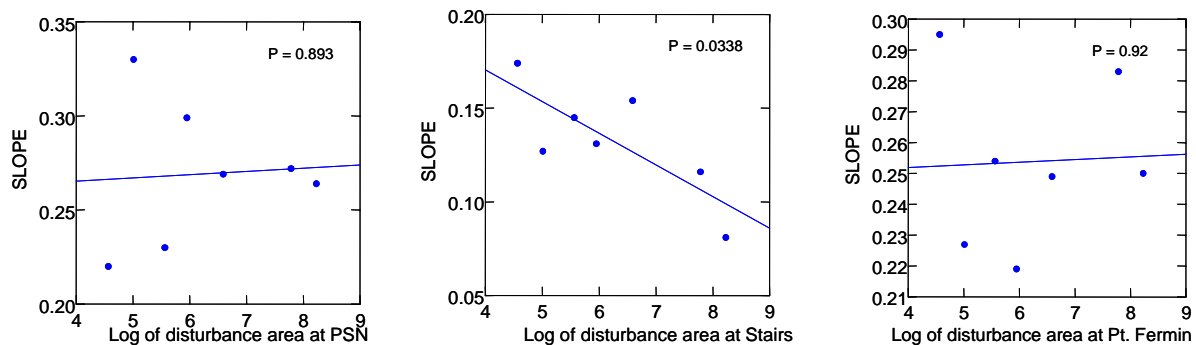

Figure 9. Results of regression analysis of recovery rate as a function of disturbance area in *Chthamalus* plots at Point Sierra Nevada, Stairs and Point Fermin. . Relationship between recovery rate and disturbance size in *Chthamalus* plots at Point Sierra Nevada (left), Stairs (middle) and Point Fermin (right).

These results are consistent with the idea that gregariousness among conspecific barnacles could be occurring at Stairs, resulting in the observed pattern of faster establishment of barnacles in smaller plots (Figure 9). One outlier plot size was left out of the analysis at all three sites (plot size 6).

Mytilus - Overall, *Mytilus* plots at Point Fermin showed much higher percent recovery than Point Sierra Nevada and Stairs, which exhibited similar overall recovery (Figure 10).
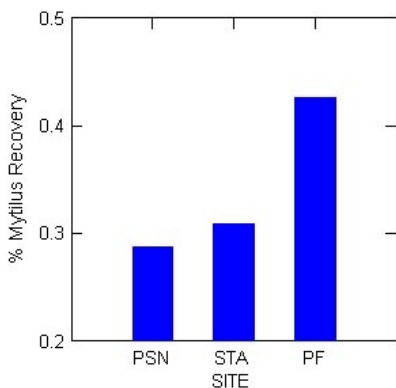

Figure 10. Mean % *Mytilus* recovery (Mean Recovery/Mean Control) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) in June 2005.

At Point Sierra Nevada, *Mytilus* showed much faster recovery in smaller plots than larger ones (Appendix C). Both Stairs (Appendix C) and Point Fermin (Appendix C) showed this pattern as well. Control plots at all three sites were relatively stable over time (Appendix D). ANCOVA revealed that there was a larger plots showed significantly slower recovery rates than small ones and that this was consistent across all three sites (Table II; Figure 11). Plots with recovery rates of zero were omitted from the analysis.
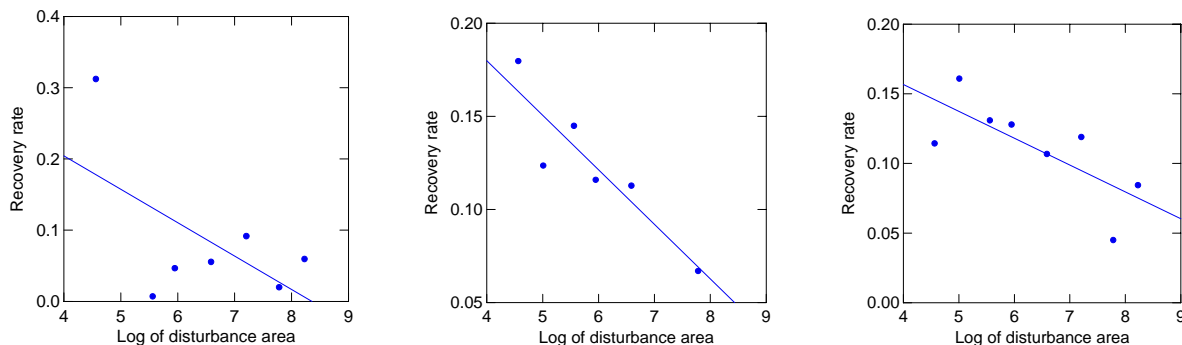

Figure 11. Results of regression analysis of recovery rate as a function of disturbance area in *Mytilus* plots at Point Sierra Nevada, Stairs and Point Fermin. . Relationship between recovery rate and disturbance size in *Mytilus* plots at Point Sierra Nevada (left), Stairs (middle) and Point Fermin (right) 2005.

Table II: ANCOVA of *Mytilus* recovery rate as a function of site and initial disturbance size.

	SS	df	MS	F	p
site	0.0032	2	0.0016	0.4948	0.6192
plot size	0.0275	1	0.0275	8.5989	0.0102
site x plot size	0.004	2	0.0021	0.6577	0.5323
error	0.0480	15	0.0032		

Comparison of Chthamalus and Mytilus recovery rates – A two-way ANOVA revealed that despite the fact that both of these invertebrates are long-dispersing, recovery rates were significantly different between them and across sites (Table III) such that *Chthamalus* recovery overall was much more rapid than that of *Mytilus* at Point Sierra Nevada and at Point Fermin while at Stairs, the two species exhibited very similar recovery rates (Figure 12), indicating that there may be an important interplay among lifespan, recruitment rate and geographic location in determining recovery rates.
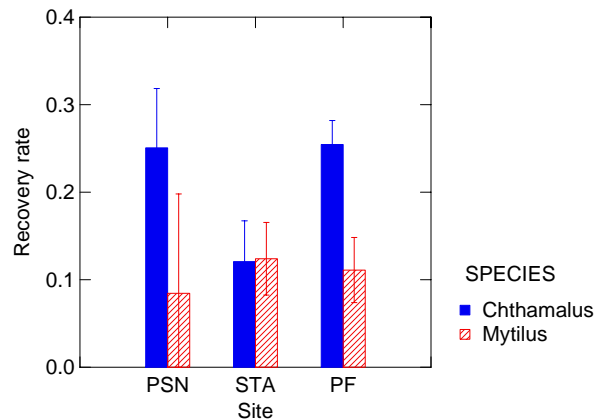
Figure 12. Comparison of *Chthamalus* (solid) and *Mytilus* (striped) recovery rates at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF). Data are mean ± SD.

Table III: Two-way ANOVA of Mytilus and Chthamalus recovery rates across sites.

	SS	df	MS	F	p
species	0.1159	1	0.1159	35.9299	< 0.0001
site	0.0286	2	0.0143	4.4413	0.01829
species x site	0.0599	2	0.0299	9.2947	< 0.0001
error	0.1258	39	0.0032		

Endocladia – Overall *Endocladia* recovery was much higher at Stairs than at Point Sierra Nevada and Point Fermin (Figure 13).
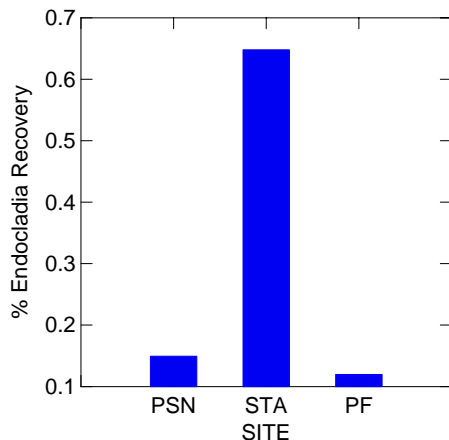
Figure 13. Mean % *Endocladia* recovery (Mean Recovery/Mean Control) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) in June.

Endocladia at Point Sierra Nevada showed faster recovery in small plots than in large ones (Appendix E) although percent cover in all plots was low. By contrast, at Stairs, there was a trend towards larger plots exhibiting faster recovery than smaller ones, although percent cover in all plots was low (Appendix E). At Point Fermin, all plots exhibited very little recovery during the time of this study. There was no pattern with respect to clearing size in those plots that did exhibit some recovery (Appendix E). *Endocladia* control plots at Point Sierra Nevada were relatively stable while control plots at Stairs and Point Fermin showed some decline over time (Appendix F). ANCOVA confirmed this pattern by showing that the effect of clearing size caused different recovery patterns across sites (Table IV)(Figure 14). Plots with recovery rates of zero were omitted from the analysis.

Table IV. ANCOVA of *Endocladia* recovery rate as a function of site and initial disturbance size.

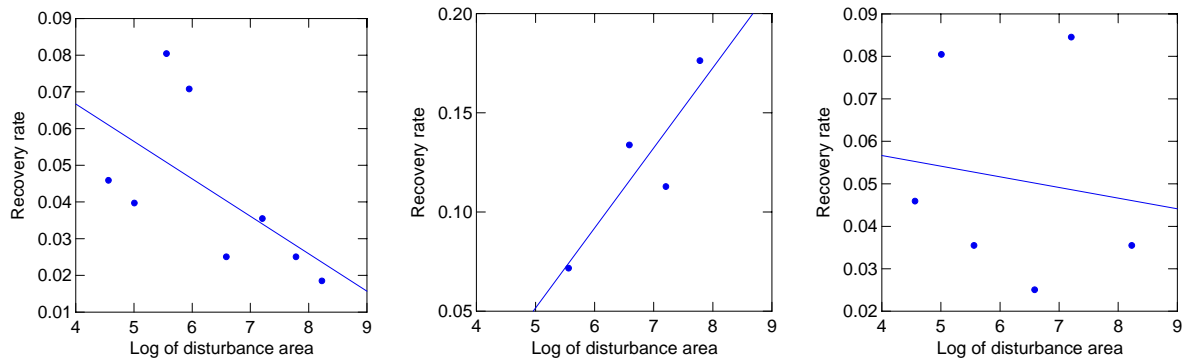|	SS	df	MS	F	p
site	0.0032	2	0.0016	2.9200	0.0926
plot size	0.0014	1	0.0014	2.5118	0.1389
site x plot size	0.0056	2	0.0028	5.1637	0.0241
error	0.0066	12	0.0005		

Figure 14. Results of regression analysis of recovery rate as a function of disturbance area in *Endocladia* plots at Point Sierra Nevada, Stairs and Point Fermin. Relationship between recovery rate and disturbance size in *Endocladia* plots at Point Sierra Nevada (left), Stairs (middle) and Point Fermin (right).

Silvetia – *Silvetia* benthic cover was very low in both recovery and control plots over time (Appendix G). While *Silvetia* canopy cover was high in both recovery and control plots, it fluctuated seasonally more in recovery plots, increasing in the winter and decreasing in the summer (Appendix G). Overall, *Silvetia* % recovery was highest at Point Fermin and Stairs while % recovery at Point Sierra Nevada was the lowest (Figure 15).
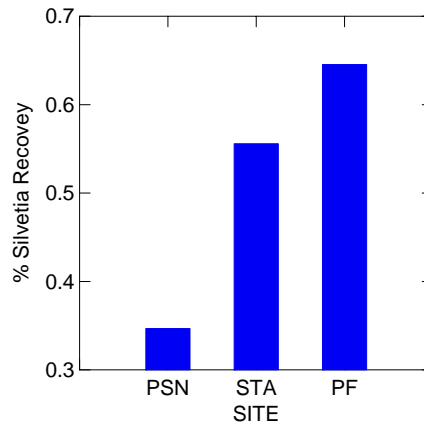

Figure 15. Mean % *Silvetia* recovery (Mean Recovery/Mean Control) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) in June 2005.

Life history characteristics – The assemblage exhibiting the most degree of recovery when compared to control plots was *Chthamalus*, followed by *Silvetia*, *Mytilus*, and *Endocladia*, respectively (Figure 16).
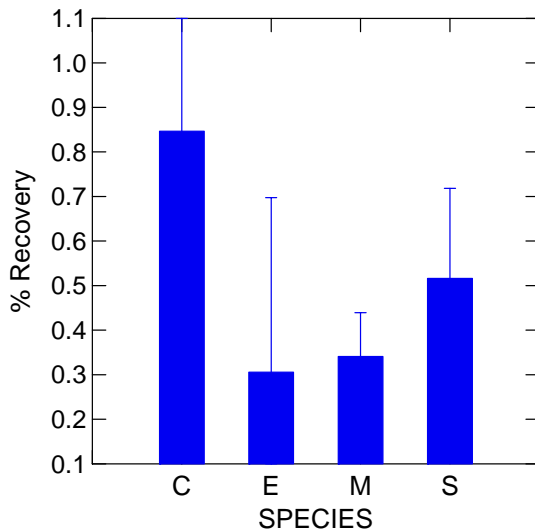
Figure 16. Overall Mean ± SD % recovery of *Chthamalus* (C), *Endocladia* (E), *Mytilus* (M) and *Silvetia* (S).

Recovery rates - community level response:

Chthamalus - All plots in the *Chthamalus* assemblage showed community compositions that differed the most between before the plots were cleared and the first time the plots were sampled after clearing. This was the case at all three sites (Appendix H). In most plots, community composition appeared to be in the process of converging with the composition of the plot before it was cleared. The second-stage MDS analysis revealed that recovery dynamics appear to be site-specific, rather than being driven solely by disturbance size (Figure 17). An ANOSIM test revealed that in the *Chthamalus* assemblage, all three sites showed significantly different recovery trajectories from one another (R = 0.732; p = 0.001).
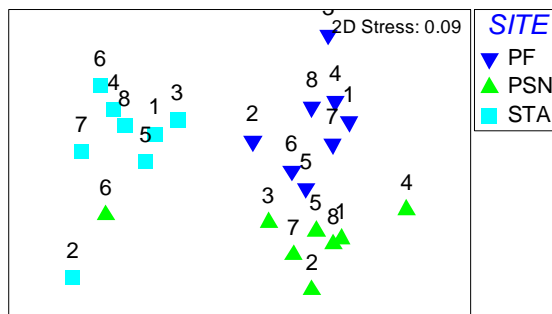

Figure 17. Community recovery trajectories for all plots in the *Chthamalus* zone at Point Fermin (blue downwards triangles), Point SierraNevada (green upwards triangles), and Stairs (turquoise squares). Numbers 1-8 represent clearing sizes where 1=smallest and 8=largest.

Mytilus – Community composition of the recovery plots in the *Mytilus* assemblage at all three sites also appeared to be the process of becoming more similar to the composition of the plots

before they were cleared (Appendix I). Smaller plots were closer to their initial composition than larger ones at all three sites (Appendix I). The second-stage MDS analysis showed that all three sites exhibited similar recovery trajectories (Figure 18) (R = 0.102; p = 0.25).
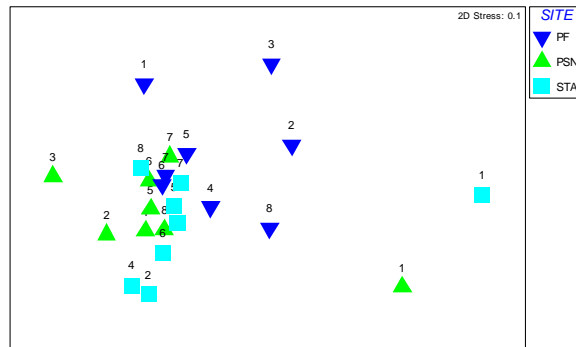

Figure 18. Community recovery trajectories for all plots in the *Mytilus* zone at Point Fermin (blue downwards triangles), Point Sierra Nevada (green upwards triangles), and Stairs (turquoise squares). Numbers 1-8 represent clearing sizes where 1=smallest and 8=largest.

Endocladia – At Point Sierra Nevada, *Endocladia* community composition changed over time among all plots. None of the plots were similar to their initial composition (Appedix J). At Stairs, some of the larger plots appeared to be closer to their initial community composition than smaller ones (Appendix J). The *Endocladia* community at Point Fermin changed over time but was still different from the way the community was prior to clearing (Appendix J). Second-stage MDS showed that all three sites had significantly different community recovery trajectories from one another in the *Endocladia* assemblage (R = 0.552; p = 0.01) (Figure 19).
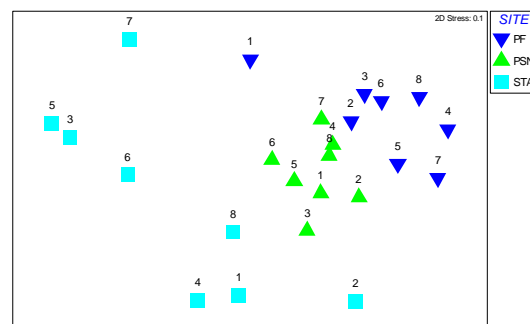

Figure 19. Community recovery trajectories for all plots in the *Endocladia* zone at Point Fermin (blue downwards triangles), Point SierraNevada (green upwards triangles) and Stairs (turquoise squares). Numbers 1-8 represent clearing sizes where 1=smallest and 8=largest.

Silvetia – Despite high canopy cover in recovery plots, the *Silvetia* assemblage did not show signs of converging with the community composition prior to clearing at Point Sierra Nevada (Appendix K). At Stairs, community composition in the *Silvetia* assemblage for some plots appeared to be approaching convergence (Appendix K). At Point Fermin, community

composition was still very different in nearly all plots from that of before they were cleared (Appendix K). A second-stage MDS and ANOSIM test revealed that all three sites have significantly different recovery trajectories (R = 0.414; p = 0.01) (Figure 20).
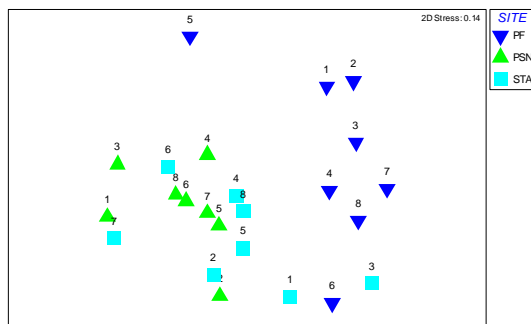

Figure 20. Community recovery trajectories for all plots in the *Silvetia* zone at Point Fermin (blue downwards triangles), Point SierraNevada (green upwards triangles) and Stairs (turquoise squares). Numbers 1-8 represent clearing sizes where 1=smallest and 8=largest.

Discussion

Biogeographic region: Recovery dynamics changed dramatically among biogeographic regions for all four assemblages. Point Fermin exhibited the most recovery for *Chthamalus*, *Mytilus* and *Silvetia* but the least for *Endocladia*. Since Point Fermin is located south of Point Conception where water temperatures are typically higher than locations north of Point Conception, it is possible that higher temperatures at Point Fermin lead to faster growth rates of these species and faster recolonization of benthic substrata. If this were the case, then *Endocladia* did not respond in a positive way to such temperature differences. However, given that Stairs exhibited the highest degree of *Endocladia* recovery and temperature differences between Point Sierra Nevada and Stairs are not great, it is likely that *Endocladia* recovery dynamics are not driven by temperature.

Since Stairs is located near Point Conception, we hypothesized that it would experience the slowest recovery of the long-dispersing invertebrates *Mytilus* and *Chthamalus*. While recovery of *Chthamalus* was the lowest at Stairs, *Mytilus* recovery was the same at Point Sierra Nevada and Stairs, indicating that forces other than the oceanographic currents near Point Conception may be driving *Mytilus* recovery. This is not surprising given the fact that *Mytilus* in general are much more likely to be dependent upon interactions with conspecific adults than *Chthamalus*. Thus, the establishment of *Mytilus* is likely to be more dependent than *Chthamalus* on post-settlement or density-dependent processes.

Silvetia recovery was the lowest at Point Sierra Nevada and considerably higher at Stairs and Point Fermin. This indicates that recovery dynamics are very different among regions. This could be related to biogeographic differences in recruitment or to differences in important species interactions such as Facilitation or Inhibition or some combination of both types of processes.

Recruitment: While recruitment differed significantly across sites, it does not appear to completely explain differences in recovery. For example, all three sites had very comparable levels of *Endocladia* recruitment onto natural substrata but Stairs had the highest degree of *Endocladia* recovery. This shows that post-settlement processes may be important in determining the degree of *Endocladia* establishment into recovery plots. This idea is supported by the fact *Endocladia* recruitment to plates was the highest at Stairs, indicating that the plates may have represented a more benign environment for recruitment than the plots and that dynamics in the recovery plots became more similar to the plates (barnacle mimics) over time. *Chthamalus* recruitment appeared to at least partially explain geographic differences in recovery such that the lowest recruitment site (Stairs) also had the least recovery and Point Fermin experienced the most recruitment and also the highest degree of recovery. Since the amount of recovery at Point Fermin does not appear to scale in a linear way with recruitment, there could be density-dependent processes occurring to explain these dynamics. For *Silvetia*, post-settlement processes are clearly very important since the lowest recruitment site (Point Fermin) was the site that experienced the highest recovery. This indicates that the few *Silvetia* sporelings that settled at Point Fermin likely experienced very high per capita survivorship. It is also possible that differences in substrata quality (rugosity, etc) or grazer abundances could explain some of the differences in *Silvetia* establishment across sites.

Disturbance size: Initial disturbance size was only important for *Chthamalus* at Stairs, where there was a negative relationship between clearing size and rate. Since Stairs was also the site with the lowest recruitment of *Chthamalus* onto natural substrata, it appears that gregariousness among conspecific barnacles is likely to be occurring at lower recruitment levels. Conversely, at Point Sierra Nevada and Point Fermin, gregariousness does not appear to be an important driver of recovery dynamics since large plots experienced the same rates of recovery as smaller ones. For *Mytilus*, initial disturbance size was a strong predictor of recovery rate such that the smallest plots experienced the fastest recovery rates at all three sites. This is likely due to encroachment from surrounding mussels in the small plots, a process which occurs more rapidly in small plots due to the higher perimeter:area ratio. For *Endocladia*, Point Sierra Nevada showed the fastest recovery in the smallest plot sizes whereas at Stairs, smallest plots experienced the slowest recovery. Such a pattern could be explained by grazer densities such that if there were more grazers at Stairs, the centers of large plots would represent a refuge for *Endocladia* recruits. Since smaller plots permit more access to grazers, it is unlikely that grazers are an important source of mortality for *Endocladia* recruits at Point Sierra Nevada. It is also possible that abiotic factors could be driving the contrasting patterns at Stairs and Point Sierra Nevada. Since desiccation stress could be also be an important source of mortality for *Endocladia* sporelings, the surrounding undisturbed *Endocladia* could represent a beneficial source of shade and moisture for developing recruits. If this were the case, we would expect the *Endocladia* zone of Point Sierra Nevada to experience more desiccation than that of Stairs. Since there was not a strong pattern between initial disturbance size and *Silvetia* recovery, it is clear that other, more site-specific processes are more important in driving recovery rates.

Life history characteristics: *Chthamalus*, the long-dispersing and short-lived species, showed dramatically higher percent recovery than the other three assemblages. This is not

surprising given the combination of short population turnover and high likelihood of propagule delivery. The species that showed the lowest percent recovery, *Endocladia* is also short-lived. This indicates that species characteristics alone cannot explain observed differences in recovery rates, however it is worth noting that *Endocladia* also experienced the most amount of variability in percent recovery across sites. *Mytilus* % recovery was only slightly higher than that of *Endocladia*, indicating further that the characteristic of having long-dispersing propagules does not predict recovery rate.

Species interactions: While much of this study has focused on the relationship between surrounding conspecifics and the target recovery species, there may also be important species interactions occurring within a plot that could strongly alter the course of succession and thus the recovery rate likely to be experienced by a given species at a given site. Such interactions are likely to change over space (e.g. biogeographic region, tidal height) and time (i.e. over the course of succession). Indeed, previous research has shown species interactions during the course of succession may have profound impacts on the overall rate and trajectory of succession. Connell and Slatyer (1977) categorized such interactions as Facilitation, Inhibition and Tolerance. Subsequent studies have shown that all three mechanisms can be important, depending on the particular suite of biotic and abiotic factors at play. For example, under more stressful abiotic conditions, Facilitation may be more likely to occur, whereas in more benign environments, Inhibition may become more important (Bertness and Callaway 1994). Successional mechanisms may also change over time throughout the course of succession (Farrell 1991; Callaway and Walker 1997) or occur simultaneously among different tissues of the same organism (Chapin et al. 1994; Callaway and Walker 1997). While much work has focused on identifying the conditions under which different successional mechanisms become more important, little attention has been focused on seeing if a link exists between the dominant mechanism and the rate (or likelihood) of community recovery to a pre-disturbance state. If such a link is found to exist, our understanding of succession and our ability to predict successional rates will be greatly enhanced. Given the potential importance of species interactions in addition to species characteristics and biogeographic location, we propose the following conceptual model as a heuristic tool for understanding the manner in which recovery rates and successional trajectories may vary over space and time (Figure 21).
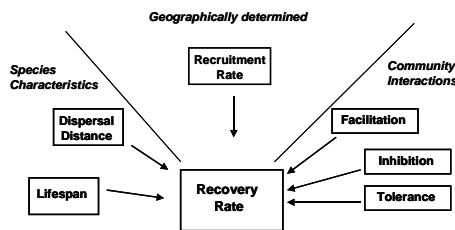

Figure 21. Conceptual diagram of possible factors affecting recovery rate.

Investigation of species interactions along with ecological variables will enhance our understanding of the way species recover after a disturbance while also providing key insight to the way communities develop over time, a process that is both fundamental and ubiquitous in nature.

ACKNOWLEDGEMENTS

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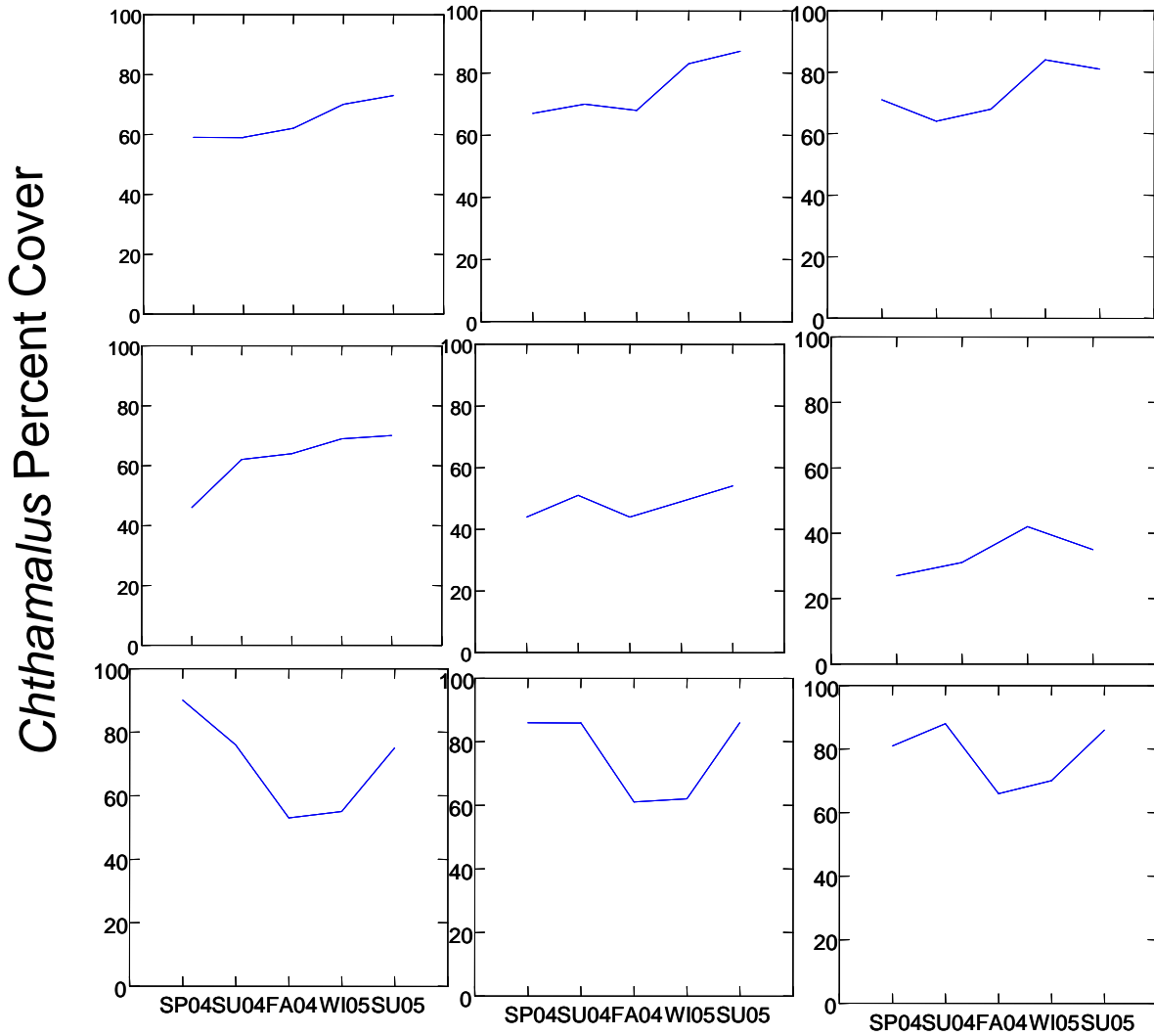
APPENDIX A

Appendix A. *Chthamalus* percent cover over time in Recovery plots from Spring 2004 - Summer 2005 at Point Sierra Nevada (PSN), Stairs (STA), and Point Fermin (PF) where R1 represents the smallest plots and R8 the largest.
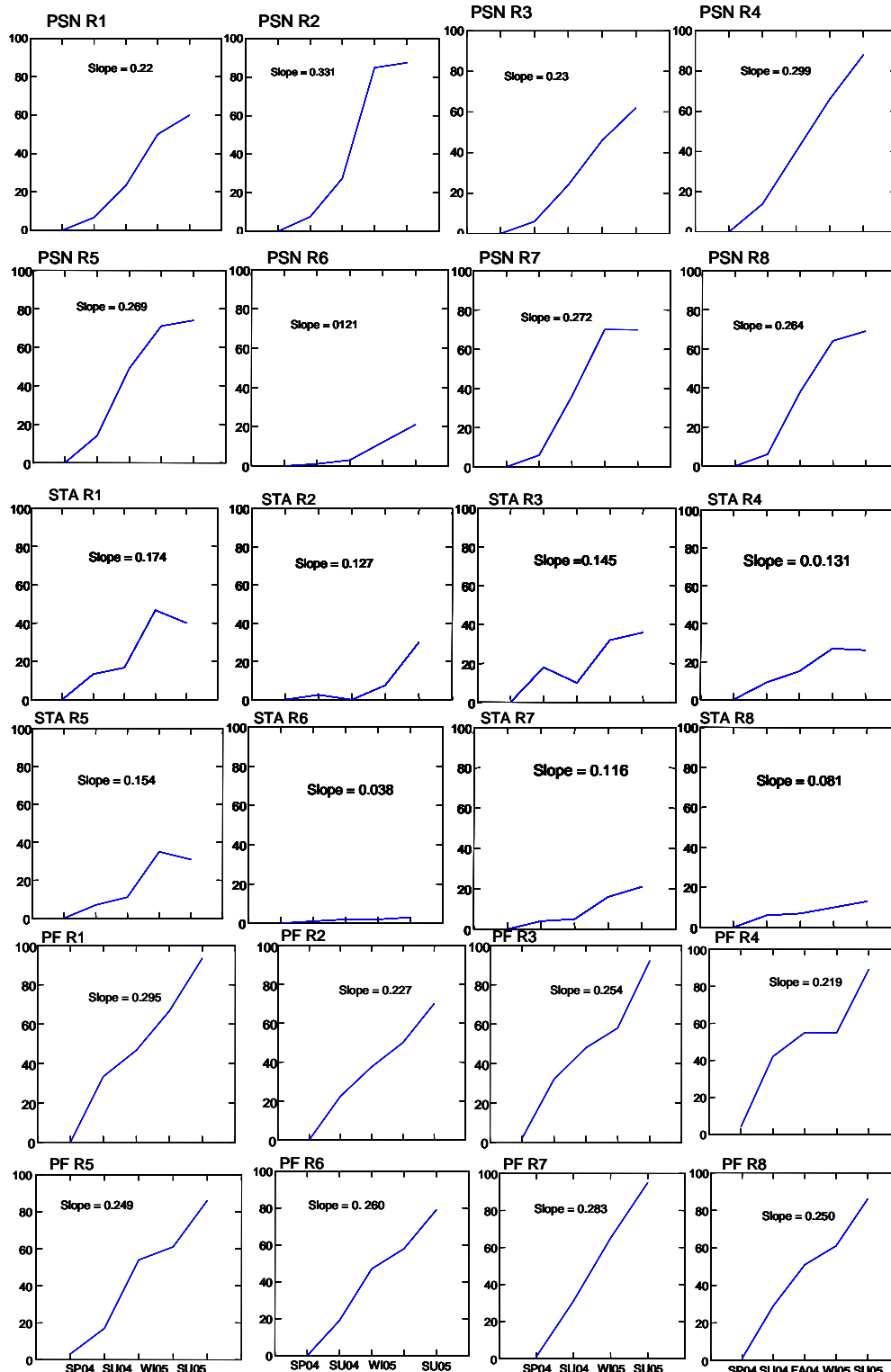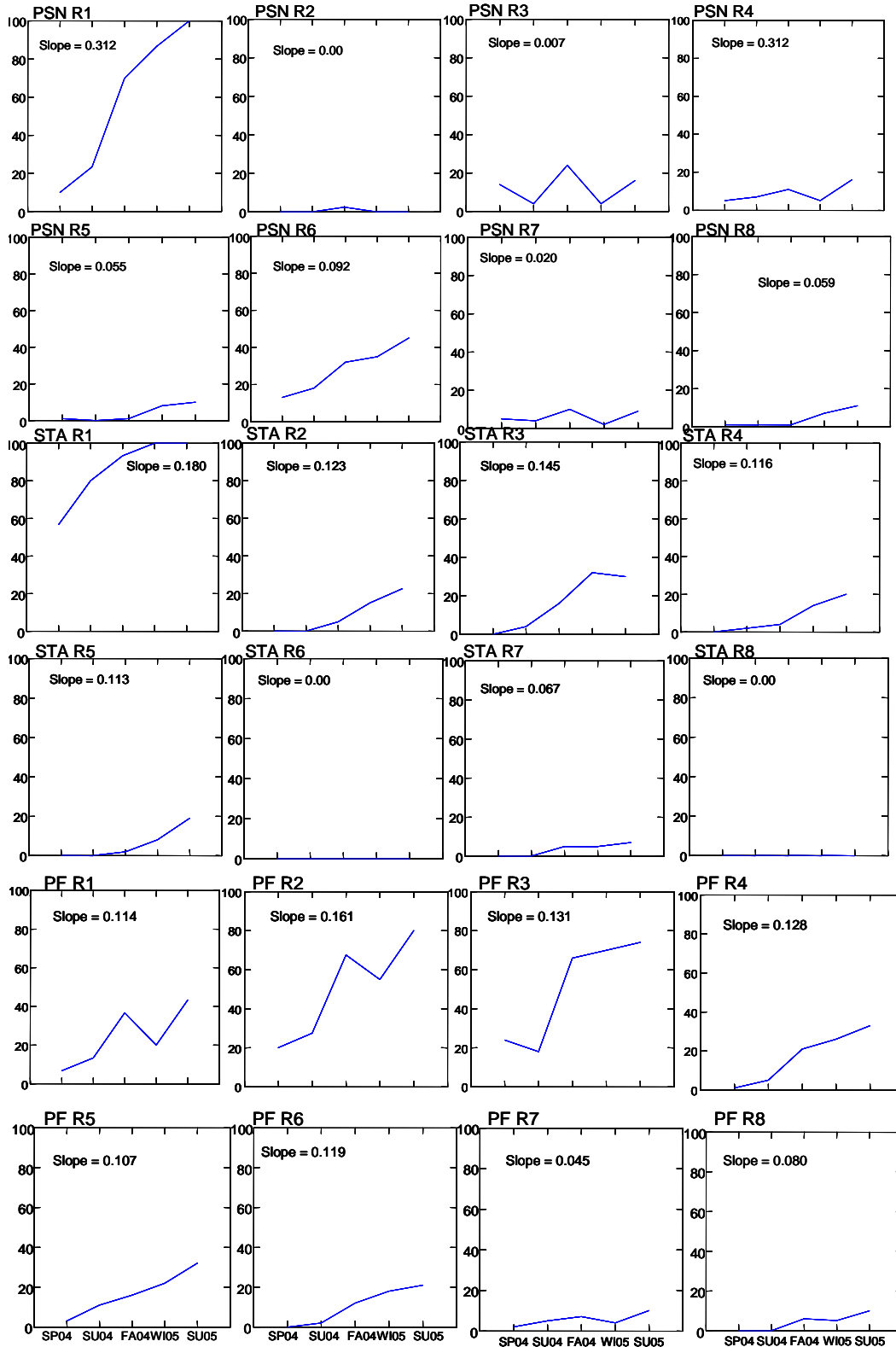
APPENDIX B

Appendix B. *Chthamalus* percent cover over time in Control from Spring 2004 - Summer 2005 at Point Sierra Nevada (PSN), Stairs (STA), and Point Fermin (PF).
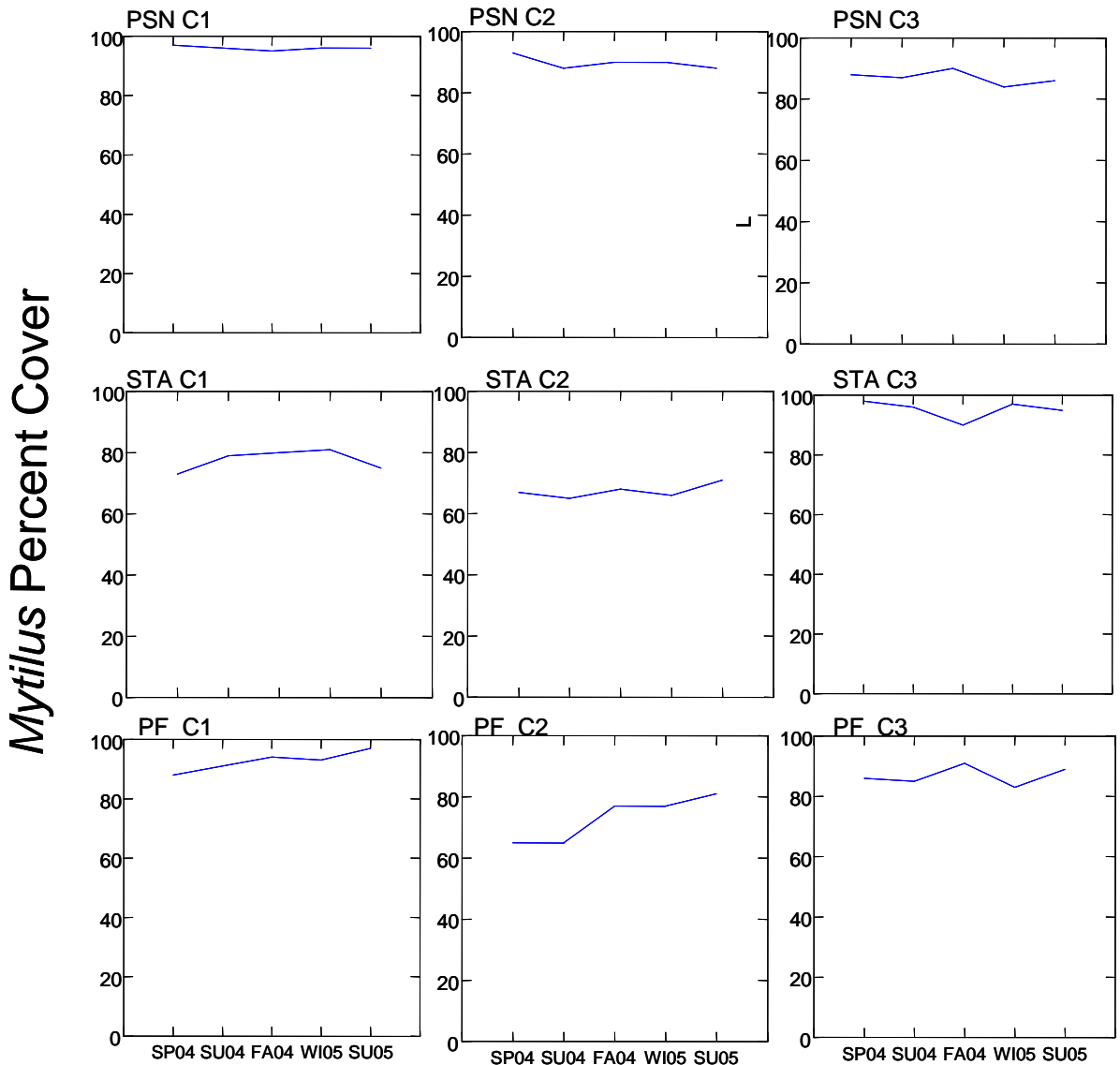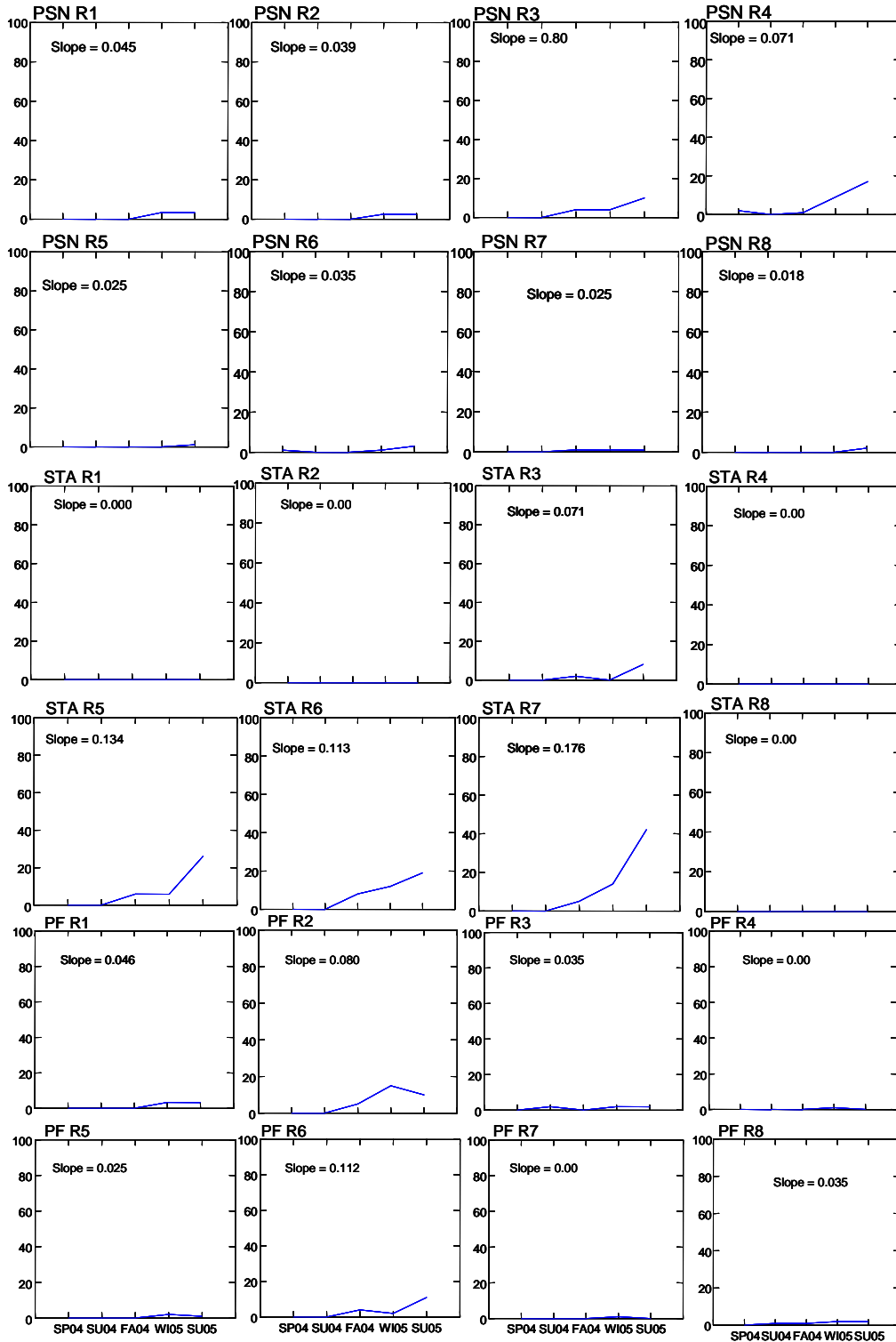
APPENDIX C

Appendix C. *Mytilus* percent cover over time in Recovery plots from Spring 2004 - Summer 2005 at Point Sierra Nevada (PSN), Stairs (STA), and Point Fermin (PF) where R1 represents the smallest plots and R8 the largest.

APPENDIX D

Appendix D. *Mytilus* percent cover over time in Control from Spring 2004 - Summer 2005 at Point Sierra Nevada (PSN), Stairs (STA), and Point Fermin (PF).
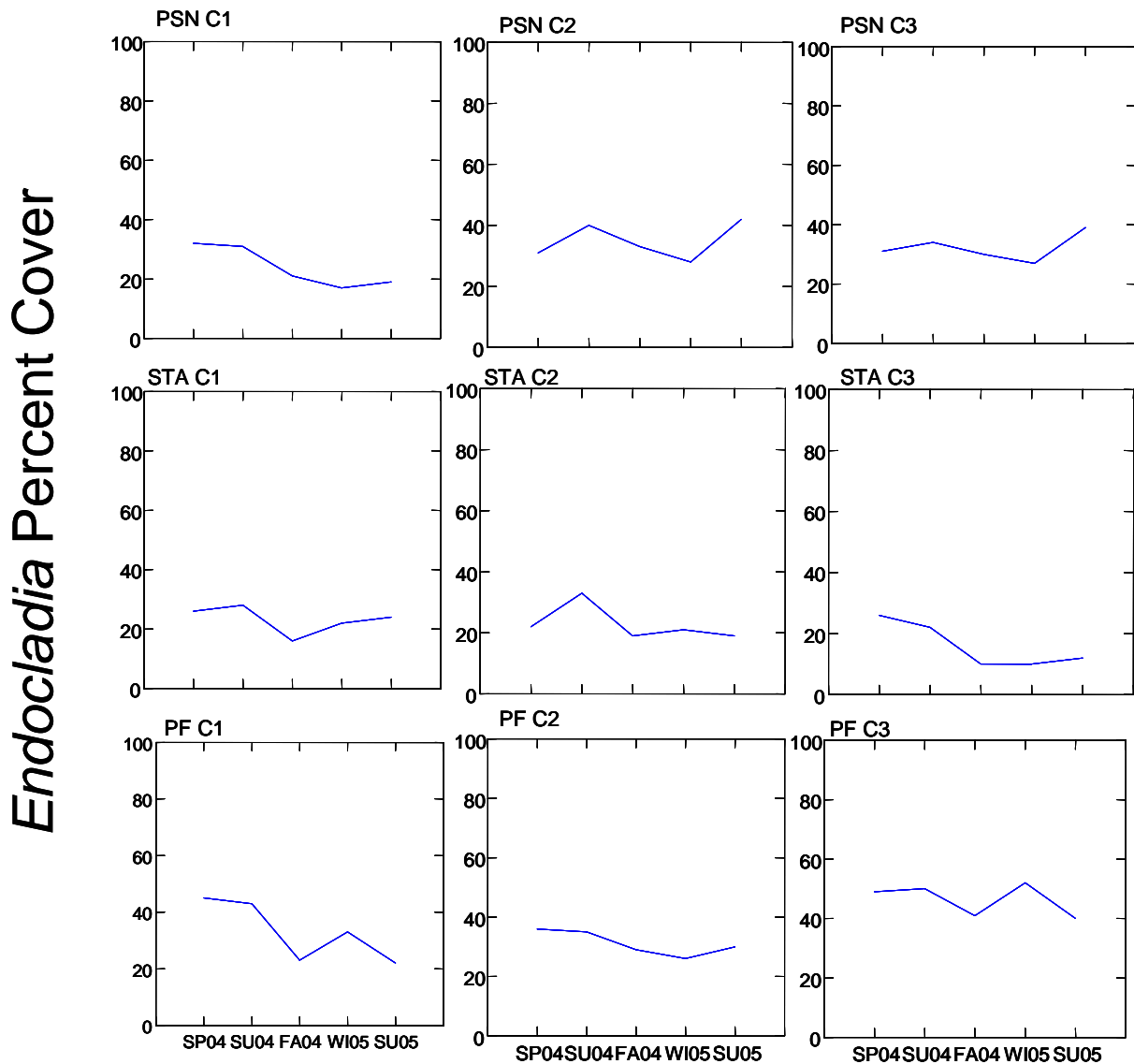
APPENDIX E

Appendix E. *Endocladia* percent cover over time in Recovery plots from Spring 2004 - Summer 2005 at Point Sierra Nevada (PSN), Stairs (STA), and Point Fermin (PF) where R1 represents the smallest plots and R8 the largest.
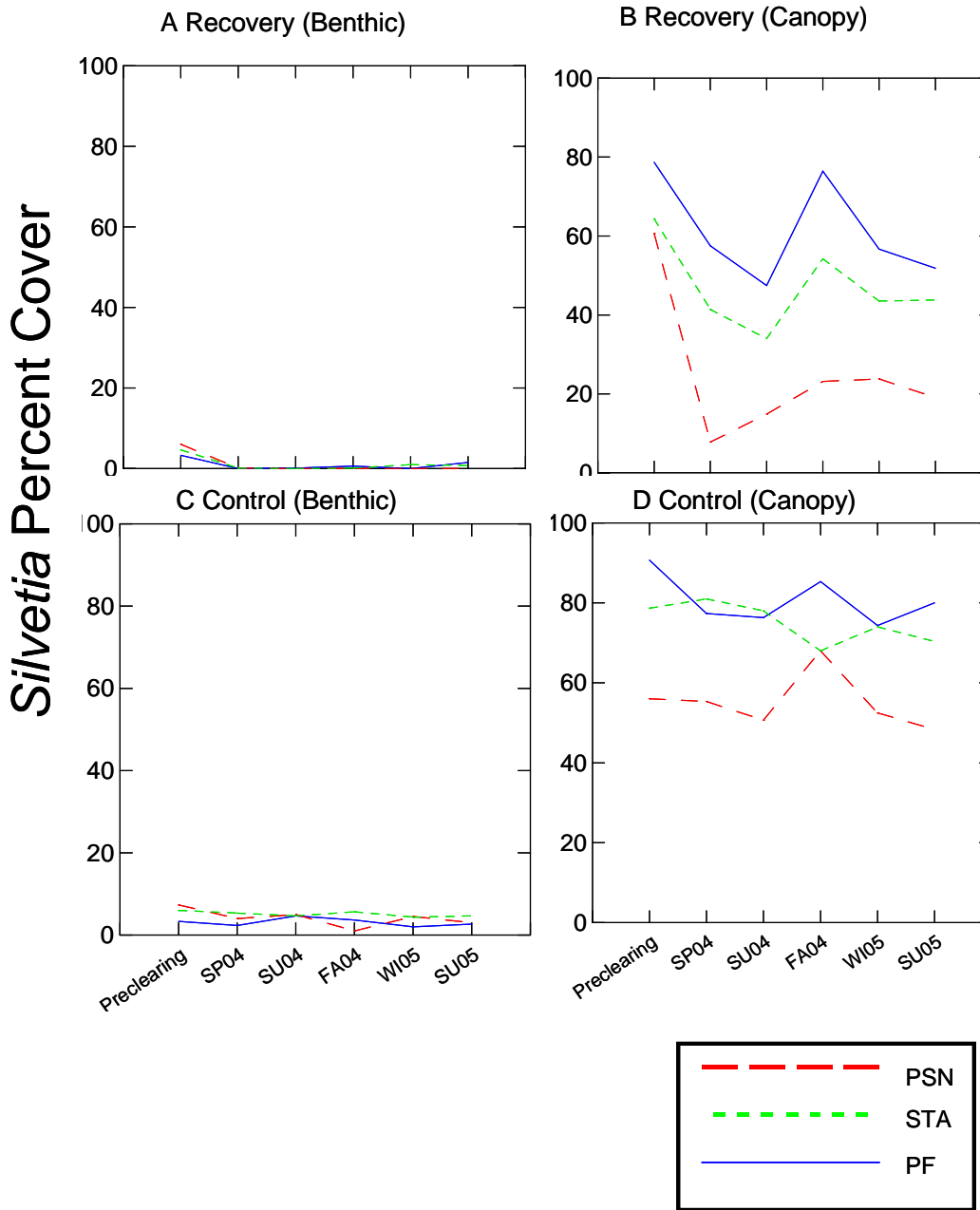
APPENDIX F

Appendix F. *Endocladia* percent cover over time in Control from Spring 2004 - Summer 2005 at Point Sierra Nevada (PSN), Stairs (STA), and Point Fermin (PF).
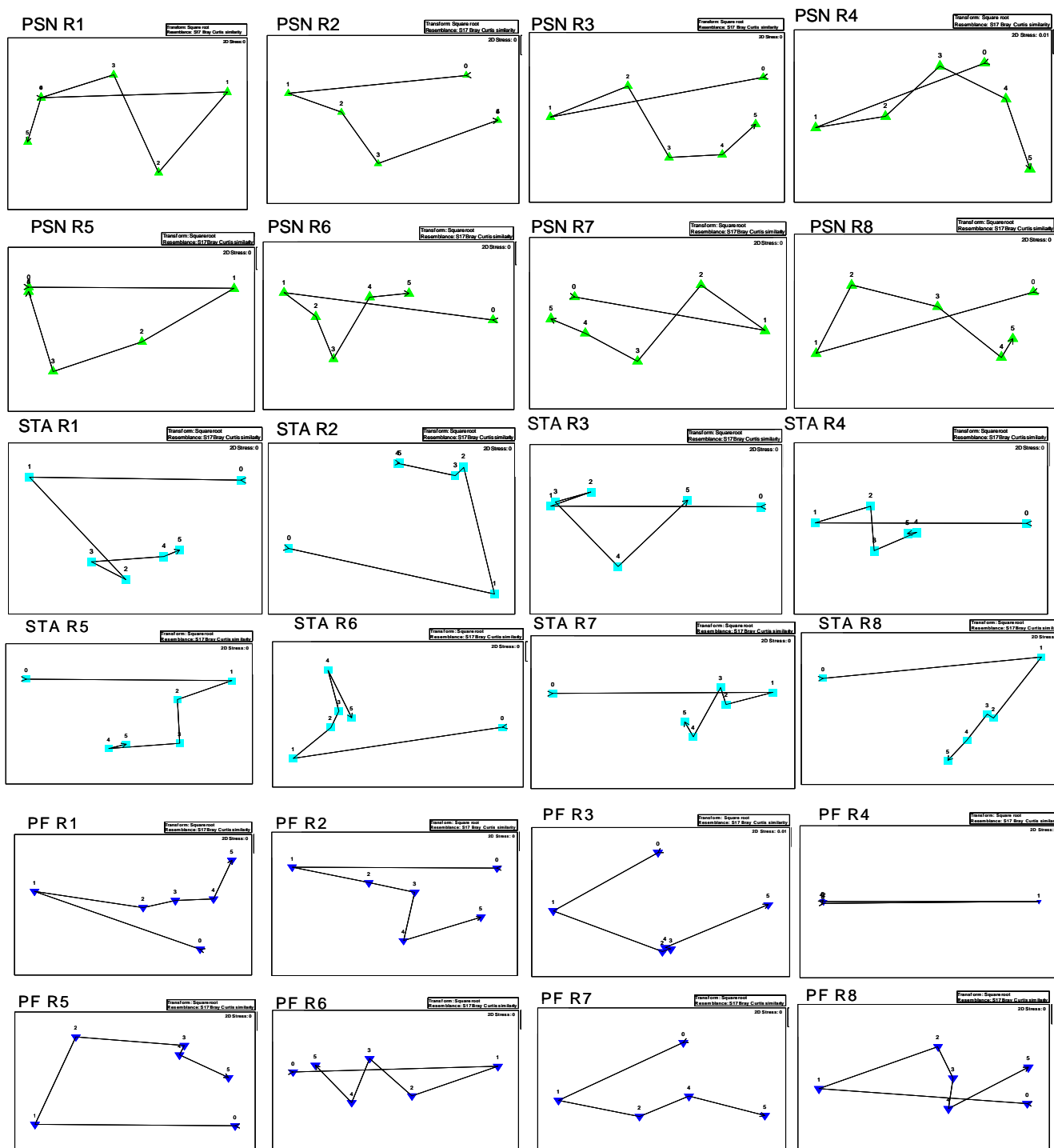
APPENDIX G

Appendix G. Mean *Silvetia* benthic and canopy cover over time in recovery and control plots from prior to clearing (Preclearing) to Summer 2005) at Point Sierra Nevada (dashed), Stairs (dotted) and Point Fermin (solid).
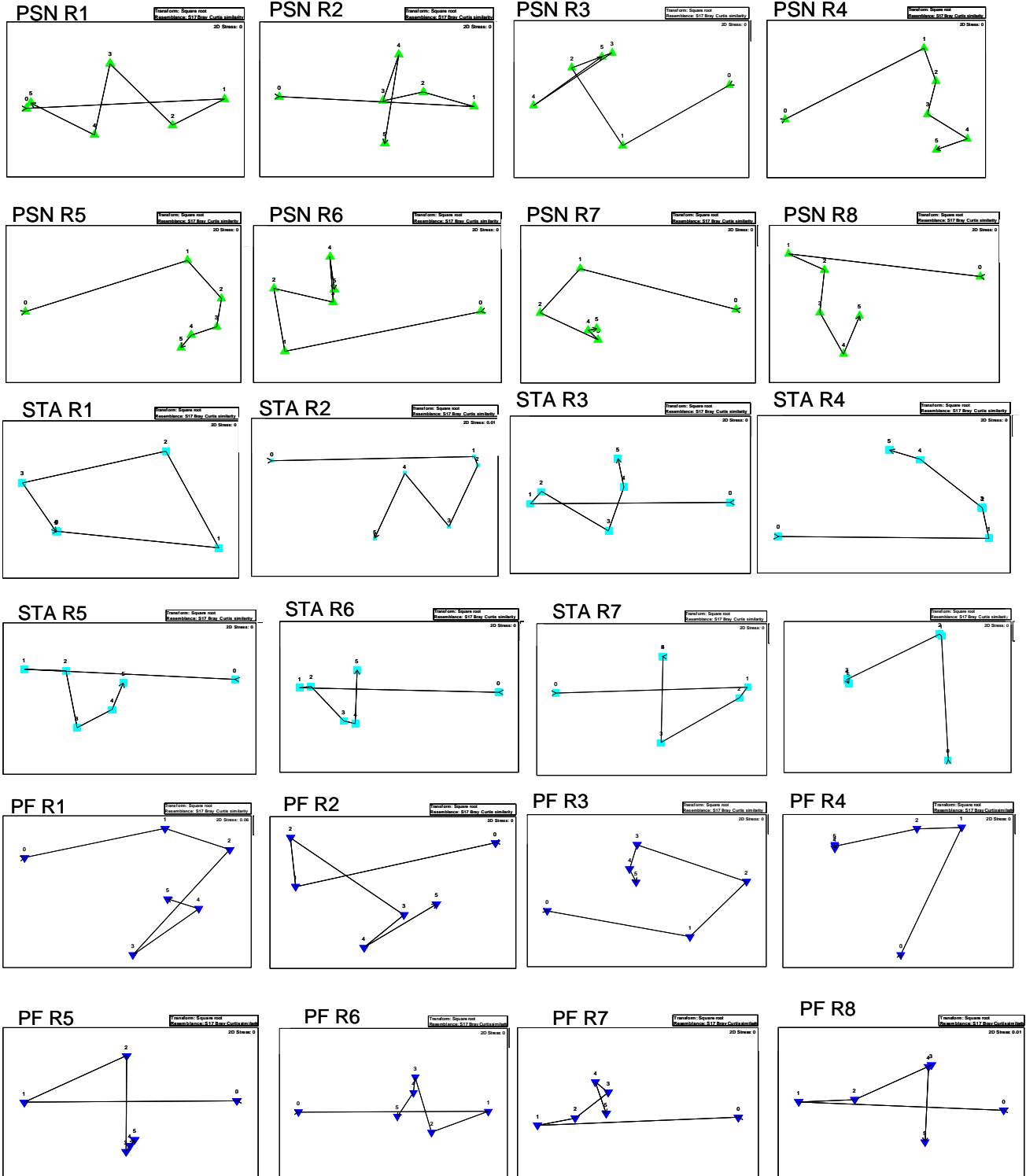
APPENDIX H

Appendix H. MDS plots of *Chthamalus* community recovery of each clearing size (R1 = smallest, R8 = largest) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) where 0 represents the community before the plot was cleared and points 1-5 represent subsequent sampling intervals.

APPENDIX I

Appendix I. MDS plots of *Mytilus* community recovery of each clearing size (R1 = smallest, R8 = largest) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) where 0 represents the community before the plot was cleared and points 1-5 represent subsequent sampling intervals.
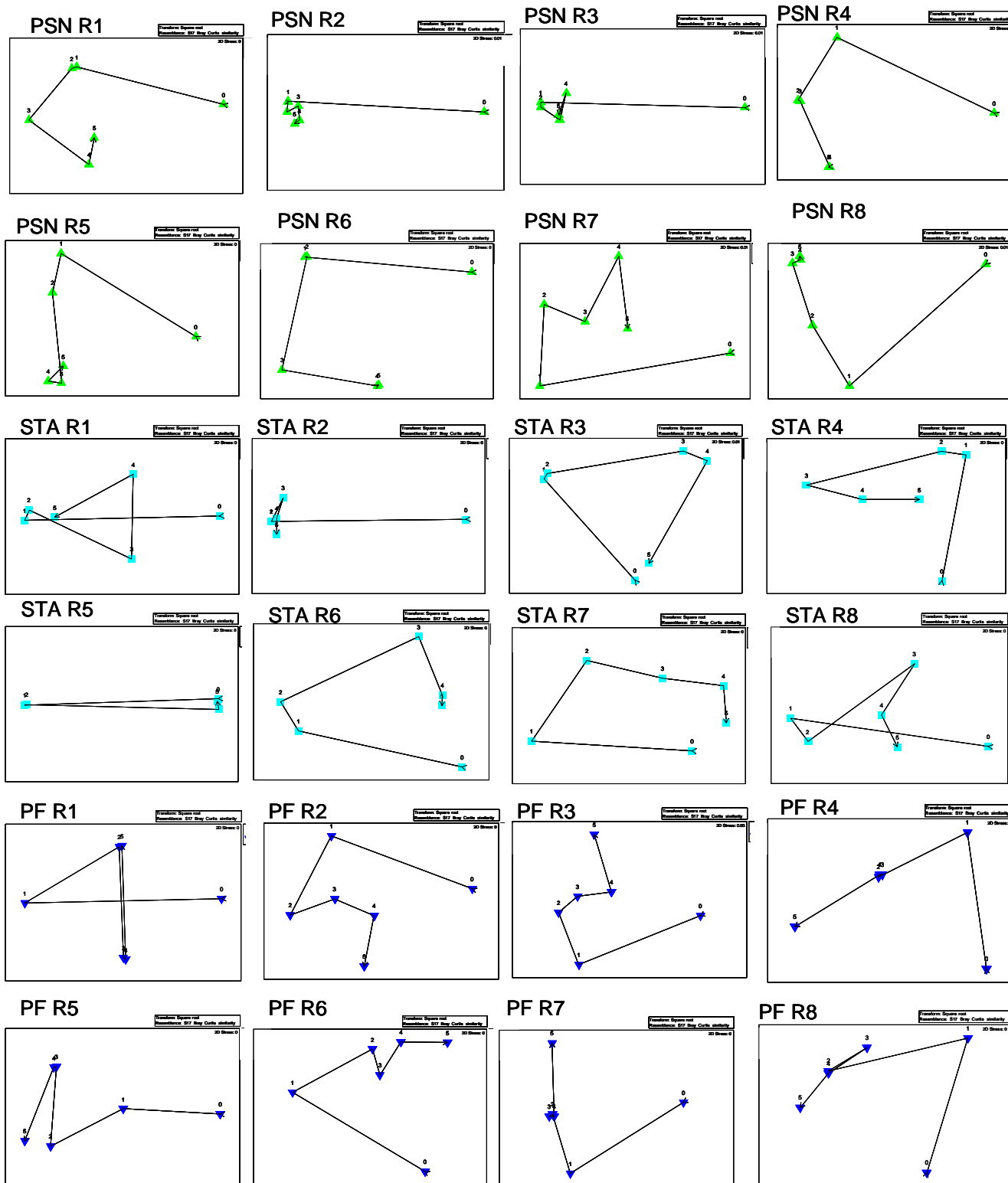
APPENDIX J

Appendix J. MDS plots of *Endocladia* community recovery of each clearing size (R1 = smallest, R8 = largest) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) where 0 represents the community before the plot was cleared and points 1-5 represent subsequent sampling intervals.
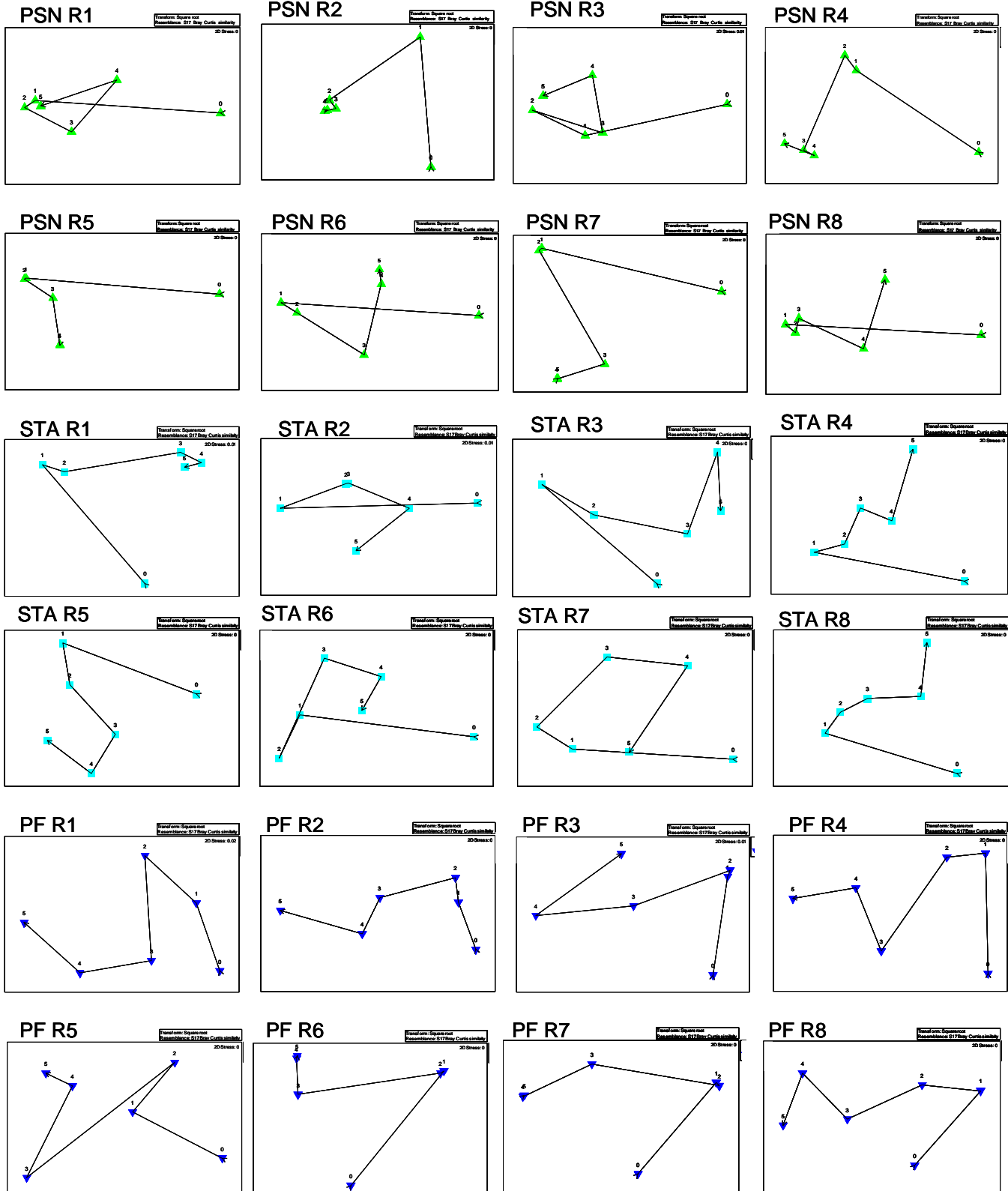
APPENDIX K

Appendix K. MDS plots of *Silvetia* community recovery of each clearing size (R1 = smallest, R8 = largest) at Point Sierra Nevada (PSN), Stairs (STA) and Point Fermin (PF) where 0 represents the community before the plot was cleared and points 1-5 represent subsequent sampling intervals. 5 represent subsequent sampling intervals.

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.