Title

Assessing Decline and Recovery of Rocky Intertidal Foundation Species Using Long-Term Data

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Assessing Decline and Recovery of Rocky Intertidal Foundation Species Using Long-Term Data

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Environmental Science and Management

by

Stephen Gregory Whitaker

Committee in charge:
Professor Steven D. Gaines, Chair
Professor Robert J. Miller
Professor Hunter S. Lenihan

December 2023

The dissertation of Stephen Gregory Whitaker is approved.

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ACKNOWLEDGMENTS

As a lifelong sufferer of imposter syndrome, I never trusted I had what it takes to be a 'Ph.D.', let alone be admitted into a program. Yet, my desire to be in academia has nagged me for as long as I can remember. The circuitous path I chose to get here was far from traditional. There were many people I feel fortunate enough to have encountered along the way who contributed to my success by offering valuable mentorship and experiences.

Thanks to Rick Ware, I was provided some of my first opportunities to work in many types of coastal habitats including marshes, seagrass beds, rocky intertidal reefs, sand beaches, and kelp forests. Rick's partnerships with various museums and universities even allowed us to work in some exotic, far-flung destinations like Fiji and the British Virgin Islands. As a result of all these experiences, my interests and focus gradually refined to the study of seaweeds and rocky shorelines.

My desire to study rocky intertidal ecosystems led me to apply for graduate school with the hope of earning a master's degree in the famed Murray Intertidal Lab at California State University, Fullerton. At CSUF, Dr. Steven Murray, along with Dr. Jayson Smith, contributed critical guidance as I learned how to conduct field experiments and test hypotheses. I attribute some of my greatest improvement and overall understanding of the art of scientific writing to the advice I received from both Dr. Murray and Dr. Smith. Moreover, both mentors contributed compelling reference letters for me which I presume were primary drivers for my acceptance into a Ph.D. program at UCSB.

If not for Dr. Robert (Bob) Miller of UCSB, I most certainly would never have dreamed of entering a Ph.D. program, especially while remaining fully employed. I am deeply indebted to Bob for all that he has done to help me get into UCSB and successfully navigate challenges as a student. I am also grateful for the freedom my committee chair, Dr. Gaines, and committee member, Dr. Lenihan have provided me as a student to decide what to work on and how to implement my project. At the same time, Dr. Gaines and Dr. Lenihan have always made time to provide guidance when I needed it most.

Returning to school and maintaining my position at the park was only possible with the vision and trust of my supervisors, David Kushner and Ken Convery. Both recognized the value of using National Park Service long-term monitoring data to characterize trends in rocky intertidal populations, and subsequently, identify factors driving the trends. More importantly, David and Ken supported my growth as an individual and employee. For that, I am most appreciative.

Perhaps like many other Ph.D. students, I underestimated the effort involved in completing my dissertation. After all, you only need to write three papers – so I thought. Writing is one thing. Statistical analysis is another. I took many courses on statistics during my tenure as a student, and I learned a lot. However, if not for the numerous consults I received from Dr. Pete Raimondi of UC Santa Cruz, many of which occurred after working hours in the evenings and weekends at my late request, I would likely still be stuck in that awful place wondering whether I did my analyses correctly. Thank you, Pete.

And that brings me to my family. My parents have supported me from the beginning. I will forever appreciate the financial hardship they faced by paying for my undergraduate tuition to attend the College of Charleston out of state so that I could major in marine biology. I am also grateful for all the opportunities they provided to support my life-long interest in working on the coast. Working full-time and being a student has impacted my ability to be present much of the time. As a result, I have missed many family occasions. My parents have always been understanding of this shortcoming, and again, I am grateful for having such wonderful, accepting, and supportive individuals in my life.

Perhaps more than anyone, my wife, Stacey, and son, Sebastian, have suffered the most from my disengagement as a husband and father over the last five years while I have been a student. Even when I was home with them, I was often preoccupied with studying and writing. Instead of spending weekends and evenings together as a family, I could reliably be found sitting in my home office staring at my computer. This placed an undue hardship on Stacey to provide for Sebastian in my absence. The sacrifices they both made for me to fulfill my lifelong dream of completing a Ph.D. are unmatched and I may never be able to adequately express my appreciation to them. Thank you, Stacey and Sebastian. You too are now rockweed experts!

This project would not have been possible without the rich data painstakingly collected by my predecessor at Channel Islands National Park, Dan Richards, along with numerous members of the Multi-Agency Rocky Intertidal Network (MARINe) which I am most grateful for. Funding for my tuition was provided by a grant from the California Ocean Protection Council (Agreement C0302106) to restore rockweed along with the NASA Biodiversity and Ecological Forecasting Program (Grant no. NNX14AR62A), the Bureau of Ocean Energy Management, Environmental Studies Program (BOEM Agreement MC15AC00006), and the National Oceanic and Atmospheric Administration in support of the Santa Barbara Channel Marine Biodiversity Observation Network.

One last note, as I was finalizing this dissertation and stressing over the formatting issues I was encountering, Dr. Rich Ambrose graciously offered to help. Dr. Ambrose not only resolved the problems I was having, but he also instructed me on how to work more efficiently in Microsoft Word. Thank you, Rich! I have long considered you one of my mentors, and now you have shown me that you are also a friend.

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EMPLOYMENT

- Marine Ecologist, Rocky Intertidal/Kelp Forest/Sand Beach Long-Term Ecological Inventory and Monitoring Programs; U.S. Department of the Interior, National Park Service, Channel Islands National Park, California; April 2013-Present
- Biological Technician, Rocky Intertidal/Kelp Forest/Sand Beach Long-Term Ecological Monitoring Programs; U.S. Department of the Interior, National Park Service, Channel Islands National Park, California; April 2009-April 2013
- Resource Advisor, U.S. Department of the Interior, National Park Service, South Florida/ Caribbean Network; July 2010
- Graduate Research Assistant, Marine Ecology Laboratory, Department of Biological Science, California State University, Fullerton, California; October 2006- May 2009
- Principal/Marine Biologist, Coastal Biome Consulting, San Clemente, California; February 2003- April 2009

EDUCATION

Ph.D. 2023. Bren School of Environmental Science and Management, University of California, Santa Barbara.
Dissertation: Assessing decline and recovery of rocky intertidal foundation species using long-term data

M.S. 2009. California State University, Fullerton (Marine Biology)
Thesis: Experimental re-establishment of the rocky intertidal brown alga *Silvetia compressa* at Little Corona del Mar

B.S. 1998. College of Charleston (Marine Biology)

ACADEMIC HONORS

- Sigma Xi Scientific Research Honor Society, University of California, Santa Barbara Chapter. 2023
- Fellowship ($67,846.50), Bren School of Environmental Science and Management, University of California, Santa Barbara. September 2018 – May 2023
- Phi Kappa Phi Honor Society, California State University, Fullerton Chapter. 2008
- Best Student Paper, Oral Presentation, Northwest Algal Symposium, Seattle Pacific University, Whidbey Island, Seattle, WA. May 2009

PEER REVIEWED PUBLICATIONS

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GRANTS

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- U.S.NPS, **Assessing endangered black abalone recruitment at CHIS, PORE and GOGA.** PMIS 202202, $97,033.58, FY19-21
- U.S.NPS, **Characterization of differential vulnerability to ocean acidification between Park Service networks in the Pacific West region.** PMIS 228189, $255,780, FY19-21
- NOAA Marine Debris Program, **Cultivating Santa Barbara Channel stewards.** $100,000, FY17-18

PAPERS PRESENTED AT SCIENTIFIC MEETINGS

(PRESENTED WHEN FIRST AUTHOR)

- Poster: Smith, J.R., Whitaker, S.G., Anderson, L.M., Fales, R.J., Sutton, S.G., Miller, R.J. **Ecological restoration using intertidal foundation species: considerations and potential for rockweed restoration**. Western Society of Naturalists, Monterey, CA. 2023.
- Poster: Smith, J.R., Sutton, S., Burnaford, J., Ambrose, R., Raimondi, P., Bell, C., Gaddam, R., Miner, M., Caselle, J., Parsons-Field, A., Boydston, E., Gilbane, L., Whitaker, S.G. **Long-term coastal monitoring by the Multi-Agency Rocky Intertidal Network (MARINe).** Western Society of Naturalists, Monterey, CA. 2023.
- Oral: Whitaker, S.G, Raimondi, P.T., Smith, J.R., Lenihan, H.S., Gaines, S.D., and Miller, R.J. **Decline of a North American rocky intertidal foundation species linked to extreme dry, downslope Santa Ana winds.** California Islands Symposium, Ventura, CA. 2023.
- Oral: Whitaker, S.G, Raimondi, P.T., Smith, J.R., Lenihan, H.S., Gaines, S.D., and Miller, R.J. **Decline of a North American rocky intertidal foundation species linked to synoptically driven offshore winds.** Western Society of Naturalists, Oxnard, CA. 2022.
- Poster: Miller, P.M., Whitaker, S.G., Raimondi, P.T., Smith, J.R., and Miller, R.J. **Population genetics and drivers of decline of a foundation species: the rockweed *Silvetia compressa***. 13th International Temperate Reefs Symposium. Hobart, Tasmania. 2023.
- Oral: Whitaker, S.G. **Long-term sustainability of ecological monitoring: perspectives from the Multi-Agency Rocky Intertidal Network.** DOI Talent. Virtual. 2022.
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- Oral: Whitaker, S.G. **North American rocky intertidal zones (tidepools): A diverse community in flux**. Naturally Speaking Series, Cabrillo National Monument, San Diego, CA. 2021.
- Oral: Emery, K.A., Dugan, J.E., Miller, R.J., Page, H.M., Schooler, N.K., Hubbard, D.M., Schroeder, D.M., Whitaker, S.G., Castorani, M.C.N., Bell, T.W. **Distribution and productivity of nearshore rocky outcrops influences trophic connectivity between kelp forests and sandy beaches.** GeoHab 2019, Saint Petersburg, Russia. 2019.
- Poster: Burnaford, J.L., Miner, C.M., Raimondi, P.T., Whitaker, S.G. and Gilbane, L. **Latitudinal variation in long-term stability and resilience of North American rocky intertidal communities.** Ocean Sciences Meeting, San Diego, CA. 2020.
- Oral: Smith, J.R., Gilbane, L., Ambrose, R.F., Bell, C.A., Burnaford, J.L., Gaddam, R., Miner, C.M., Parsons-Field, A., Raimondi, P.T. and Whitaker, S.G. **Long-term monitoring by the Multi-Agency Rocky Intertidal Network (MARINe).** Ocean Sciences Meeting, San Diego, CA. 2019.
- Oral: Whitaker, S.G. **The value of long-term monitoring: Channel Islands National Park Rocky Intertidal Monitoring Program.** NOAA Fisheries West Coast Region Protected Resources Division Workshop, San Diego, CA. 2018.

- Oral: Whitaker, S.G., Dilly, G.F., Ambrose, R.F., Yap, T.A. and Richards, D.V. **Widespread decline in abundances of the rocky intertidal rockwed *Silvetia compressa* at Channel Islands National Park.** California Islands Symposium, Ventura, CA. November 2016.
- Oral: Bell, C.A., Raimondi, P.T., Ambrose, R.F., Amman, K.A., Anderson, L.A., Burnaford, J.L., Douglas, M.A., Fletcher, N.C., Gaddam, R., George, M.K., Gilbane, L.A., Lee, S.F., Smith, J.R., Whitaker, S.G. and MARINe. **Patterns from decades of rocky intertidal monitoring.** Western Society of Naturalists Conference, Monterey, CA. November 2016.
- Oral: Raimondi, P.T., Gilbane, L., Ostermann, S., Whitaker, S.G., Lee, L., Richards, D.V., Ambrose, R.F., Lee, S., Bell, C.A., Miner, C.M., Gaddam, R., Burnaford, J.L., Smith J.R. and Murray, S.N. **Multi-Agency Rocky Intertidal Network: Trends and assessment of long-term surveys on both sides of the Santa Barbara Channel.** 9th California Islands Symposium, Ventura, CA. 2016.
- Oral: Gilbane, L.A., Helix, M.E., Bell, C.A., Miner, C.M. and Whitaker, S.G. **Why Long Term Rocky Intertidal Monitoring Matters.** Western Society of Naturalists, Sacramento, CA, 2015.
- Oral: Whitaker, S.G. and Raimondi, P.T. **Rocky intertidal monitoring at Channel Islands National Park responds to challenges of the 21st century.** George Wright Society, Oakland, CA. April 2015.
- Oral: Ostermann-Kelm, S., Allen, S., Anderson, D., Becker, B., Fong, D., Fradkin, S., Lombardo, K., Miner, M., Whitaker, S. and Raimondi, P. **Unprecedented outbreak of sea star wasting disease in west coast national parks.** George Wright Society Conference on Parks, Protected Areas, and Cultural Sites. Oakland, CA, 2015.
- Oral: Whitaker, S.G. **Rocky intertidal monitoring at Channel Islands National Park and Cabrillo National Monument.** MEDN I&M Program Science Symposium. Santa Monica Mountains National Recreation Area, Thousand Oaks, CA. November, 2015.
- Oral: Whitaker, S.G. **Sand beach and lagoon monitoring at Channel Islands National Park.** MEDN I&M Program Science Symposium. Santa Monica Mountains National Recreation Area, Thousand Oaks, CA. November, 2015.
- Oral: Whitaker, S.G. and Richards, D.V. **Revisiting a trampling study following 30 years of intertidal monitoring at Cat Rock, Anacapa Island.** Channel Islands Symposium, Ventura, CA. November 2012.
- Oral: D.V. Richards and S.G. Whitaker. **Tidepooling through time: 30 years of rocky intertidal community monitoring at Channel Islands National Park.** Channel Islands Symposium, Ventura, CA. November 2012.
- Oral: D.V. Richards and S.G. Whitaker. **Icons of the rocky intertidal zone: black abalone persevere at the northern Channel Islands.** Channel Islands Symposium, Ventura, CA. November 2012.
- Poster: Whitaker, S.G. and Richards, D.V. **Widespread declines in abundances of rocky intertidal ecosystem modifiers and associated motile invertebrate species.** Western Society of Naturalists, San Diego, CA. November 2010.
- Poster: D.V. Richards and S.G. Whitaker. **Monitoring black abalone movement and aggregating behavior.** Western Society of Naturalists, San Diego, CA. November 2010.

- Oral: Whitaker, S.G. **The National Park Service's response to the Deepwater Horizon oil spill.** Ventura Audobon Society, Ventura, CA. September 2010.
- Oral: Whitaker, S.G., Smith, J.R., and Murray, S.N. **Experimental re-establishment of the intertidal rockweed *Silvetia compressa* on urban southern California shores.** Northwest Algal Symposium, Seattle Pacific University, Whidbey Island, Seattle, WA. May 2009.
- Oral: Whitaker, S.G., Smith, J.R. and Murray, S.N. **Experimental restoration of the intertidal rockweed *Silvetia compressa* at Little Corona.** Multi-Agency Rocky Intertidal Network workshop, Cabrillo Aquarium, Long Beach, CA. October 2008.
- Oral: Smith, J.R., Navarro, C.N., Whitaker, S.G. and Murray, S.N. **Seaweed communities in a heavily urbanized environment in southern California.** Coastal Studies Consortium, Universidade Federal Fluminense, Niteroi, Brazil. July 2007.
- Poster: Whitaker, S.G., Smth, J.R. and Murray, S.N. **Experimental restoration of the intertidal rockweed *Silvetia compressa* at Little Corona del Mar, CA.** Southern California Academy of Sciences, CSUF, Fullerton, CA. June 2007.

INVITED LECTURES

- Whitaker, S.G. **Rocky intertidal monitoring with a special focus on rockweed restoration.** University of California, Santa Barbara. Biological Conservation. Fall 2014.

STUDENT ADVISING

- Coty, A. **Santa Rosa Island lagoons monitoring: two highly variable systems.** Environmental Science and Resource Management Undergraduate Capstone Project. California State University, Channel Islands. 2016.
- Miller, M. **Ventura County marine debris trends: 30 years of change on mainland and Channel Island beaches.** Environmental Science and Resource Management Undergraduate Capstone Project. California State University, Channel Islands. 2016.

PROFESSIONAL SERVICE

- NOAA Channel Islands National Marine Sanctuary, Subject-matter expert for State of the Sanctuary Reports and Climate Vulnerability Workshop. 2016-Present.
- NOAA Channel Islands National Marine Sanctuary Advisory Council Member. 2022-Present.
- Southwest Climate Adaptation Science Center Advisory Committee. 2023-Present.
- NOAA NMFS Black Abalone Recovery Team. 2016-Present.
- NOAA CINMS Marine Shipping Working Group. 2015-2016.
- NRDA Rocky Intertidal Survey for Refugio Oil Spill. 2015.
- CDFW OSPR Refugio Oil Spill Rocky Intertidal Technical Working Group. 2015-2018.
- Reviewer: Marine Pollution; NOAA NMFS; CDFW

- Member of the Multi-Agency Rocky Intertidal Network (MARINe). 2006-Present.
    - Additional service on the Database Team

RELEVANT CERTIFICATIONS

- 40 Hour Blue-Card Refresher, National Park Service Scientific Diving, Channel Islands National Park. 2012, 2015, 2018
- Operational Leadership, National Park Service. 2010
- HAZWOPER, 24 Hour. Updated Annually
- Blue-Card Certified National Park Service Scientific Diver, Channel Islands National Park. 2009-Present
- American Academy of Underwater Sciences Research Diver, University of Southern California. 2001
- Master Diver, NAUI. 2001
- Nitrox, NAUI. 2001
- Advanced Open Water, PADI. 1996
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ABSTRACT

Assessing Decline and Recovery of Rocky Intertidal Foundation Species Using Long-Term Data

by

Stephen Gregory Whitaker

Rocky intertidal ecosystems in California have been significantly degraded. Of particular concern is the precipitous population decline of rockweeds attributed to increased urbanization and accompanying impacts. As foundation species, rockweeds modify the physical environment of rocky intertidal habitats and increase biodiversity by decreasing environmental stress under their canopy. No substitute macrophyte species in southern California provides a comparable function to rockweeds in the intertidal zone. Recovery of impacted rockweed populations is typically slow and unpredictable, due to their poor dispersal capacity. To determine the status of the dominant rockweed species in southern California, *Silvetia compressa*, I analyzed canopy cover data from 30 sites spanning 18 years. I found that the rockweed had declined markedly at sites south of the major biogeographic break, Point Conception (PC), including the California Channel Islands and southern California mainland. Analyses using climatological data revealed that substantial declines in *Silvetia* cover in southern California were associated with strong, hot offshore Santa Ana wind events. To assess the recovery of disturbed rocky intertidal ecosystems, I analyzed 28 years of data from a controlled disturbance experiment at a remote site with limited human visitation. I found the recolonization rates for species cleared to be highly variable ranging from years to decades, and that even relatively mild disturbances from pedestrian traffic can have long-lasting effects on rockweeds. Long-lived species such as rockweeds and mussels took more time to recover from extreme disturbances than species with shorter lifespans such as barnacles and turfweed. Since rockweeds foundational to ecosystem functioning have sustained extensive degeneration and range contractions worldwide, and recovery of impacted rockweed populations is typically slow and unpredictable due to their limited dispersal capacity, I propose that rockweeds are optimal candidates for restoration. In my third chapter, I summarize the current knowledge of rockweed ecology, highlighting studies that could inform restoration practices, and recommend ways to improve our ability to implement scalable restoration of rockweeds and accompanying ecosystem-wide benefits.

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Introduction

Rocky intertidal habitats harbor diverse and productive communities of marine species. Along the western coast of North America, particularly in densely populated southern California, these ecosystems have been significantly altered and degraded. Examples include the near extinction of black abalone, declines in body size of owl limpets, reduction in extent and diversity of mussel bed communities, and the widespread mortality of ochre sea stars. Of particular concern is the precipitous decline of habitat-forming rockweed species, specifically *Silvetia compressa* and *Pelvetiopsis californicus*, along their ranges, including within established Marine Protected Areas. Declines of rockweeds in California have been attributed to increased urbanization and accompanying impacts, and climate change and sea level rise are expected to exacerbate these impacts.

Rockweeds are foundation species that modify the physical environment of rocky intertidal habitats and increase biodiversity. In the middle and high intertidal zone, rockweed canopies provide shade and trap moisture during low tides, protecting a diverse community (>100 species) from desiccation and UV stresses that will likely increase in the future with climate change. Rockweed canopies also facilitate the recruitment of numerous species, including the rockweeds themselves, positive feedback that contributes to their long-term population stability. In addition, rockweeds are highly productive relative to many other intertidal macrophytes, providing an important source of food for herbivores. No substitute macrophyte species in southern California provide a comparable function to rockweeds in the intertidal zone, and the biodiversity and ecosystem function of intertidal habitats are depressed without the presence of these foundational species.

Recovery of impacted rockweed populations is typically slow and unpredictable, due in part to their low dispersal capacity - rockweed gametes are non-motile and most settlement occurs <1m from parent populations. While fertilization rates are nearly 100%, post-settlement mortality of rockweed zygotes and germlings is high due to abiotic stresses and biotic interactions, and survival outside the adult canopy is likely lower. Thus, when a local population declines, this can lead to a downward spiral to extirpation. Recovery is unlikely with no local source population.

My dissertation uses long-term monitoring data from dozens of Multi-Agency Rocky Intertidal (MARINe) sites to investigate patterns of decline for rockweeds in California. I tested the hypothesis that strong, dry, and often warm downslope winds, commonly referred to as *Santa Ana* winds are driving declines in rockweed populations. To gain a stronger understanding of how damaged rockweed populations recover, I analyzed data from a multidecadal controlled disturbance experiment to identify rates of recovery for rockweeds and other intertidal assemblages dominated by taxa with varying dispersal capabilities and life expectancies. Finally, I summarize the current knowledge of rockweed ecology, highlighting studies that could inform restoration practices, and recommend ways to improve our ability to implement scalable restoration of rockweeds and accompanying ecosystem-wide benefits.

In Chapter 1, I analyzed rockweed canopy cover data from 30 sites in California spanning 18 years. Using a Generalized Linear Model with explicit spatial effects, I identified regional trends among the sites and found that the rockweed had declined markedly, particularly at sites south of the major biogeographic break, Point Conception (PC), including the California Channel Islands and southern California mainland. Above PC, *Silvetia* trends were highly variable, but most populations remained stable or increased in cover during the survey period. This latitudinal pattern suggests that rockweed may be more stressed in its southern range. Further analyses indicated that substantial declines in *Silvetia* cover in southern California were associated with strong, hot offshore Santa Ana wind events, most notably between 2008 and 2015. Using climatological data, I found a highly significant negative effect of dewpoint depression, a measure of moisture content in the atmosphere, on *Silvetia* cover across all three regions in this study. My results support the hypothesis that *Silvetia* population trends are tightly linked to atmospheric climate conditions, particularly Santa Ana wind events.

In Chapter 2, I assessed recovery rates for rockweeds relative to other rocky intertidal foundation species following disturbance. I used data from a remote site with limited human visitation that was surveyed annually for 28 years following a controlled disturbance experiment including human trampling to mimic light visitor usage and clearing to represent more intense disturbance. I found the recolonization rates for species cleared to be highly variable ranging from years to decades. The one-time trampling treatment significantly reduced the cover of rockweeds but not turfweed, barnacles, or mussels. Recovery took approximately one decade for the fucoid assemblage following trampling. The results of this long-term field experiment indicate that longer-lived species including mussels and rockweeds take more time to recover from extreme disturbances than species with shorter lifespans such as barnacles and turfweed. Even relatively mild disturbances from pedestrian traffic can have long-lasting effects on some intertidal species.

In Chapter 3, I (1) explain why rockweeds are prime subjects for restoration, (2) summarize published evidence of changes in rockweed populations, (3) identify and discuss the factors limiting population recovery, and (4) review past restoration activities and provide recommendations for future ecological restoration efforts. I show that restoring key foundation species, such as rockweeds, is an efficient way to achieve broader benefits to ecosystem integrity since rockweed recovery can increase the biodiversity of the entire rocky intertidal ecosystem dependent on them. My review indicates that it is critically necessary to identify effective methods for restoring rocky intertidal communities at meaningful spatial scales to counter future large- and small-scale impacts to this ecologically important and valuable marine ecosystem. Restoring foundational rockweeds and their associated communities is one of them and will help buffer against the impacts of climate change and other catastrophic events in the future as well as prevent larger-scale losses of intertidal communities.

[redacted] Decline of a North American Rocky Intertidal Foundation Species Linked to Extreme Santa Ana Winds

Introduction

Foundation species define much of the structure of the community they occupy by modulating fundamental ecosystem processes and creating locally stable conditions for other species (Dayton, 1985; Ellison et al., 2005). Examples include mangroves (Duke et al., 2007), corals (Hughes et al., 2003), seagrasses (Short et al., 2006), kelps (Steneck et al., 2002), oysters (Lenihan et al., 2001), cordgrass (Zedler et al., 2001), and many tree species including redwood, hemlock, and birch (Ellison et al., 2005). These species share commonness and high local abundances, hence the tendency to name ecosystems after them – seagrass beds, kelp forests, oyster beds, and hemlock forests. Maintaining their foundational role in ecosystems, and the resulting effects on biodiversity, community composition, and ecosystem function, requires high local abundances, not simply species survival. However, many foundation species are declining due to coastal development (Zedler et al., 2001; Duke et al., 2007), pollution (Duke et al., 2007), invasive species (Steneck et al., 2002), introduced pathogens (Ellison et al., 2005), over-harvesting (Jackson et al., 2001; Steneck et al., 2002; Ellison et al., 2005), and climate change (Sagarin et al., 1999; Hughes et al., 2003), likely resulting in cascading impacts on associated communities (Sarà et al., 2021; Smale et al., 2022; Wernberg et al., 2023 and references therein).

In temperate rocky intertidal ecosystems, perennial fucoid macroalgae, commonly referred to as rockweeds, are often important foundation species (Chapman, 1995; Schiel and Foster, 2006). At low tide, rockweed canopies protect the substratum and communities beneath the canopy from sun exposure, desiccation, and heat stress (Bertness et al., 1999; Sapper and Murray, 2003; Råberg and Kautsky, 2007; Marzinelli et al., 2014) and thereby enhance biodiversity (Råberg and Kautsky, 2007; Marzinelli et al., 2014). Via this protection, as well as hydrodynamic effects, rockweed canopies also facilitate the recruitment of numerous intertidal species, including the rockweeds themselves (Bertness et al., 1999; Viejo et al., 1999), a positive feedback loop that likely contributes to their long-term population stability (Bertness et al., 1999). In addition to these ecosystem engineering effects, rockweeds are highly productive (Golléty et al., 2008; Tait and Schiel, 2010; Tait et al., 2014; Bordeyne et al., 2015), providing an important source of food for intertidal herbivores (Moore, 1977; Lubchenco, 1983; Steinberg, 1985; Bertness and Leonard, 1997; Jenkins et al., 2004; Hawkins et al., 2008) and detrital consumers (Bishop et al., 2010; Golléty et al., 2010; Renaud et al., 2015), and contributing to nutrient cycling (Schmidt et al., 2011).

Silvetia compressa (J.Agardh, E.ASerrão, T.O.Cho, S.M.Boo, and S.H.Brawley, 1999), (Phaeophyceae, hereafter *Silvetia*) is the dominant rockweed species in the northeast Pacific from Monterey County, California to Punta Baja, Baja California, Mexico (Abbott and Hollenberg, 1992; Silva et al., 2004). *Silvetia* can live at least eight years (Gunnill, 1980) and is slow to recover from population declines due to the short-range dispersal of its gametes (Hays, 2006). Attaining frond lengths of 90 cm with up to 20 orders of branching (Silva et al., 2004), *Silvetia* can form large and dense beds (Figure 1.1) that harbor a diverse understory community. For example, Sapper and Murray (2003) documented 47 species of algae, 20 sessile and 44 mobile invertebrate species under the canopy formed by *Silvetia* at a rocky intertidal site in southern California.

Upper and middle intertidal rockweeds, including *Silvetia,* are regularly subjected to prolonged periods of aerial exposure (i.e., emersion) during low tides. Rapidly fluctuating atmospheric variables, such as temperature, irradiance, wind speed, and relative humidity, impose increasingly greater stress on intertidal biota as a function of shore height (e.g., Hawkins and Hartnoll, 1985). Physiological stress generally results in increased rates of mortality (Graham and Wilcox, 2000) and reduced physiological performance (Schonbeck and Norton, 1980), and individuals living higher on the shore often exhibit morphological differences in response, such as thickened and stunted body forms (Sideman and Mathieson, 1985; Davison and Pearson, 1996). As a result, stress from emersion, and particularly desiccation, is considered among the most important drivers of species performance and abundance in the rocky intertidal zone (Brinkhuis et al., 1976; Brawley and Johnson, 1993; Davison and Pearson, 1996; Stengel and Dring, 1998; Helmuth and Hofmann, 2001 and references therein).

The coast from central California to northern Baja California including southern California and the Channel Islands in the Southern California Bight is periodically exposed to strong, dry, and often warm downslope winds, commonly referred to as *Santa Ana* winds (SAWs) (Abatzoglou et al., 2021; Guirguis et al., 2023). These harsh winds result from sharp gradients between high-pressure systems across the interior of the western United States and low pressure at the coast. As the air masses move from the dry Great Basin to the west over the coastal mountain ranges, they are compressed down the mountains and through canyons where they accelerate, heat, and dry in the process termed downsloping. SAWs can reach sustained speeds of 7-13 m s^{-1} (and gusts of >25 m s^{-1}) and are characterized by low humidity

(<15%) and warm air (>21 °C) (Rolinski et al., 2019). SAWs can occur any time of the year, but they peak in late fall through early spring.

Recent modeling studies have revealed marked interannual variation in the frequency, intensity, and spatial coverage of SAWs (Jones et al., 2010; Abatzoglou et al., 2013; Guzman-Morales et al., 2016; Dye et al., 2020), and these temporal trends have been linked to variation in environmental indices, including the El Niño-Southern Oscillation (Raphael, 2003), Pacific Decadal Oscillation, and the Atlantic Multi-decadal Oscillation (Li et al., 2016). SAWs are well studied due to their impact on vegetation and catastrophic wildfire threats (e.g., Moritz et al., 2010; Dye et al., 2020), but research on their impacts on marine life and oceanographic patterns is scarce. Intertidal organisms in southern California are severely stressed in late fall and winter when SAWs frequently coincide with extreme low tides (Seapy and Hoppe, 1973; Gunnill, 1980; Littler, 1980), and die-backs of *Silvetia* and other species have been attributed to prolonged aerial exposure (Seapy and Littler, 1982).

According to the Santa Ana Wildfire Index, a model derived from the climatological data used in this study to generate time series representing the trend for SAWs from 1981-2016, the annual frequency gradually increased beginning in 2000 (Li et al., 2016; Rolinski et al., 2019) (Figure S1.1). By 2006, the mean number of SAW days had increased 54% from 46 days per year (1981-2005) to 71; a trend that persisted through the remainder of the climatology (Rolinski et al., 2019). This trend appears inversely proportionate to changes in *Silvetia* cover observed at numerous long-term monitoring study sites in the region affected by SAWs, with the most precipitous losses in cover occurring after 2005.

Here, we test the hypothesis that SAW events are driving declines in *Silvetia* populations in southern California. To perform our test, we used climatological time series data along with long-term monitoring data for *Silvetia* measured throughout much of its geographical range, extending across ca. 900 km of shoreline from Los Angeles, California to near the California /Mexico border, including several of the offshore Channel Islands in southern California.

Materials and Methods

Study sites

Thirty long-term monitoring sites (Figure 2.1; Table S1.1) were established by the Multi-Agency Rocky Intertidal Network (MARINe; pacificrockyintertidal.org), a consortium of government agencies, academic institutions, and nonprofit groups, from 1981 to 1999 across *Silvetia's* range. Sites were established on bedrock benches with *Silvetia* beds. Refer to Engle et al. (2022) for detailed descriptions of methods.

Sites were grouped consistent with biogeographic regions described in Blanchette et al. (2008): central California (CEN, n = 4), defined as sites north of Point Conception (PC), a major biogeographic barrier separating the southern California sites (SOU, n = 10). Although located in the Southern California Bight, the offshore Channel Islands are exposed to a latitudinal gradient in environmental and oceanographic conditions that differs from the mainland (Dailey et al., 1993; Harms and Winant, 1998; Kapsenberg and Hofmann, 2016). Therefore, we grouped the Channel Islands (CHA, n = 16) sites separately from the southern California mainland sites. The sites were primarily limited to the northern Channel Islands which are subjected to colder water temperatures than the southern Channel Islands.

Survey methods

At each of the sites, five fixed rockweed plots (50 x 75 cm) were established mostly in the mid-1980s to 1990s and were originally chosen haphazardly at each site in areas of high canopy cover of *Silvetia* (Engle et al. 2022) (Figure 1.1). Stainless steel hex bolts were installed in three corners of each rectangular plot so they could be relocated. Percent cover of *Silvetia*, as well as other species or bare substrate when *Silvetia* was absent, was scored in each plot using a point contact method with a grid of 100 points, either in the field or using a digital photo of the plot (Engle et al. 2022). Until 2015, fixed plots were photographed and sampled biannually in the spring (March–May) and fall (October – January) during daytime low tides. Beginning in 2015, plots were sampled annually to reduce survey effort since seasonal differences in *Silvetia* cover were not significant (Raimondi et al., 2018), and most annual monitoring was conducted during the fall period. The long-term monitoring, fixed-plot approach used by MARINe was established to support a reasonable sampling effort while providing effective statistical power to detect changes over space and time. To maximize spatial and temporal coverage, we included all data on *Silvetia* cover from 2002-2020. The initial year was chosen based on the period when protocols and the resolution of taxonomic identifications were standardized across monitoring sites.

Climatology

For each *Silvetia* monitoring site, daily mean and max statistics (3-km horizontal resolution) for dewpoint depression (D_d) (°C) and wind velocity (W_s) (km h^{-1}) were generated using a numerical weather prediction and atmospheric simulation system, the Weather Research and Forecasting (WRF) model (Rolinski et al., 2016). Daily values for D_d and W_s for each site were averaged between sampling events to provide a synopsis of the environmental conditions prior to measuring the percent cover of *Silvetia*. Dewpoint depression, the difference between air temperature and dewpoint temperature, together with near-surface wind gust time series, represents the drying process characteristic of synoptically driven offshore *Santa Ana* winds. Refer to Rolinski et al. (2016) and Skamarock et al. (2008) for detailed descriptions of how the atmospheric data used in this study were generated.

Statistical analysis

Data exploration of SAW patterns was carried out following the protocol described by Zuur et al. (2010). Dewpoint depression (D_d) and W_s climatological data were visually inspected using QQ plots, histograms, and a pair plot. Collinearity between D_d and W_s was assessed using scatterplots. Data transformations were deemed unnecessary, since the time series appeared approximately normally distributed, and various transformations including square root, cubic root, and logarithmic calculations did not significantly improve the linearity of the time series (Akaike, 1974). Data examination revealed nonlinear temporal and covariate effects.

To test for relationships between *Silvetia* cover and SAW time series data, trends in *Silvetia* populations were modeled as a function of the covariates using generalized additive mixed-effects models (GAMM) via restricted maximum likelihood (REML) in the mgcv package (Wood, 2011) using R Ver. 4.2.2 (R Core Team, 2022). Fixed covariates included *Season_number* (ordered integer with 36 levels), *Region* [categorical with three levels, central California (CEN), southern California (SOU), and the Channel Islands (CHA)], and a summary statistic (mean or maximum) for SAW time series data (D_d and W_s). S*ite* (30 levels) was used as a random intercept to incorporate dependency among observations from the same site. A smoother for the *Site* spatial coordinates (*Xkm, Ykm*) was included to account for spatial dependency among sites.

We used interactions to test for regional differences in SAW time series data (e.g., *meanD*$_d$ × *Region*) and time (i.e., *Season_number* × *Region*) resulting in four full models: 1) interactions of *Region* with *maxW2*, *max*D$_d$, and *Season_number*, 2) interactions of *Region* with *mean*W$_s$, *mean*D$_d$, and *Season_number*, 3) interactions of *Region* with *max*W$_s$, *mean*D$_d$, and *Season_number*, and 4) interactions of *Region* with *mean*W$_s$, *max*D$_d$, and *Season_number*. We compared multiple reduced models based on the full models to test whether to include the interactions and both covariates (W$_s$ and D$_d$) (Table S1.2). The Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) were used to identify the preferred model (i.e., lowest AIC and BIC) (Akaike, 1974; Schwarz, 1978). A beta distribution with a logistic link was used to ensure that the fitted values ranged from 0 to 1 for the response variable, mean percent cover of *Silvetia* [Equation (1)].

Using GAMM, we analyzed the following equation:

$$Cover_{ij} \sim Beta(\pi_{ij})$$

$$E(Cover_{ij}) = \pi_{ij}$$

$$Var(Cover)_{ij} = \pi_{ij} \times (1 - \pi_{ij})/(1 + \theta)$$

$$\begin{aligned} logit(\pi_{ij}) = Intercept + Region_{ij} + s\left(Sample_{season_{number}\,ij} \times Region_{ij}\right) \\ + s(D_d statistic \times Region_{ij}) + s(W_s statistic \times Region_{ij}) \\ + s(Xkm \times Ykm) + Site_i \end{aligned}$$

$$Site_i \sim N(0, \sigma^2_{Site})$$

$$(eqn\ 1)$$

where Cover$_{ij}$ is the *j*th observation in site *i*, and *i* = 1, …, 30, θ is an unknown parameter controlling the variance, and Site$_i$ is the random intercept, which is assumed to be normally distributed with mean 0 and variance σ^2.

To account for temporal dependency observed in the time-series data, we incorporated an autoregressive component [AR(1) correlation structure] into the model in which the random intercept *w_it* at time *t* and location *i* is similar to *w_i*, *t-1* at time *t-1* at location *i*. The AR(1) generates a latent variable that is spatially correlated, slowly changes over time, and captures any spatial and temporal patterns that are not modeled by the covariates. This latent variable ensures that the model residuals are independent and imposes a dependency structure on the response variable, *Silvetia* cover.

Underlying model assumptions including independence and absence of residual patterns were verified by plotting residuals versus fitted values and each covariate in the model. Temporal autocorrelation was assessed via partial autocorrelation function (PACF) plots of the model residuals. We then simulated 10,000 datasets from the preferred GAMM and calculated a frequency table for each simulated dataset. An average frequency table was generated from the simulated data and compared with the frequency table of the observed data.

Nonlinear trends and linear fits for *Silvetia* cover were generated at the region and site levels along with the regional relationship between *Silvetia* cover and $max\mathrm{D}_d$ using JMP Ver. 14.2.0 (SAS Institute Inc., 2018).

Results

Trends

Cover of the rockweed *Silvetia compressa* was highly variable in space and time across California. At the regional level, central California (CEN) *Silvetia* cover was relatively stable over time with slight declines until around 2009 and after 2015 (Figure 1.3). Channel Islands (CHA) *Silvetia* cover declined precipitously until around 2012 followed by a period of stabilization. Similarly, southern California (SOU) *Silvetia* cover followed a relatively steep negative trajectory but failed to recover.

Most sites (22 of 30) exhibited significant declines in rockweed cover over the study period. Declines were most prevalent south of Point Conception on the Channel Islands and the southern California mainland (Figure 1.4). The SOU sites exhibited high incidence (90% of sites) of decline, and nearly all declines exceeded 50% cover followed by minimal or no recovery. Within the CHA region, *Silvetia* cover decreased at all but five sites (ANSFC, SBLC, SBSLR, SRFR, SRNWT) with similar trajectories. CEN rockweed populations appeared most resilient, with one site (CAY) increasing in cover significantly during the study period and two sites (BOA, PSN) declining. The remaining sites across the three regions had relatively stable populations of rockweed over time (CEN 25%, CHA 25%, SOU 10%).

Most *Silvetia* declines occurred steadily after 2005 until approximately 2015 when *Silvetia* cover either slightly increased or continued declining for the remainder of the study period (Figure 1.3-1.4). Sites that had stable or increasing *Silvetia* populations generally peaked in cover near the beginning of the study period and/or after 2015. Sites that precipitously declined more than 30% failed to recover.

Model Results

The model (M17) with the lowest AIC and BIC included a smoother for time (i.e., *Season_number*) and an interaction with *Region* and a smoother for the covariate $maxD_d$ (Table 1.1, Table S1.2). Based on ΔAIC, M9, M11 and M13 were considered comparable to M17 since AIC values for each were < 5 points apart. However, M9, M11 and M13 each were more complex than M17. Therefore, we identified M17 as the preferred model. Based on ΔBIC, only one other model (M18) was comparable to the preferred model (M17).

Residuals from M17 met regression assumptions including normality and homogeneity of variance, and no clear patterns were seen when the residuals were plotted against covariates included and not included in the model. The AR(1) correlation structure markedly reduced the autocorrelation of the model residuals for M17 (Figure S1.2). Residuals for the spatial coordinates represented variation in *Silvetia* cover not captured by covariates modeled with the GAMM (Figure S1.3). Slightly higher residuals were observed in the middle latitudes corresponding with the CHA region. Lower residuals occurred in the southern latitudes near the lower portion of the SOU region. Low variability in the residuals was observed in the remaining study areas.

Dewpoint depression

Maximum dewpoint depression (maxD_d) was negatively correlated with *Silvetia* cover in all three regions (Table 1.1, Figures 1.5-1.6). The relationship between *Silvetia* cover and maxD_d appeared nonlinear for the three regions (Figures 1.5-1.6). Model selection indicated that an interaction between maxD_d and Region was not necessary since AIC for the full models was not substantially lower compared with the models excluding the interaction.

Simulating the preferred model (M17) 10,000 times, we found strong correspondence between the actual data and our modeled data (Figure 1.5). *Silvetia* cover across all three regions declined steadily as $maxD_d$ increased according to the actual data and the modeled fit. At the regional level, *Silvetia* cover in CEN and SOU responded similarly to increasing $maxD_d$ by decreasing precipitously until approximately 8°C then stabilizing (Figure 1.6). At the CHA region, *Silvetia* cover remained relatively stable until around 20°C before declining as $maxD_d$ increased (Figure 1.6).

Wind

Mean near-surface wind gust (meanW_s) and max near-surface wind gust (maxW_s) were not significantly correlated with *Silvetia* cover in the three regions (Table S1.2). Collinearity between D_d and W_s was low (Figure S1.4). Model selection indicated that neither meanW_s nor maxW_s should be included in the preferred model based on AIC and BIC (Table S1.2).

Discussion

We found large declines of the intertidal foundation species, *Silvetia* putatively driven by harsh, desiccating wind events across most of its geographical range, particularly the California Channel Islands and southern California mainland (Figures 1.3-1.4). This pattern mirrors worldwide declines and range shifts in rockweeds and other fucoids (Bokn and Lein, 1978; Kautskyl et al., 1986; Vogt and Schramm, 1991; Munda, 1993; Sagarin et al., 1999; Thompson et al., 2002; Lotze and Milewski, 2004; Keser et al., 2005; Torn et al., 2006; Airoldi and Beck, 2007; Ugarte et al., 2009; Lamela-Silvarrey et al., 2012; Martínez et al., 2012; Nicastro et al., 2013; Riera et al., 2015; Buonomo et al., 2018; Whitaker et al., 2023 and references therein). Spatio-temporal modeling revealed a pervasive trend of declining abundance for *Silvetia* populations at the Channel Islands and the California mainland south of Point Conception (PC), an important biogeographic break. Sites north of PC were characterized by a heterogeneous combination of trends, most of which indicated that *Silvetia* was relatively stable or increasing in cover during the study period.

Although declining rockweed populations were most prevalent in the southern California region, trends varied by site, and all three regions had examples of declining and stable sites (Figure 1.4). The possible causes of this complexity may, like the between-region patterns, reflect variability in meteorological and oceanographic climate, but on different spatial scales. The central California region is influenced primarily by the cool California current, while the California Current and the opposing, warmer Southern California Countercurrent (Hickey, 1979) combine to form a more complex seascape in the SCB (the region below PC including the islands). As a result, SST along the southern California mainland and the southern islands is consistently warmer, and onshore winds and fog are generally lighter relative to central California and the northwestern islands, San Miguel, and Santa Rosa Islands (Dailey et al., 1993). The islands in between occupy a transitional zone where these currents mix and SST can be highly variable (Dailey et al., 1993).

At the site level, variations in substratum aspect, slope (Harley, 2008) and extent (Gedan et al., 2011) interact with atmospheric and oceanographic variables to affect the conditions experienced by intertidal organisms including aerial temperature (Helmuth and Hofmann, 2001), wave energy (Harley and Helmuth, 2003), solar radiation (Schoch and Dethier, 1996), wind velocity, relative humidity and fog (Helmuth and Hofmann, 2001; Helmuth et al., 2006). A high degree of spatial heterogeneity exists across the network of sites in this study given its broad spatial scale, which likely corresponds to significant site-level variation in abiotic conditions (Choi et al., 2019). As a result, the mosaic of trends for *Silvetia* likely reflects environmental heterogeneity at both the local and regional levels, thereby influencing the population dynamics of *Silvetia*.

During the study period, sea surface temperatures (SST) rose more rapidly in southern California than in most other regions of the world (Hobday and Pecl, 2014). Anomalously high SSTs occurred in the northeastern Pacific Ocean during El Niño events in 2009-10 and 2014-16. The latter event, one of the strongest El Niño's in recent history (Huang et al., 2016), resulted in exceptionally high SST anomalies in part due to the concurrence of a widespread marine heat wave in the North Pacific (Jacox et al., 2016). In addition, the average annual air temperature in southern California steadily increased from 1950 to 2010 (Gonzalez, 2020). Macroalgae including *Silvetia* can be stressed by oceanographic parameters including seawater temperature (Breeman, 1988; Hurd et al., 2014; Wernberg et al., 2011; Graham et al., 2018) and wave energy (Vadas et al., 1990), as well as by atmospheric conditions such as high temperatures (Bell, 1995) and high irradiance (Henley, 1992). These changes in regional atmospheric and oceanographic conditions are consistent with the general latitudinal pattern of trends we identified in *Silvetia* cover and suggest that declines in southern California may be linked to overall warming conditions both in the coastal ocean and on land.

Downsloping, offshore wind is a natural occurrence in western North America due to gradients between high-pressure systems in the inland Great Basin and low pressure over the Pacific Ocean. As low-pressure systems offshore of California pull air masses from inland desert areas, winds more than 25 m s^{-1} (56 mi h^{-1}) (Keeley et al., 2004; Cao and Fovell, 2013) are generated through canyons and mountain passes compressing, drying, and heating the air in the process. Below PC, these conditions are called Santa Ana winds (SAWs), and recent studies suggest that downslope wind systems in central and northern California coincide with SAWs (Gershunov et al., 2021; Guirguis et al., 2023). SAWs occur annually between September and June (Cao and Fovell, 2016). However, SAW frequency and intensity are greatest during the winter months of December and January, respectively, (Guzman-Morales et al., 2016) a time of year coincident with periods of day-time aerial exposure for intertidal ecosystems in southern California. More than any other environmental variable, the seasonal pattern of diurnal emersion has been attributed to changes in the abundances of intertidal algae in the Southern California Bight (SCB) (Emerson and Zedler, 1978; Gunnill, 1980; Seapy and Littler, 1982; Littler et al., 1991).

The Santa Ana Wildfire Index (SAWTI), a model generated from the climatological data used in this study, indicates that the monthly and seasonal SAW day counts were variable but mostly remained near average or below average from 1981 to the early 2000s (Figure S1.1). After 2006, the number of SAW days per season was significantly elevated for the remainder of the study period through 2016 (Rolinski et al., 2019). This trend corresponds with negative changes in *Silvetia* cover observed at many study sites in the two regions, Channel Islands (CHA) and southern California mainland (SOU) which exhibited gradual declines from the beginning of the study period through around 2015 with the most precipitous losses in percent cover occurring after 2005 (Figures 1.3-1.4).

Despite rockweeds being very desiccation-resistant for a large frondose alga (Schonbeck and Norton, 1978), extreme conditions during warm and dry periods, especially with strong, dry winds, can be detrimental. During SAW events occurring during low tide periods, *Silvetia* is often observed exhibiting severe drying out with fronds turning crispy. Desiccation stress is known to affect various physiological processes and conditions in rockweeds and other fucoids, including oxidative damage (Martins et al. 2021), reduced net photosynthesis, survival, and growth (Dethier et al. 2005), increased susceptibility to loss from wave action (Haring et al. 2002), and limited recruitment success (Dudgeon and Petraitis, 2001). Over time, these effects are likely to cause population declines, as observed at our monitoring sites.

SAW activity has been linked with environmental cycles including the Atlantic multi-decadal oscillation (AMO), the PDO, and the ENSO, with elevated periods of SAW activity typically coinciding with cool phases of the PDO (Rolinski et al., 2019) and ENSO (Raphael, 2003; Rolinski et al., 2019), and the warm phase of the AMO (Li et al., 2016). Although Guzman-Morales (2016) found seasonal SAW intensity to increase during the warm phases of the PDO and ENSO and vice versa. This information is critical for projecting SAW activity. However, it remains unclear how SAW events will change under anthropogenic climate warming conditions. Projections of SAW activity due to climate change remain mixed due, in part, to differences in approaches used to distinguish and downscale the events (e.g., Miller and Schlegel, 2006; Hughes et al., 2011; Abatzoglou et al., 2013; Guzman-Morales et al., 2016). Some studies indicate a reduction of SAW events as anthropogenic warming increases due to a weakening in the temperature gradient between the ocean and the Great Basin (Hughes et al., 2009, 2011; Guzman-Morales, 2018). Others suggest that anthropogenic warming will increase the frequency of strong SAWs in late fall (Yue et al., 2014), or that more SAW days may occur at the beginning (September) and end (June) of the SAW season (Rolinski et al., 2019). Clearly, more research is needed to increase the accuracy of projecting SAW variability as climate warms. Based on patterns discussed here, however, any increases in the frequency or intensity of SAWs are likely to lead to large declines and possible extirpation of *Silvetia*, as well as the important ecological services the species provides.

Our results demonstrate that *Silvetia*, like many other fucoids throughout the world (Sagarin et al., 1999; Lamela-Silvarrey et al., 2012; Martínez et al., 2012; Nicastro et al., 2013; Riera et al., 2015), has declined significantly in southern California and the Channel Islands. This trend corresponds with elevated dewpoint depression, an indicator of SAW activity, which, in turn, may represent the phases of environmental cycles such as PDO, ENSO, and AMO that the data in this study were collected or anthropogenic forcing on SAW activity. Spatial and temporal patterns in rockweed populations, however, are complex, varying between sites as well as across regions. The network of long-term monitoring sites established by the Multi Agency Rocky Intertidal Monitoring Network (MARINe) that provided the data for this study is an ideal milieu for a detailed comparative and experimental program to elucidate the causes of rockweed declines. This information, along with more accurate future projections of SAW activity under climate change, are critical for informing conservation, and potentially restoration, of this important foundation species and the rocky intertidal biodiversity it supports.

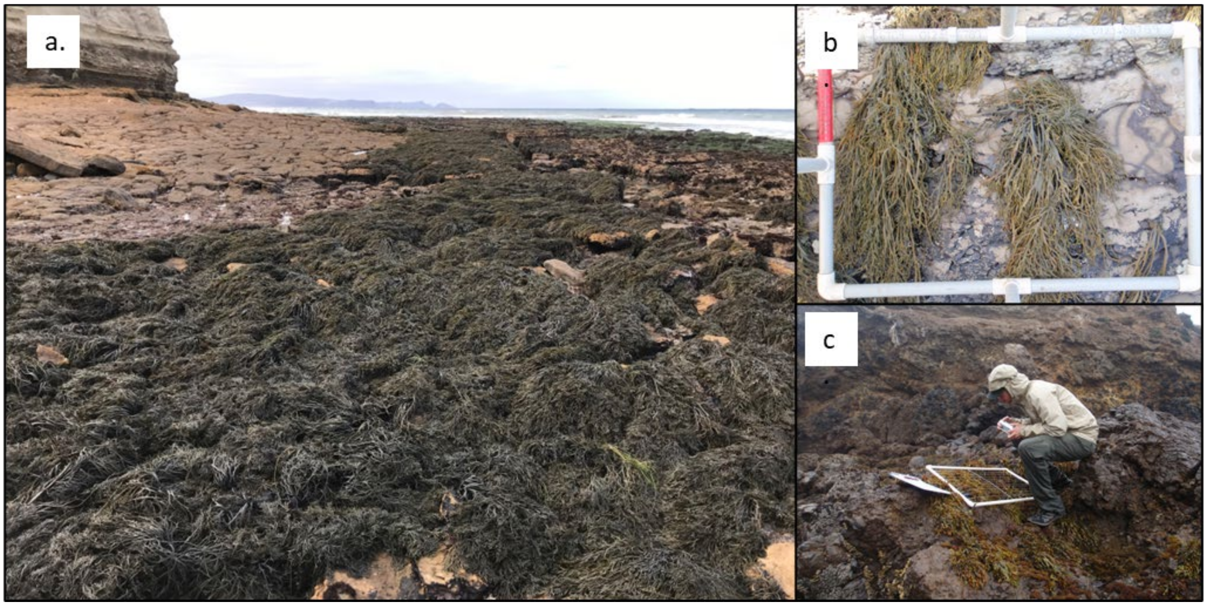

Figure 1.1. Rockweed, *Silvetia compressa*.

Forming large beds in the middle intertidal zone on the northwest side of Santa Rosa Island (a); fixed plot established to document the percent cover of the rockweed, *Silvetia compressa* (b) (photos, S. Whitaker); lead author S. Whitaker scoring a fixed plot for rockweed (c) (photo, K. Chan).

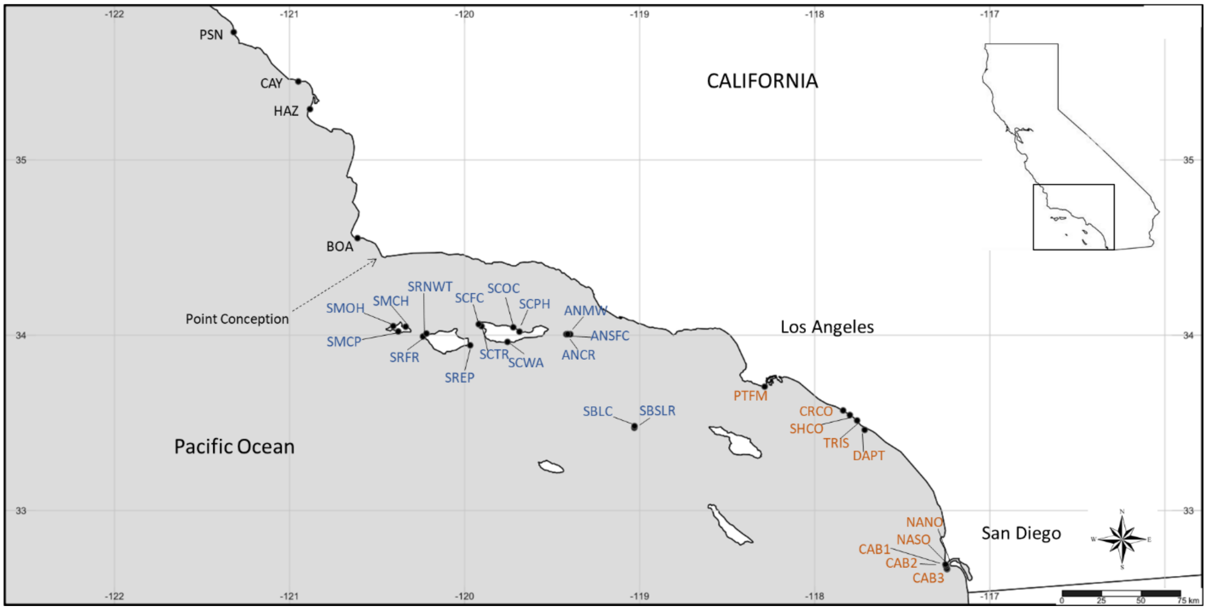

Figure 1.2. Map of long-term monitoring sites for *Silvetia compressa* used in this study.

See Table S1.1 for full site names and positions. Site abbreviations are color-coded by region (black = central California, blue = Channel Islands, orange = southern California).

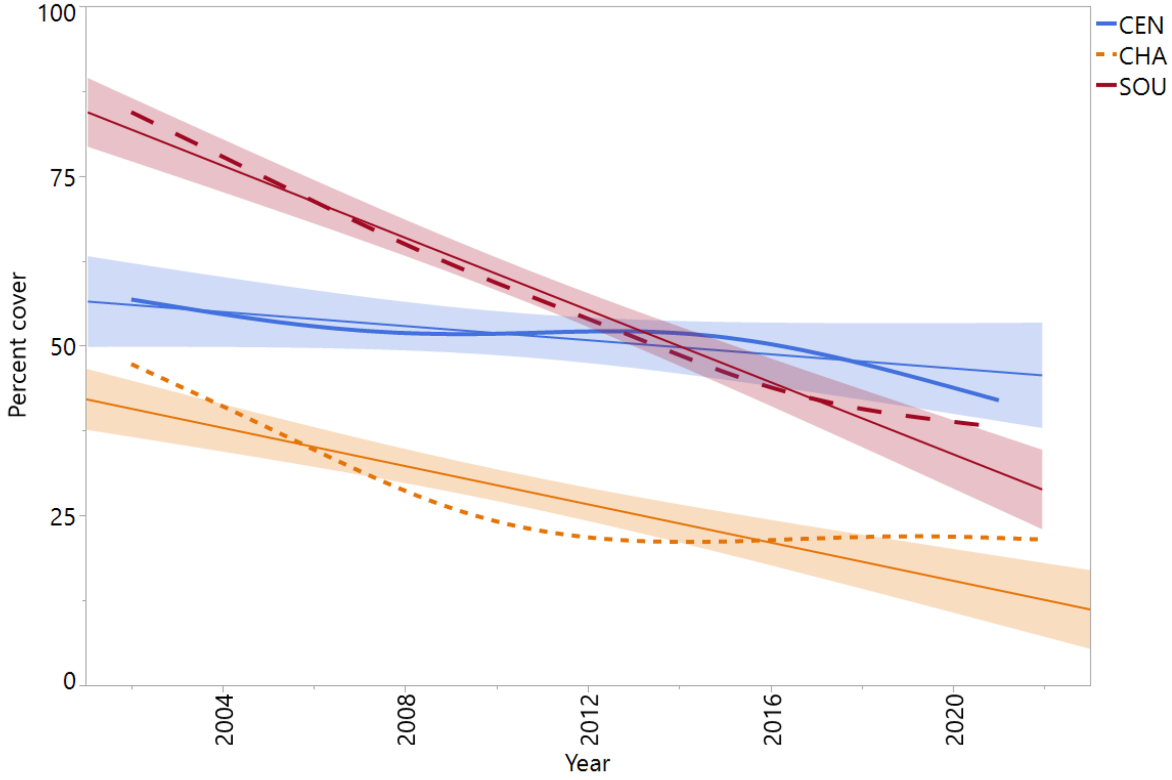

Figure 1.3. Mean annual percent cover data for *Silvetia* by region.

Shade lines represent approximate linear fit. CEN = Central California region (P = 0.0982), CHA = Channel Islands region (P < 0.0001), SOU = Southern California region (P < 0.0001).

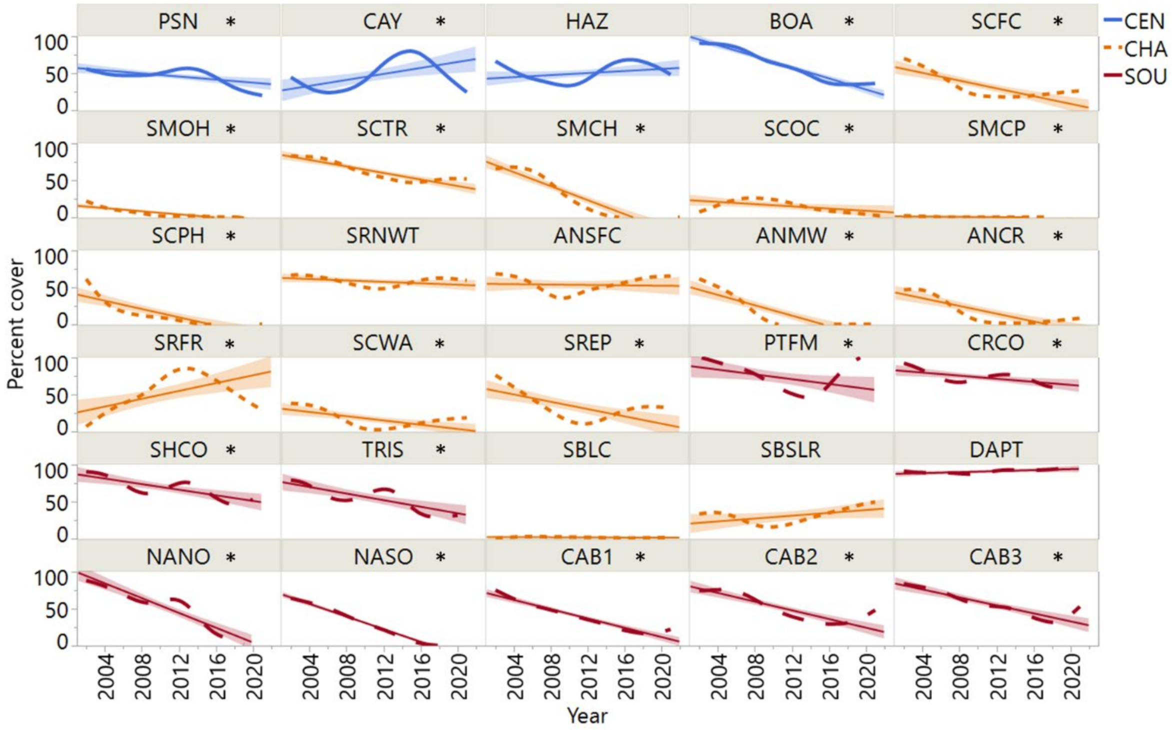

Figure 1.4. Mean annual percent cover data for *Silvetia* at each of the thirty sites arranged by latitude.

Site codes are defined in Table 1.1. Asterisk denotes significance of the linear regression slope (P = <0.05). CEN = Central California region, CHA = Channel Islands region, SOU = Southern California region.

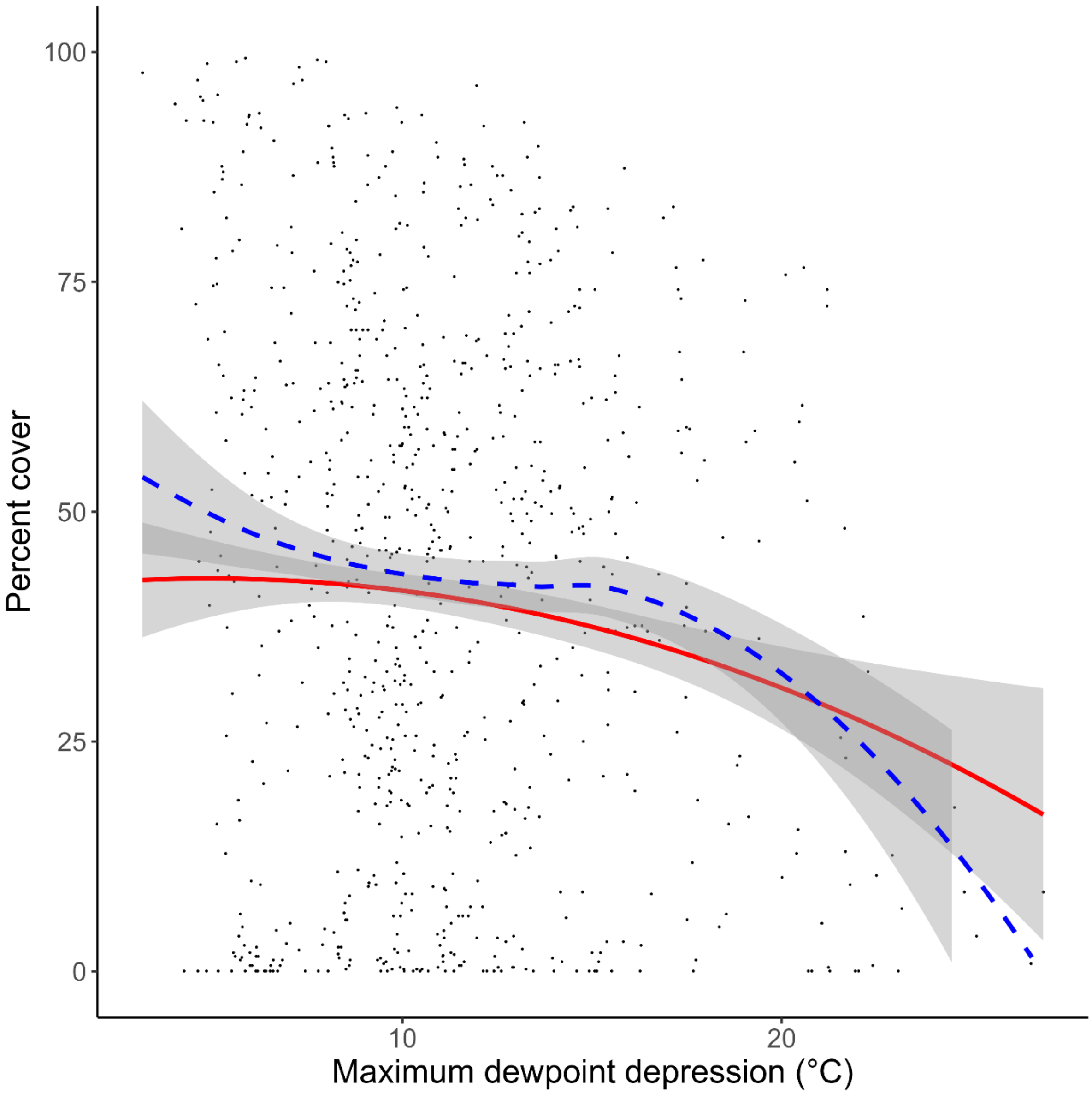

Figure 1.5. Effect of max dewpoint depression (maxD$_d$) on *Silvetia* cover at an average site and year plotted on the original scale.

The blue dashed line represents a smoothed fit using the actual data. The red line represents a smoothed fit using the model (predicted data). The grey areas indicate the 95% confidence interval for the actual data and the modeled fit. Points denote measured data.

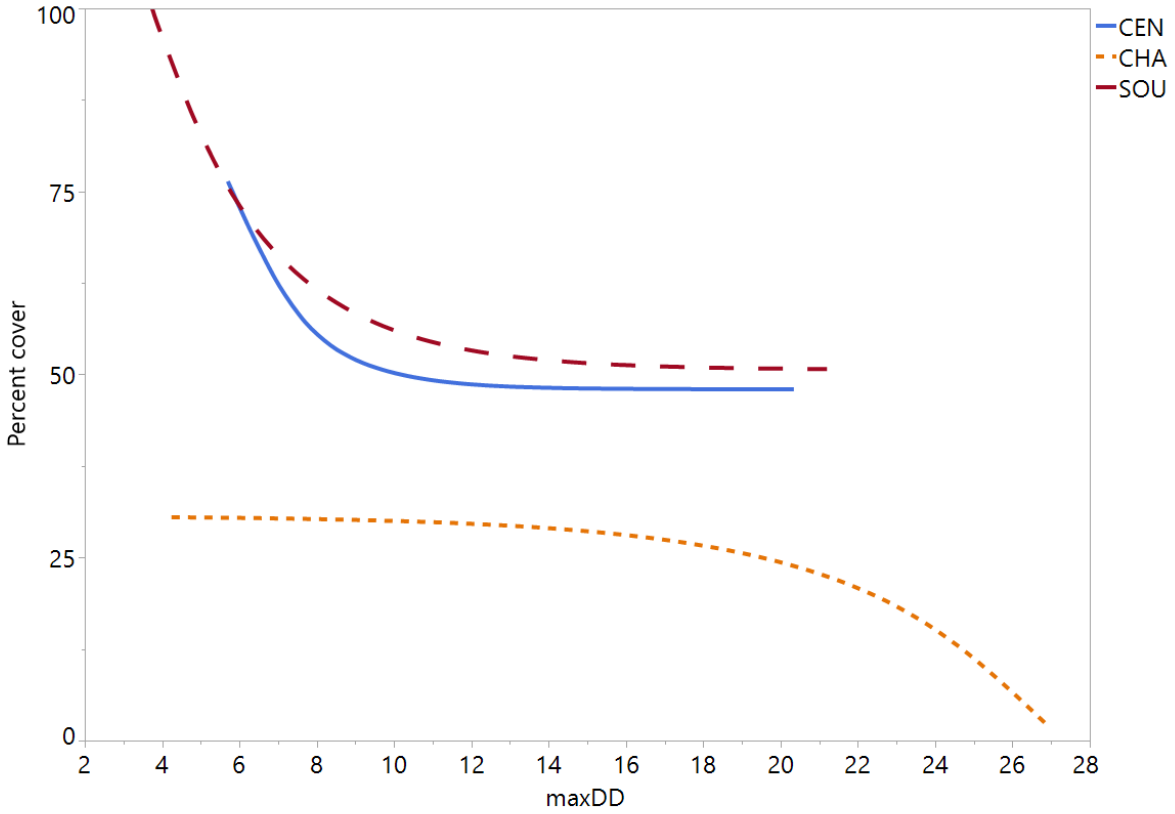

Figure 1.6. ***Silvetia*** **percent cover plotted on scale of maximum dewpoint depression (°C).**

Regression slopes are all significant (P = 0). CEN = Central California, CHA = Channel Islands, SOU = Southern California.

Table 1.1. ***Silvetia*** **cover GAMM (beta response distribution with logit link function) summary.**

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-0.227	1.475	-0.154	0.8780	
	georegionCHA	-1.504	1.379	-1.090	0.2759	
	georegionSOU	2.092	1.908	1.096	0.2733	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(event):georegionCEN	1.944	2.459	1.076	0.2786	
	s(event):georegionCHA	3.355	4.271	26.697	0.0000	***
	s(event):georegionSOU	5.375	6.651	12.220	0.0000	***
	s(maxDD)	3.450	4.397	18.996	0.0000	***
	te(Xkm.std,Ykm.std)	3.000	3.000	1.809	0.1439	
	s(site_code)	22.412	25.000	12.131	0.0000	***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

Adjusted R-squared: 0.739, Deviance explained 0.835

fREML : -57.440, Scale est: 1.000, N: 841

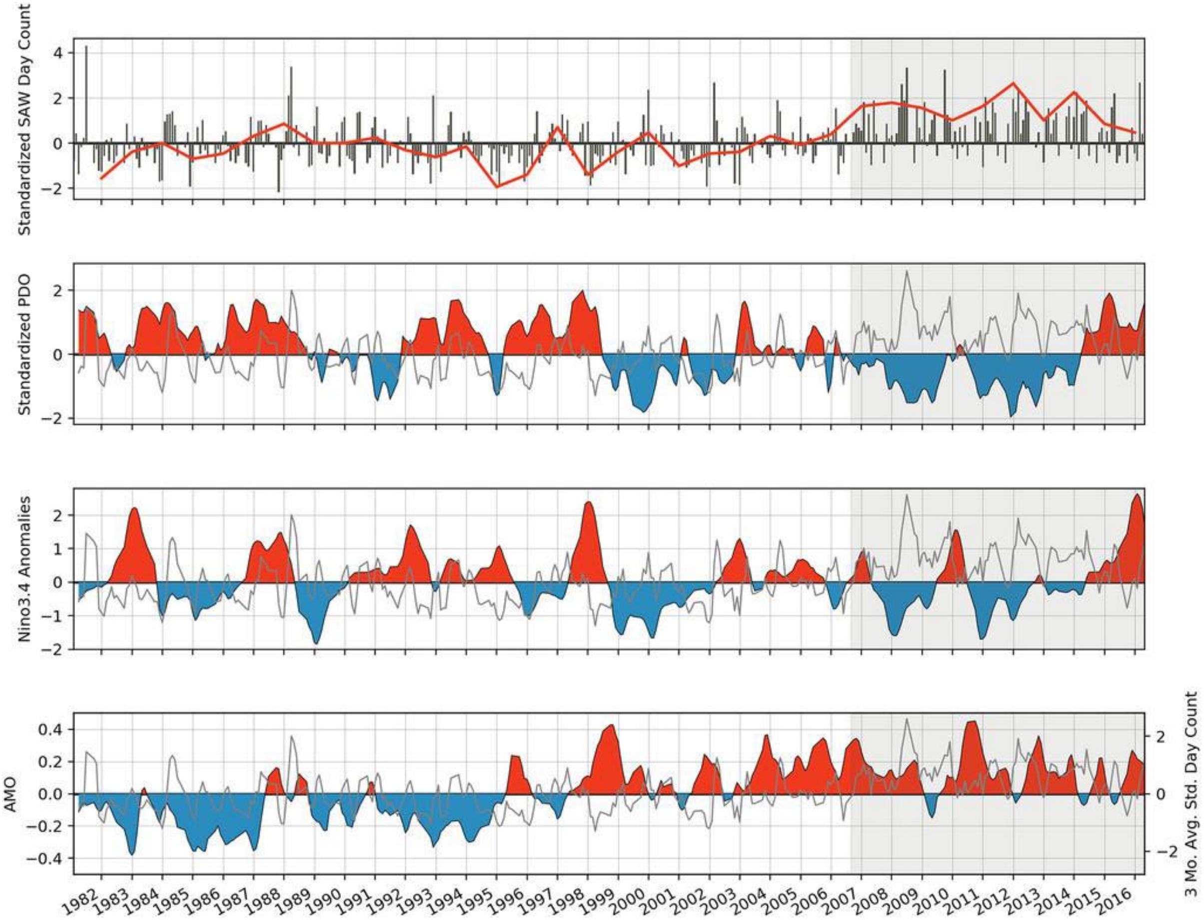

Figure S1.1. Time series representing the modeled trend for standardized Santa Ana wind (SAW) day count from 1981-2016 (top), along with standardized PDO, Nino3.4 Anomalies, and AMO (Rolinski et al. 2019).

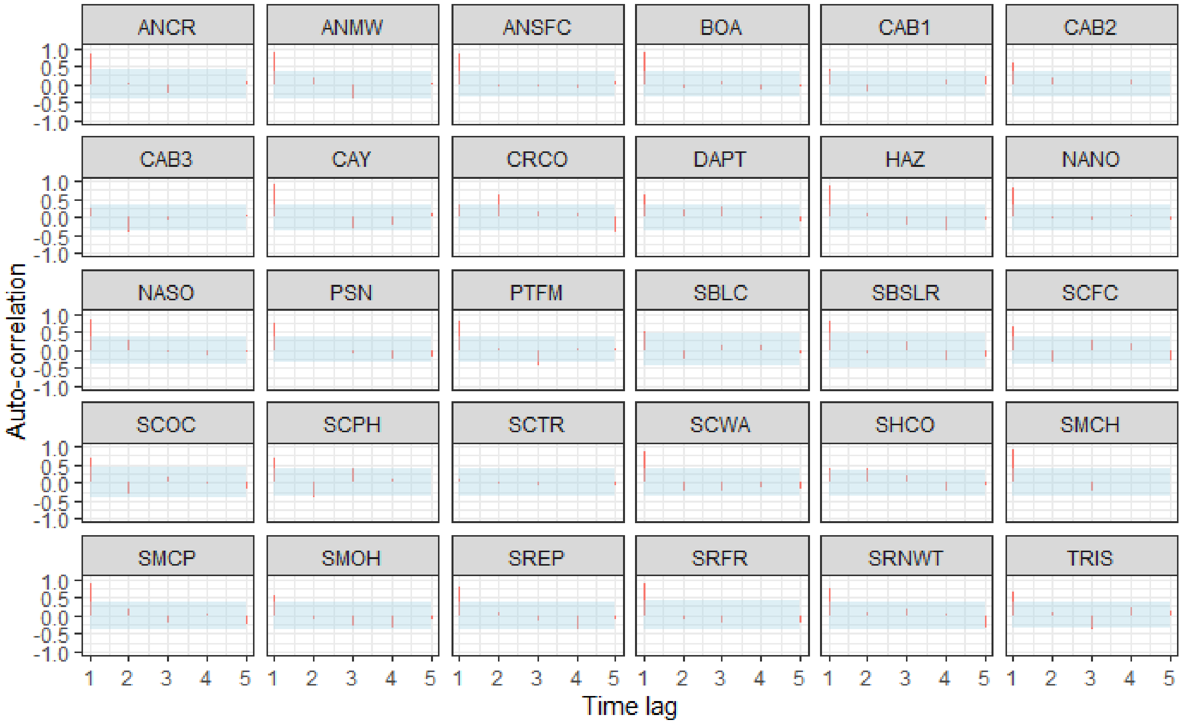

Figure S1.2. Partial autocorrelation function graphs for the residual time series at each site. See Table S1 for full site names and positions.

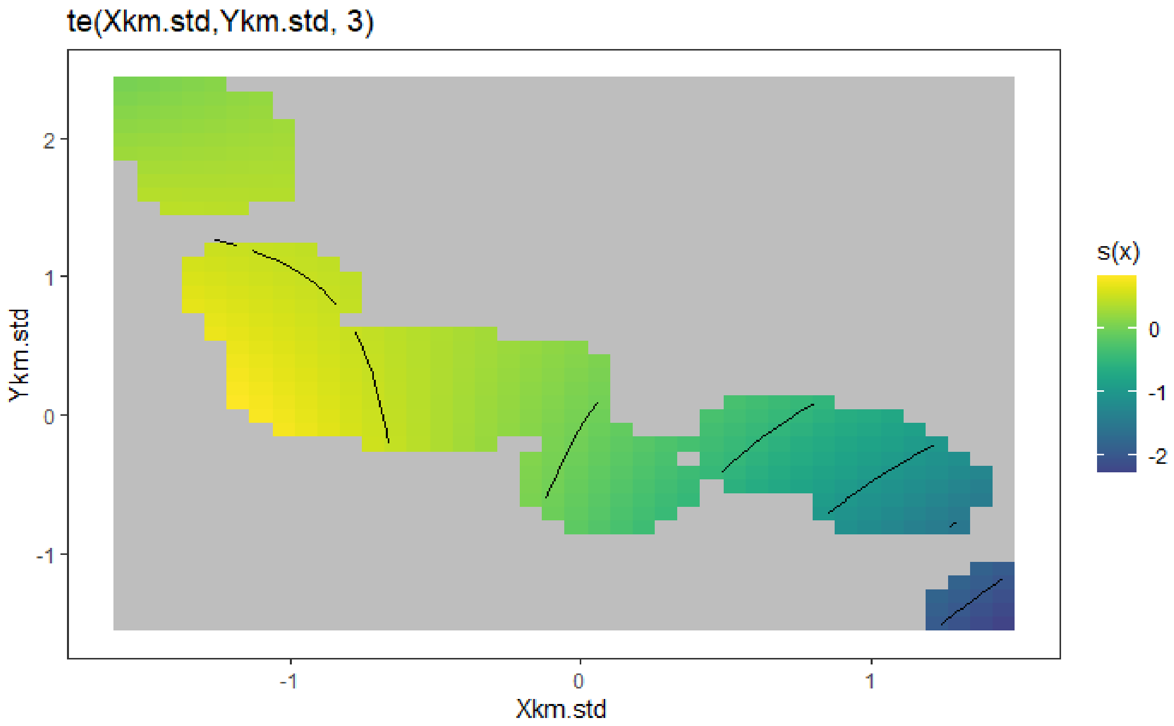

Figure S1.3. Residuals from the tensor smoother of the spatial coordinates for each monitoring site.

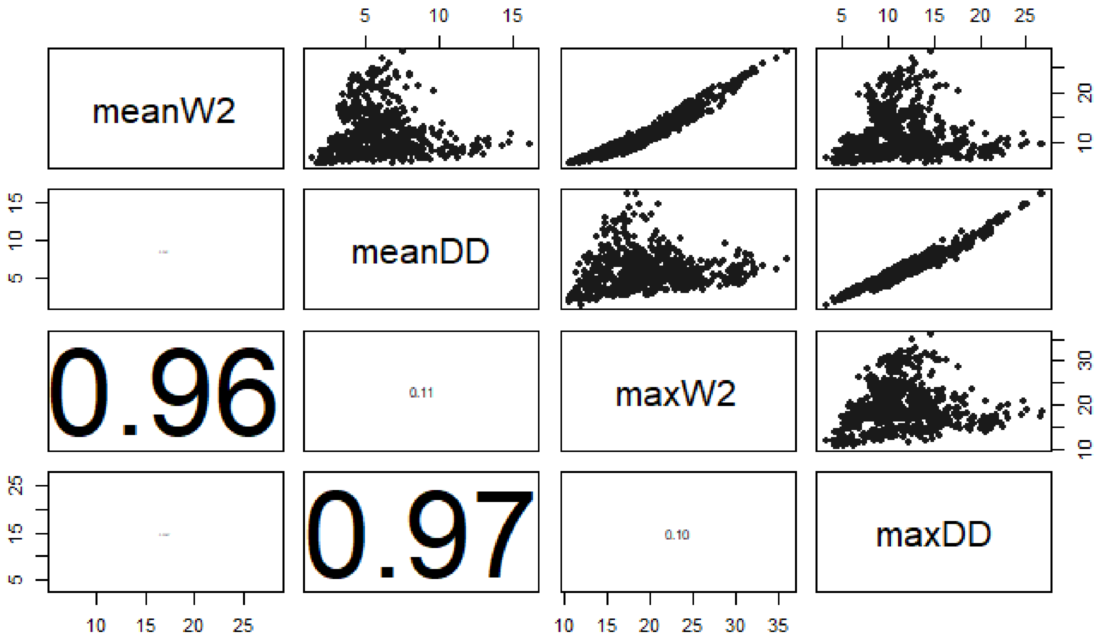

Figure S1.4. Scatterplots displaying collinearity between mean/max dewpoint depression (DD) and mean/max wind velocity (W2).

Table S1.1. Site information, including code, name, region, latitude, and longitude. Regions are designated as central California (CEN), southern California mainland (SOU), and the Channel Islands (CHA).

Site code	Site name	Region	Latitude	Longitude
PSN	Point Sierra Nevada	CEN	35.729	-121.319
CAY	Cayucos	CEN	35.447	-120.950
HAZ	Hazards	CEN	35.290	-120.883
BOA	Boat House	CEN	34.554	-120.612
SCTR	Santa Cruz Trailer	CHA	34.052	-119.903
SMCH	San Miguel Cuyler Harbor	CHA	34.049	-120.336
SMCP	San Miguel Crook Point	CHA	34.022	-120.379
SCPH	Santa Cruz Prisoner's Harbor	CHA	34.020	-119.687
SCOC	Santa Cruz Orizaba Cove	CHA	34.010	-120.218
SMOH	San Miguel Otter Harbor	CHA	34.010	-120.218
SRNWT	Santa Rosa Northwest-Talcott	CHA	34.010	-120.218

ANSFC	Anacapa South Frenchy's Cove	CHA	34.007	-119.411
ANCR	Anacapa Cat Rock	CHA	34.005	-119.419
SCWA	Santa Cruz Willows Anchorage	CHA	33.962	-119.755
SCFC	Santa Cruz Fraser Cove	CHA	33.943	-119.968
SREP	Santa Rosa East Point	CHA	33.943	-119.968
SRFR	Santa Rosa Fossil Reef	CHA	33.943	-119.968
ANMW	Anacapa Middle-West	CHA	33.482	-119.03
SBLC	Santa Barbara Landing Cove	CHA	33.482	-119.030
SBSLR	Santa Barbara Sea Lion Rookery	CHA	33.472	-119.031
PTFM	Point Fermin	SOU	33.707	-118.286
CRCO	Crystal Cove	SOU	33.571	-117.838
SHCO	Shaw’s Cove	SOU	33.545	-117.799
TRIS	Treasure Island	SOU	33.513	-117.758
DAPT	Dana Point	SOU	33.460	-117.715
NANO	Navy North	SOU	32.693	-117.253
NASO	Navy South	SOU	32.683	-117.250
CAB1	Cabrillo I	SOU	32.670	-117.246
CAB2	Cabrillo II	SOU	32.668	-117.245
CAB3	Cabrillo III	SOU	32.666	-117.244

Table S1.2. Comparisons of alternative models describing changes over time in each region and covariate effects on *Silvetia* percent cover.

Model	Model Description	ΔAIC	ΔBIC	*df*
M17 (preferred)	Region x Season_number + maxD$_d$	——	——	47.857
M11	Region x Season_number + Region x meanW$_s$ + maxD$_d$	0.61	14.85	50.864
M9	Region x Season_number + Region x maxW$_s$ + maxD$_d$	1.85	29.58	53.715
M13	Region x Season_number + maxW$_s$ + maxD$_d$	4.57	16.31	50.336
M14	Region x Season_number + meanW$_s$ + maxD$_d$	5.16	19.41	50.867
M18	Region x Season_number + meanD$_d$	5.45	3.09	47.358
M10	Region x Season_number + Region x maxW$_s$ + meanD$_d$	5.70	31.96	53.403
M16	Region x Season_number + meanW$_s$ + meanD$_d$	7.30	25.08	51.611
M15	Region x Season_number + maxW$_s$ + meanD$_d$	7.55	18.82	50.237
M5	Region x Season_number + maxW$_s$ + Region x maxD$_d$	7.86	26.90	51.878
M1 (full)	Region x Season_number + Region x maxW$_s$ + Region x maxD$_d$	8.24	50.00	56.678
M4 (full)	Region x Season_number + Region x meanW$_s$ + Region x maxD$_d$	8.38	36.52	53.800
M12	Region x Season_number + Region x meanW$_s$ + meanD$_d$	9.30	38.41	54.006
M6	Region x Season_number + meanW$_s$ + Region x maxD$_d$	11.45	38.30	53.528
M3 (full)	Region x Season_number + Region x maxW$_s$ + Region x meanD$_d$	11.99	52.61	56.436
M19	Region x Season_number + maxW$_s$	13.22	18.14	48.896
M20	Region x Season_number + meanW$_s$	14.57	24.15	49.882
M7	Region x Season_number + maxW$_s$ + Region x meanD$_d$	15.41	36.41	52.290
M8	Region x Season_number + meanW$_s$ + Region x meanD$_d$	15.42	42.30	53.533
M2 (full)	Region x Season_number + Region x meanW$_s$ + Region x meanD$_d$	17.03	57.27	56.356

[redacted] Long-Term Recovery Rates of Rocky Intertidal Foundation Species Following Mechanical Disturbance

Introduction

Disturbances are events that remove biota and create space for the colonization of new individuals, a process that is often referred to as patch dynamics (Thompson, 1978). The complete or partial mortality that results from disturbance can affect species diversity (Connell 1978) and even switch ecosystem states (Holling, 1973). Many natural phenomena can cause ecological disturbances, including fire, hurricanes, ice storms, drought, flash floods, lava flows, landslides, and disease, thereby contributing to the patchiness of ecosystems across a wide range of temporal and spatial scales (Oliver, 1981; Sousa, 1984).

Human activities such as development, agriculture, logging, bottom trawling, and off-road driving can also cause disturbances. Anthropogenic disturbances can impact ecosystem community structure through reductions in biodiversity (Barlow et al., 2016), decreases in evenness (Mishra et al., 2004), and habitat fragmentation (Antongiovanni et al., 2020). Relative to natural disturbance regimes, anthropogenic disturbances can impact larger areas and last longer (Ellison and Farnsworth 2001). Moreover, anthropogenic and natural disturbances can interact synergistically, resulting in greater impacts on ecosystems (Lenihan and Peterson, 1998; Hegland et al., 2010; Gaoue and Ticktin, 2010; Mandle and Ticktin, 2012) and increased time to recovery (Witmer and Roelke, 2014; Machado et al., 2016; Mathews and Maccarone, 2019).

Recovery rates following disturbance are highly variable, ranging from months to decades, depending on the magnitude and timing of the disturbance and traits of the species involved, including lifespan, growth rate, and dispersal capacity (Sousa 1979, 1984; Paine and Levin 1981; Farrell 1989; Kim and DeWreede 1996; Foster et al. 2003; Bertocci et al. 2005; Conway-Cranos 2012). Edge effects, gradients at the boundary of disturbances, can also influence recovery rates (Laurance et al., 1997). Positive edge effects can speed recovery as a function of improved environmental conditions (Bertness and Shumway, 1993), density dependence (Kent et al., 2003), and propagule availability (Sousa, 1984b). Conversely, negative edge effects can slow recovery through processes including variances in microclimate (Pinto et al., 2010), whiplash and shading effects from nearby macroalgae or vegetation (Bazzaz, 1979; Jenkins et al., 1999; Cervin et al., 2004), predation (Young and Gotelli, 1988), and grazing (Sousa, 1984).

Rocky intertidal ecosystems are regularly disturbed by natural processes such as wave forces (Paine and Levin, 1981; Sousa, 1984), scouring and burial from sediments (Seapy and Littler, 1982; Taylor and Littler, 1982; Littler et al., 1983) and ice (Stephenson and Stephenson, 1972; Dayton et al., 1970), and impacts of large objects such as logs, cobbles and boulders (Dayton, 1971; Dethier, 1984), especially during storms. The proximity and accessibility of rocky intertidal habitats to humans also make them susceptible to an array of anthropogenic disturbances including pollution (Islam and Tanaka, 2004; Johnston and Roberts, 2009; Rabalias et al., 2009; Lucas and Smith, 2016) and development (Rothschild et al., 1994; Lotze et al., 2006; Waycott et al., 2009). Population expansion and urbanization along coastlines worldwide have accelerated the extent and intensity of anthropogenic disturbance (Morton, 1990; Ellison et al., 1996; Sale et al., 2011; de Andrés et al., 2017), which have been linked to population and community-level impacts on rocky intertidal ecosystems (Crowe et al., 2000 and references therein).

Benign as it may seem, trampling is one of the most widespread and common forms of human disturbance on rocky shores (Brosnan and Crumrine, 1994; Keough and Quinn, 1998; Brown and Taylor, 1999; Schiel and Taylor, 1999; Smith and Murray, 2005; Araujo et al., 2009; Huff, 2011; Travaille et al., 2015). Pedestrian traffic can have detrimental effects on the functioning and biodiversity of rocky intertidal ecosystems through reductions in the abundance and reproductive potential of populations (Zedler, 1978; Ghazanshahi et al., 1983; Castilla and Bustamante, 1989; Duran and Castilla, 1989; Smith and Murray, 2005; Van De Werfhorst and Pearse, 2007). Foliose macroalgae are particularly vulnerable to trampling (Povey and Keough, 1991; Keough and Quinn, 1998; Irvine, 2005; Denis, 2003). Decreases in canopy cover, biomass, and reproductive weight have been documented for fucoid macroalgae following a single footstep (Povey and Keough, 1991), with more extreme rates of trampling causing nearly complete losses of populations (Povey and Keough, 1991; Keough and Quinn, 1998; Irvine, 2005; Denis, 2003). Similarly, common intertidal invertebrates including barnacles and mussels are susceptible to trampling, which can crush and dislodge them, sometimes facilitating an alternate community state dominated by turf-forming algae (Brosnan and Crumrine, 1994).

A century ago, rocky intertidal macrophyte communities near southern California urban centers were dominated by highly productive, large to mid-sized, fleshy macrophytes (Dawson, 1959, 1965). However, those same shores now support high abundances of less productive, small, turf-forming, and crustose algae, likely due to disturbances accompanying increased levels of urbanization during the past half century (Widdowson, 1971; Thom and Widdowson, 1978; Murray et al., 2001; Gerrard, 2005). Significant changes have also been documented for rocky intertidal invertebrate communities in southern California, including declines in the abundances of both sessile and mobile invertebrates (Goodson, 2004, Sagarin et al., 2007).

Long-lived habitat-modifying species, such as canopy-forming algae and bivalves, and the communities associated with them, typically recover slowly following disturbance. For example, the community dominated by the rocky intertidal fucoid *Ascophyllum nodosum* failed to fully recover 12 years following the experimental removal of the canopy (Jenkins et al., 2004). Paine and Levin (1981) observed that disturbed populations of the mussel *Mytilus californianus* took a minimum of approximately eight years to recover.

While numerous experimental and observational studies have been done to identify the rate of recovery for ecosystems following disturbance, many were not long enough to fully capture the process, particularly for long-lived species (Lotze et al., 2011). In addition, it is not always clear whether disturbance has ceased, particularly in the case of anthropogenic impacts such as trampling. Collectively, these issues undermine the goal of understanding the resilience of ecosystems to disturbance.

To assess the recovery of disturbed rocky intertidal ecosystems, we conducted a controlled pulse disturbance experiment at a remote site with limited human visitation and surveyed it annually for 28 years (VTN Oregon, 1983). Disturbance treatments included human trampling to mimic light visitor usage and clearing to represent more intense disturbance resulting from sustained trampling or harvesting. Species surveyed included common and important habitat-modifying taxa such as rockweeds, turf algae, mussels, and barnacles, that vary in their life history traits and dispersal capabilities. We tested the hypotheses that 1. macroalgae are more sensitive to trampling than sessile invertebrates, 2. the communities associated with slow-growing and long-lived species including rockweeds and mussels recover more slowly than those associated with ephemeral turf algal and barnacles, and 3. physical disturbance causes long-term effects on community composition.

Methods

Study system. The study site, Cat Rock (34°00'19"N, 119°25'05"W), is a rocky intertidal reef approximately 35 m long and 30 m wide located on the south-facing side of Anacapa Island, the easternmost of the northern Channel Islands group, approximately 20 km offshore of the California mainland (Figure 2.1). The site lies in Channel Islands National Park within an Area of Special Biological Significance (Santa Barbara and Anacapa Island ASBS) and the Anacapa Island Special Closure regulated by the California Department of Fish and Wildlife to protect breeding brown pelicans and their fledglings from human disturbance. The intertidal zone at the site comprises a series of highly rugose Miocene volcanic bedrock reefs lying 1-2 m above the zero-tide level and fractured by surge channels. The average reef slope is 6.8°. An offshore reef reduces the wave energy that reaches the intertidal zone at the site during low tide. Cobble beaches flank the site on both sides. Visitor usage at Cat Rock is very low due to its remoteness and restricted access from land and sea; dense kelp and underwater features make skiff landing difficult and land access requires a relatively long and arduous hike over rough terrain.

Plot establishment. Four biotic communities spanning the intertidal gradient were chosen for study: (1) the barnacle (*Chthamalus* spp. and *Balanus* spp.) community, and (2) turfweed (*Endocladia muricata*) beds, both in the upper intertidal zone, (3) the mid-intertidal fucoid rockweeds *Silvetia compressa* and *Pelvetiopsis californica* (formerly *Hesperophycus californicus*), and (4) beds of California mussel (*Mytilus californianus*) in the mid-to-lower intertidal (Figure 2.2). The barnacles and two species of rockweeds monitored in this study were lumped together, respectively, to simplify data collection. All taxa chosen for study are dominant structure-forming species upon which most other rocky shore organisms depend and are common throughout the northern Channel Islands (Dayton, 1971; Bertness et al., 1999; Sapper and Murray, 2003; Smith et al., 2006; Råberg and Kautsky, 2007; Marzinelli et al., 2014; Elsberry and Bracken, 2021). Nine fixed 50 x 50 cm (0.25 m^2) plots were established in each of the four biotic communities nonrandomly. Plots within each zone were chosen to be similar with respect to substratum rugosity, abundance of dominant species, and the level of exposure to wave energy and other environmental factors.

Experimental design and monitoring. Two levels of pulsed disturbance treatments, mild and severe, were applied to randomly chosen plots within each zone. The mild disturbance consisted of a single trampling event of 500 footsteps within each plot using hiking boots with Vibram soles, and the severe disturbance consisted of scraping plots of all biota excluding encrusting organisms using paint scrapers and wire brushes. Both treatments, along with controls, which were not trampled or scraped but were otherwise treated the same as other plots, were each established randomly in three replicate plots in each of the four communities, yielding a total of 36 plots.

All plots were photographed immediately prior to treatment, immediately afterward, then quarterly during the first year, and biannually every subsequent year from 1982 to 2014. One hundred evenly spaced points were overlain on each plot, either on the plot itself in the field using a gridded quadrat, or on a photograph of the plot, and each point was scored for species (sessile or attached mobile, e.g., sea stars), or, in the case of bare space, substratum type, to estimate cover (see Engle et al., (2022) for more detail on methodology).

To further assess community differences among treatments and controls, motile invertebrates were counted annually from 2001-2010 by carefully searching each plot. Select species were measured for size-frequency distribution. Abundant species including littorine snails (*Littorina* spp.) and small limpets were subsampled in three haphazardly placed small plots (either 20x20cm or 10x10cm, depending on density) within each fixed plot area.

Univariate analyses. Examination of percent cover data for focal species within each of the four communities (e.g., California mussels [*Mytilus californianus*] within the nine mussel plots) revealed nonlinear temporal and covariate effects. To test for differences in treatments and controls following mechanical disturbances, data were modeled as a function of the covariates using generalized additive mixed-effects models (GAMM). A beta distribution with a logistic link was used to ensure that the fitted values ranged from 0 to 1 for the response variable (percent cover). Fixed covariates were *Season_number* (ordered integer with 65 levels) and *Treatment* (categorical with three levels). The smoothed interaction term was *Season_number* × *Treatment.* To account for temporal dependency observed in the time-series data, we incorporated an autoregressive component (AR(1) correlation structure) into the model in which the random intercept *w_it* at time *t* and location *i* is similar to *w_i*, *t-1* at time *t-1* at location *i*. The AR(1) generates a latent variable that is spatially correlated, slowly changes over time, and captures any spatial and temporal patterns that are not modeled by the covariates. The latent variable ensures that the model residuals are independent and imposes a dependency structure on the response variable, percent cover (Robinson, 1978).

We used *plot* (factor with 9 levels) as a random intercept to incorporate dependency among observations from the same site. The Akaike Information Criterion (AIC) and

Bayesian Information Criterion (BIC) were used to identify the preferred model (i.e., lowest AIC and BIC) (Akaike, 1974; Schwarz, 1978). Generalized Additive Mixed Models were applied via restricted maximum likelihood (REML) in the mgcv package (Wood, 2011) using R Ver. 4.2.2 (R Core Team, 2022).

Three tests were conducted for each biotic zone. The first test was a *before-after-control-impact* (BACI) analysis to determine if any differences existed between plots in the two treatments and the controls in the four quarterly visits in the first-year post-treatment, versus the single pre-treatment visit. A second test was conducted to determine whether differences existed between the treatment and control plots over the entire sampling period (1981-2014) excluding the pre-treatment visit. A third test was conducted to determine if the treatments vary from the controls during the last five years (2009-2014) of the study period.

Underlying model assumptions including independence and absence of residual patterns were verified by plotting residuals versus fitted values and each covariate in the model. Temporal autocorrelation was assessed via autocorrelation function (ACF) and partial autocorrelation function (PACF) plots of the model residuals. We then simulated 10,000 datasets from the preferred GAMM and calculated a frequency table for each simulated dataset. An average frequency table was generated from the simulated data and compared with the frequency table of the observed data.

Multivariate analyses (community level analyses). To visualize temporal changes in community structure within the fixed plots, non-metric multi-dimensional scaling (nMDS) was used (Kruskal and Wish, 1978). Multivariate methods account for community-level variations in populations, and they can provide powerful descriptions of communities responding to stress or disturbance. For each of the four biotic zones, two nMDS plots were generated: one including sessile species (percent cover) within the plots and another using motile species (count data). Data were lumped to higher taxonomic levels and functional groups to account for differences in survey effort and reduce redundancy in taxa and influence of rare taxa characterizing community structure. Bray-Curtis similarity coefficients were calculated for every pair of samples to identify mutually similar groups that were mapped onto an ordination plot based on relative dissimilarity of species composition between pairs of samples (Clarke et al., 2014). All multivariate analyses were implemented using Primer-E 7 (Ver 7.0.10) software.

Results

The recolonization rates for species in the four biotic zones following the scrape disturbance spanned a wide range, from years for barnacles and turfweed, to decades for rockweeds and mussels (Figures 2.3b, 2.6b, 2.9b, 2.12b). The one-time trampling treatment significantly reduced cover of rockweeds (*S. compressa* and *P. californica*, $p<0.01$) but not turfweed (*E. muricata*) or barnacles and mussels (Figures 2.3a, 2.6a, 2.9a, 2.12a and Tables 2.1, 2.4, 2.7, 2.10). Recovery for the rockweed assemblage following the trampling treatment took approximately one year (Figure 2.9b and Tables 2.7, 2.8).

Barnacles. The barnacle complex (*Chthamalus* spp./ *Balanus* spp.) was not significantly affected by the trample treatment (Figure 2.3a, Table 2.1). Recolonization of barnacles following severe disturbance occurred within approximately two years (Figure 2.3b). The nMDS plot for the barnacle assemblage shows that the severely disturbed plots had more bare rock than the control and trample plots near the beginning of the study before converging with the control and trample plots around quarter 5 post-disturbance (i.e., Year 2) (Figure 2.4).

Temporal trends were similar for the severe disturbance treatment and control: cover declined to approximately 10-20% between the late 1980s and early 2000s, before increasing to approximately 30-40% for the remainder of the study period (Figure 2.3b, c). Barnacle cover in the trampled plots remained relatively steady, between 30-40% during the entire study (Figure 2.3b, c). These trends are supported by the nMDS plot, which indicates that the severely disturbed plots transitioned away from the control and particularly the trample plots mid study period, as they were colonized by rockweeds, before gradually converging with both treatments by the end of the study. We detected no significant differences in barnacle cover between the treatments and controls during the last five years (2009-2014) (Figure 2.3c, Table 2.3). Similarly, we found no indication that the motile invertebrate community from 2001-2010 differed markedly between treatment and control plots (Figure 2.5).

Turfweed. Endocladia muricata cover was significantly affected only by the severe disturbance (Figure 2.6a, Table 2.4). Following complete removal, it took approximately eight years for *Endocladia muricata* cover to reach pre-treatment abundances in the severely disturbed plots (Figure 2.6b). The nMDS plot for the turfweed community also indicates that the severely disturbed plots diverged from the control and trample plots until around survey event 16 in year 7 (Figure 2.7).

Endocladia muricata cover in the control plots and trample treatment declined markedly from 1981 to 1985 before rebounding to approximately 40-50% the remainder of the study period (Figure 2.6b, c). These trends can be observed in the nMDS plot as both treatments and controls transition towards communities dominated by miscellaneous algae (mostly red turf algae other than *E. muricata*) and barnacles several years after the beginning to the middle of the study period (Figure 2.7). Post-treatment trends over time (1981-2014) revealed significant fluctuations in cover of *E. muricata* in both treatments and the controls, but no significant differences between treatments and controls were detected (Table 2.5). *E. muricata* cover in the scrape and trample plots was similar to and statistically indistinguishable from cover in the controls during the last five years (2009-2014) of monitoring (Figure 2.6c, Table 2.6). The motile invertebrate community from 2001-2010 was also similar between treatment and control plots (Figure 2.8).

Rockweed. The rockweed species complex (*Silvetia compressa* and *Pelvetiopsis californica*) significantly declined following both disturbance treatments (Figure 2.9a, Table 2.7). The one-time trampling event reduced cover of rockweed by approximately 20% (Figure 2.9a). Following the severe disturbance treatment, rockweed failed to recover above 10% in any of the plots until the late 1980s (Figure 2.9b, Table 2.8). These trends are apparent in the nMDS plot, as communities in the scraped and trampled treatments were less dominated by rockweeds near the beginning of the study (Figure 2.10).

Rockweed cover in the trampled and scraped plots followed a precipitous negative trajectory through the mid-1980s and late-1980s, respectively, stabilized between 30-40% cover until 2005, and then declined to near 0% by the end of the study (Figure 2.9b, c). Similarly, control plots had relatively stable rockweed cover until approximately 2005 when they declined precipitously (Figure 2.9b, c). The nMDS plot showed that communities in both treatments and controls during survey events corresponding with the last several survey years were predominantly composed of *E. muricata*, *Mytilus* spp., and bare rock (Figure 2.10). Post-treatment trends over time (1981-2014) revealed significant fluctuations in the cover of *S. compressa* and *P. californica* in both treatments and the controls, but no significant differences between treatments and controls were detected (Figure 2.9b, Table

2.8). Rockweed cover in the scrape and trample plots was comparable and statistically similar to cover in the controls during the last five years (2009-2014) of monitoring (Figure 2.9c, Table 2.9). The motile invertebrate community from 2001-2010 appeared similar regardless of treatment type (Figure 2.11).

Mussels. California mussel (*Mytilus californianus*) cover was not significantly reduced by the one-time trampling event (Figure 2.12a, Table 2.10). The temporal trend for the trample treatment and control fluctuated significantly, but no significant differences in *M. californianus* cover were detected between trample and control plots (Figure 2.12b, Table 2.11). Over time, mussel cover in the trample and control plots decreased gradually to about 30% through the early-1990s, increased steadily to approximately 40-50% by 2005, and then declined slightly the remainder of the study (Figure 2.12b). The nMDS plot for the mussel communities represents the temporal trends as two clouds of points, with one corresponding primarily to the later period (post 2000) that is more highly associated with *Mytilus* spp (Figure 2.13).

The severe disturbance resulted in significant, long-lasting impacts to *M. californianus* (Figure 2.12a, Table 2.10). Recovery for the species was gradual over the course of nearly two decades, when mussel cover finally approached pre-treatment abundance (Figure 2.12b). Like the trample and control abundances, *M. californianus* cover peaked around 2005 and gradually decreased through the remainder of the study. These temporal trends in mussel cover are apparent in the nMDS plot, as the community of the severely disturbed plots shifted from being dominated by bare rock early in the study period to *Mytilus* spp. later (Figure 2.13). Post-treatment linear trends over time (1981-2014) revealed significant differences between cover of mussels in the severely disturbed treatment and the controls (Figure 2.12b, Table 2.11). Yet, the effects of removal were not visible from 2009-2014, when mussel cover was statistically comparable in the scrape and control plots (Figure 2.12c, Table 2.12). We also detected no marked differences between treatment and control plots in the motile invertebrate communities from 2001-2010 (Figure 2.14).

Discussion

The results of this long-term field experiment demonstrate that some rocky intertidal species take decades to fully recover from even very small-scale (0.25 m^2) severe disturbances. Other species returned to their initial, undisturbed state within one year. Longer-lived species including mussels and rockweeds took much more time to reach pre-disturbance population size following complete removal than species with shorter lifespans including barnacles and turfweed. These results generally mirror those in freshwater (Yount and Niemi, 1990), brackish, forest, terrestrial, and other marine ecosystems (Jones and Schmitz, 2009 and references therein).

Severely disturbed mussel and rockweed community plots in our study took approximately 10 years to recover (Figures 2.9, 2.12). Previous studies have demonstrated that recovery time for mussels and rockweeds is highly variable. However, most studies did not last long enough for populations to return to their initial state (Underwood, 1998, 1999; Jenkins et al., 1999, 2004; Peterson et al., 2003; Ingolfsson and Hawkins, 2008; Conway-Cranos, 2012). As a result, without monitoring data, most recovery times for longer-lived species including fucoids and mussels are based on predictions that are 2-10-fold higher than the recovery rates we observed (MMS and Kinetic Laboratories, 1992; Underwood, 1998, 1999; Jenkins et al., 1999, 2004; Speidel et al., 2001; Peterson et al., 2003; Cervin et al. 2005; Ingolfsson and Hawkins, 2008; Conway-Cranos, 2012; Schiel and Lilley, 2011).

Paine and Levin (1981) suggested that mussel community recovery in Washington, USA takes at least 8 years, but that mussel (*Mytilus californianus*) bed regeneration is highly spatially variable, and the process may require up to 35 years. Similarly, Conway-Cranos (2012) estimated that recovery time ranged widely from 5 to 47 years for disturbed *M. californianus* assemblages at three sites spanning the California biogeographic break, Point Conception. Mussels cleared at six sites in central California required at least 12 years to fully rebound based on the trajectory of incomplete recovery (MMS and Kinetic Laboratories, 1992). Recovery rates for *M. californianus* are likely related to life history characteristics for the species including being slow-growing, long-lived (7 to 20 years minimum), and relatively slow to reach reproductive maturity (4-8 months) (Suchanek, 1981).

Similar estimates of recovery time ranging from several years to decades have been documented for fucoids including rockweeds (Underwood, 1998, 1999; Jenkins et al., 1999, 2004; Speidel et al., 2001; Peterson et al., 2003; Cervin et al., 2005; Ingolfsson and Hawkins, 2008; Conway-Cranos, 2012; Schiel and Lilley, 2011). Conway-Cranos (2009) cleared plots ranging in size from 8 x 12 cm to 50 x 75 cm dominated by the rockweed, *Silvetia compressa* at three sites. Recovery rates varied widely among sites and disturbance size with over half of the assemblages recovering within 6-48 months, while others failed to recover within the study period and were projected to take 5-196 years to return to a pre-disturbed state. Other studies have reported maximum recovery times for fucoids following removal ranging from less than 2 years to an estimated more than 12 years (Farrell, 1991; Devogelaere and Foster, 1994; McCook and Chapman, 1997; Underwood, 1998, 1999; Jenkins et al., 1999, 2004;

Speidel et al., 2001; Peterson et al., 2003; Cervin et al., 2005; Ingolfsson and Hawkins, 2008; Schiel and Lilley., 2011; Whitaker et al., 2023).

Several factors may contribute to the slow recovery of fucoids. While fucoids are capable of regenerating from holdfasts, they are unable to propagate vegetatively, and must instead rely primarily on dispersal of early life stages including propagules and zygotes (Schiel and Foster, 2006). Dispersal of fucoid gametes is typically limited to short distances (cm to m) (Serrao et al., 1996; Williams and Di Fiori, 1996). Many fucoids such as *S. compressa* and *P. californica* are negatively buoyant which likely affects their ability to disperse via reproductive fronds (McKenzie and Bellgrove, 2009). Moreover, some species surround spores with a thick mucilage which slows movement, and time peak gamete release to periods of low water motion or low tidal level (Pearson and Brawley, 1996). Recovery can also be delayed since fucoids are typically reproductive only during relatively short periods of time (Gunnill, 1980). Additionally, early post-settlement life stages of fucoids have extremely high mortality rates (>99.99%) (McLachlan, 1974; Gunnill, 1980; Chapman and Johnson, 1990; Brawley and Johnson, 1991; Vadas et al., 1992; Johnson and Brawley, 1998; Moeller, 2002).

Our turfweed (*Endocladia muricata*) plots took approximately 8-9 years to return to pre-scrape abundances (Figure 2.6). However, recovery may have been delayed due to environmental factors. *E. muricata* cover in the control plots and the trample treatment declined simultaneously near the beginning of the study before rebounding along with the scrape plots. One explanation for the *E. muricata* declines near the beginning of the study may be the 1982-83 El Niño Southern Oscillation event, one of the strongest El Niño’s on record. Along the western coast of North America, El Niño’s typically result in anomalously warm sea surface temperatures over prolonged periods of time. Such conditions can be deleterious to some marine species such as *E. muricata* (Schiel et al., 2004).

Prior studies indicate that *Endocladia muricata* can recover from clearing disturbances on the order of years (Northcraft, 1948; Farrell, 1991; Foster et al., 2003; Conway-Cranos, 2012). Most clearings of *E. muricata* at five study sites in central California were considered recovered in six years, though recovery rates varied significantly among sites (Foster et al., 2003). Similarly, recovery of *E. muricata* varied significantly among three sites studied across Point Conception with nearly all plots returning to their pre-disturbed state before the end of the 52-month study (Conway-Cranos, 2012). Conversely, *E. muricata* failed to recover within 37 months at a site where holdfasts were removed in Monterey, California (Northcraft, 1948). Like many other red algal species (Goldstein, 1973; Azanza-Corrales and Dawes, 1989; Hurtado-Ponce, 1990; Kain, 1991; Iima et al., 1995), *E. muricata* likely is relatively short-lived and can regenerate both vegetatively without reproducing and sexually via spores, which may improve its ability to colonize open spaces.

The barnacle community (*Chthamalus* and *Balanus* spp.) plots cleared of biota in our study recovered most quickly out of the four community types we studied, within approximately one year (Figure 2.3). Conway-Cranos (2012) measured comparable recovery rates for *Chthamalus* and *Balanus* spp. as nearly all her barnacle plots recovered within two years of being cleared. To investigate succession processes, Farrell (1991) cleared small plots at three sites in central Oregon, USA, and found that the barnacle *Chthamalus* spp. was the first to recolonize, followed by *Balanus* spp., with peak abundance occurring 4-36 months after scraping. Relatively rapid recovery of *Chthamalus* spp. may be attributed to a unique set of life history characteristics including their short lifespan (~3 years), early age of reproductive maturity (~2 months), long-range dispersal of larvae, and the ability to settle year-round on bare rock surfaces irrespective of tidal height (Morris et al., 1980).

In addition to life history traits, time to recovery depends on numerous factors including geographic location, and the size, timing, intensity, and frequency of disturbance (Kim and DeWreede, 1996; Schiel and Taylor, 1998; Spiedel et al., 2001; Conway-Cranos, 2012; Underwood, 1998). Disturbance size, in particular, has been shown to be an important factor governing the rate of recovery for some species. For example, Kim and DeWreede (1996) found that a community dominated by rockweeds (*Fucus distichus* and *Pelvetiopsis limitata*) recovered slowest in their largest 20 x 20 cm clearings. Conway-Cranos (2009) also found recovery of mussels and the rockweed, *S. compressa* to be slowest for larger 50 x 75 cm disturbances, but patch size had much less influence on barnacle and *E. muricata* recovery. We did not test the effect of disturbance magnitude on recovery rates, but the size of our plots (50 x 50 cm) and rates of recovery were comparable to that of the largest plots in the Conway-Cranos (2009) study suggesting that disturbance size may have influenced the process of recovery.

Differences in recovery time have been attributed to the intensity of disturbance (Schiel and Taylor, 1999; Underwood, 1998; Speidel et al., 2001). This is especially true for algae recovering from disturbances that cause complete removal of entire thalli including holdfasts (Underwood, 1998; Speidel et al., 2001). For example, Speidel et al. (2001) found no significant differences in recovery trends among partial canopy removal treatments for the rockweed, *Fucus gardneri*, but complete removal of *F. gardneri* adult thalli and germlings resulted in a significantly longer period of recovery. Similarly, *E. muricata* cleared (including holdfasts) from a site in Monterey, California failed to recover by the end of a 37-

month study (Northcraft, 1948). Yet, at the same site, Glynn (1965) measured recovery within 6 months for *E. muricata* that was partially cleared with holdfasts not removed. Schiel and Taylor (1999) found the scale and intensity of disturbance to be directly related to recovery rates of the rockweed, *Hormosira banksii*, with progressively more intense levels of trampling disturbance resulting in longer periods of recovery. Our results differed from these patterns, as trampled plots were less impacted than scraped plots, but remained depressed and took a similar amount of time, over two decades, as plots that were severely disturbed by scraping to completely recover relative to the control plots.

Fucoids are known to be extremely vulnerable to injury from pedestrian traffic (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Fletcher and Frid, 1996; Schiel and Taylor, 1999; Jenkins et al., 2001), and the significant reduction in the canopy cover of rockweeds caused by our single trampling event persisted for approximately one year (Figure 2.9b). Similar recovery patterns are likely for other short-dispersal fucoids. For instance, Povey and Keough (1991) documented a 20% loss in biomass of the fucoid, *H. banksii* following a single footstep and 60% reduction after 75 steps. Another study found that only 10 footsteps reduced the cover of *H. banksii* by 25%, and 200 steps caused a 96% reduction in canopy cover (Schiel and Taylor, 1999). Our trampling treatment involved a single application of 500 steps resulting in a 30% reduction in fucoid (*S. compressa* and *P. californica*) cover (Figure 2.9). By comparison, a trampling study on *S. compressa* at three sites in southern California using two monthly disturbance treatments for 16 months including 150 steps and 300 steps per plot resulted in significant reductions in *S. compressa* cover ranging from 16-38% and 25-38% across sites for each treatment, respectively (Denis, 2003). Most canopy cover loss occurred within the first 150 footsteps, suggesting that sites close to urbanized areas are subjected to high impacts from trampling.

The *Endocladia muricata* and invertebrate assemblages in our experiment were not affected significantly by the trampling treatment. Past studies support our finding that *E. muricata* is relatively resistant to trampling (VTN Oregon, 1983; Brosnan and Crumrine, 1994). Brosnan and Crumrine (1994) subjected plots dominated by *E. muricata* at two sites in Oregon, USA to low-level disturbance consisting of 250 steps one day per month for a year and found no significant changes in *E. muricata* cover. However, the same study detected significant decreases in the cover of barnacles (*Semibalanus glandula* and *Chthamalus dalli*) and mussels (*Mytilus* spp.). At one site, barnacle cover declined from 66.6 to approximately 25% after only one day of trampling and further declined to 7.2% in 4 months. Barnacle cover at the second site was initially 21.3% and fell to 5.5% after 6 months of low-intensity trampling. Mussel cover declined at one site from 97% to approximately 60% following two trampling events. At the second site, even though mussels were lost due to trampling, the primary cover of mussels remained high throughout the study since the mussel bed was multi-layered. Povey and Keough (1991) also reported significant damage to barnacles and mussels including dislodgement and crushing from pedestrian traffic.

Conspicuous organisms such as fucoids, mussels, turfweed and barnacles, collectively referred to as foundation species (sensu Dayton, 1972), provide services critical to the natural functioning of rocky intertidal ecosystems and support biodiversity principally through the provision of structurally complex three-dimensional habitat. As an example, the dense frond canopy formed by the rockweed, *S. compressa* in southern California, USA, harbored 107 epifaunal and understory taxa (Sapper and Murray, 2003). By comparison, mussel beds, primarily *M. californianus*, at the California Channel Islands supported 610 invertebrate and 141 algal species (Kanter, 1980). More than 90 species were associated with *E. muricata* tufts on the shore at Hopkins Marine Station in Pacific Grove, CA (Glynn, 1965). Declines in abundance of foundation species, therefore, can have direct, long-lasting effects on community composition (Jenkins et al., 2004; Schiel and Lilley, 2011; but see Speidel et al., 2001). For example, shifts in community structure including a significant decline in red algal turf and a 3-6-fold increase in limpets were still apparent 12 years following the removal of canopy formed by the fucoid, *Ascophyllum nodosum* at a study site in Sweden (Jenkins et al., 2004). Similarly, in New Zealand, eight years after the fucoid *H. banksii* was experimentally removed, despite the regeneration of a nearly closed fucoid canopy, the disturbed plots had lower diversity and density of *H. banksii*, and more turf algae relative to unmanipulated plots (Schiel and Lilley, 2011).

To assess long-term change in the community composition of cleared and trampled plots relative to controls in the present study, we quantified the percent cover of sessile invertebrates and algae annually for 28 years following the two pulse disturbances. We detected no significant differences between the treatments and controls during the last five years (2009-2014) in the percent cover of focal species within each of the four intertidal assemblages studied. In addition, annually from 2001-2010, we counted all motile macroinvertebrates within the plots. Non-metric multi-dimensional scaling plots used to visualize temporal changes in community structure of the motile invertebrate assemblages within the fixed plots suggest high similarity between the treatment and control plots.

Recovery of rocky intertidal organisms can vary on the order of years to decades depending on the ecological characteristics and life history of species, as well as the multitude of factors related to the extent and duration of the disturbance. Recovery is also contingent upon the availability of adult sources of recruitment and reestablishment. Some species, such as many fucoids, lack reliable long-range dispersal capabilities, which may further hinder recovery. Given the slow recovery time some species exhibit following disturbances, it may be necessary to consider assisted recovery to stabilize or initiate populations that continue to decline or have been extirpated. This is particularly true for foundational intertidal species that support entire communities, often by relieving desiccation stress (Jurgens et al., 2022, Whitaker et al., 2023). Climate change is likely to lead to increased temperature, drying winds, and depressed fog, and facilitative species like rockweeds and mussels can provide refugia from these stresses (Jurgens et al., 2022). Currently, restoration ecology in rocky intertidal habitats is in its infancy, but new approaches are being developed (e.g., Gao et al., 2017; Whitaker et al., 2010). Meanwhile, rocky intertidal ecosystems have already been impacted and are highly vulnerable to anthropogenic stresses predicted to increase in frequency and intensity, including climate change (Kay et al., 2016; Keser et al., 2005; Rugiu et al., 2018; Takolander et al., 2017; Wilson et al., 2015) and urbanization (Thompson et al., 2002). The socioeconomic benefits that rocky shores provide are vast, ranging from tourism and fisheries to recreation and research, and it is paramount to identify effective methods to restore damaged rocky intertidal ecosystems at practical scales. Conserving and restoring foundation species that are slow to recover and provide broader benefits to ecosystem integrity could bolster rocky intertidal communities and biodiversity against future climate change impacts.

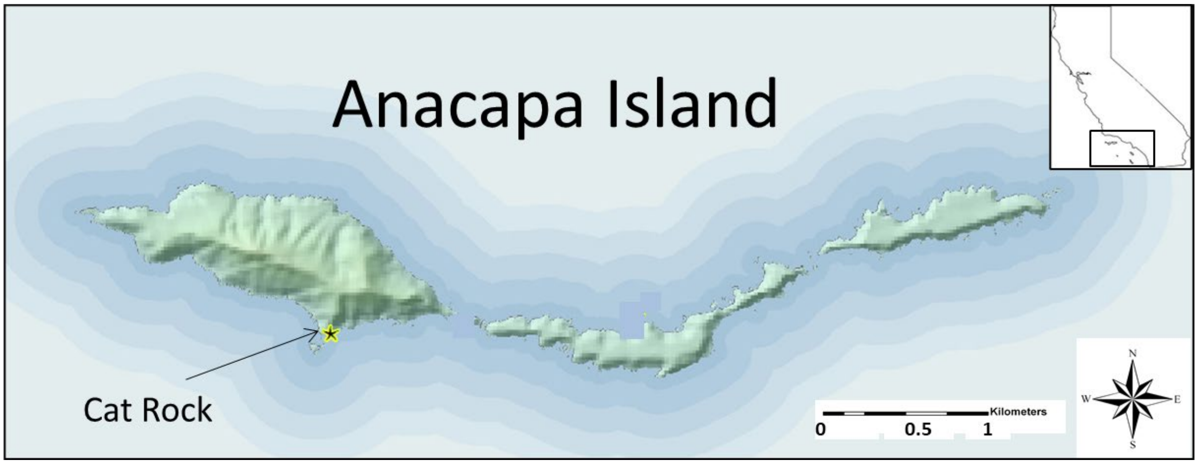

Figure 2.1. Map of the study site.

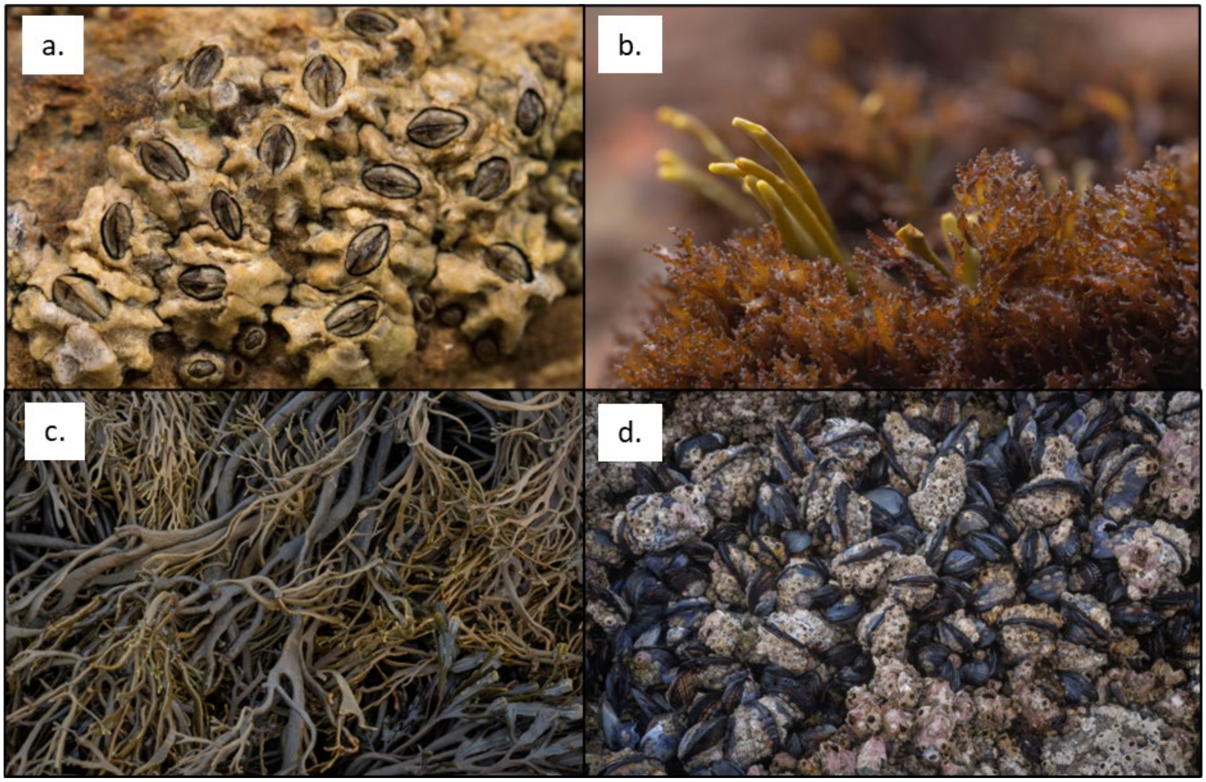

Figure 2.2. The four taxa chosen for study.

The taxa include the barnacle (*Chthamalus* and *Balanus* spp.) community (a), turfweed (*Endocladia muricata*) beds, both in the upper intertidal zone (b), the mid-intertidal fucoid rockweeds *Silvetia compressa* and *Pelvetiopsis californica* (formerly *Hesperophycus californicus*) (c), and beds of California mussel (*Mytilus californianus*) in the mid-to-lower intertidal (d). Photos: M. Ready

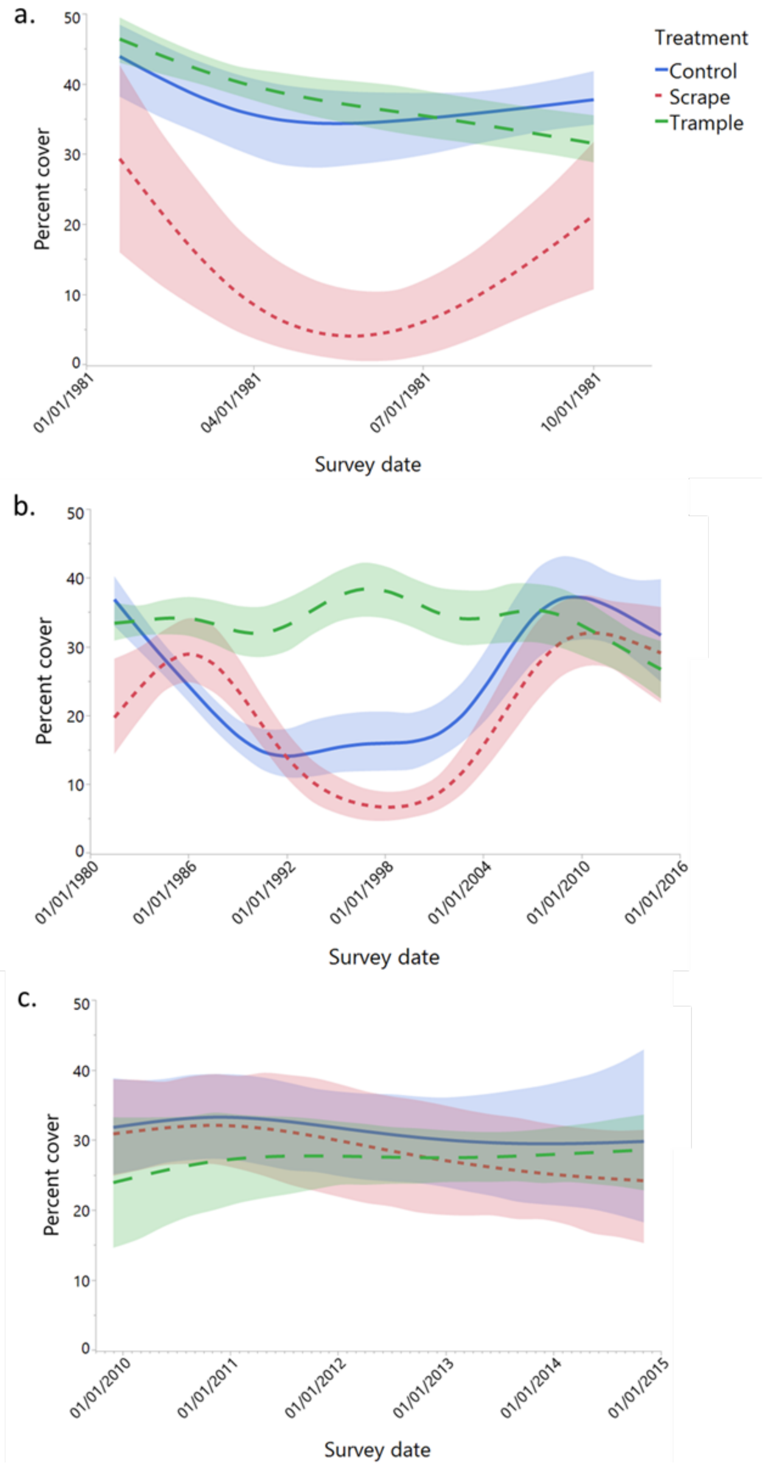

Figure 2.3. Barnacle complex (*Chthamalus* and *Balanus* spp.) percent cover.

Cover prior to and one year following the one-time disturbance treatments (a), following the one-time disturbance treatments excluding the pre-treatment (b), and during the last five study years (c). Shaded bands represent the bootstrap confidence region of each fit.

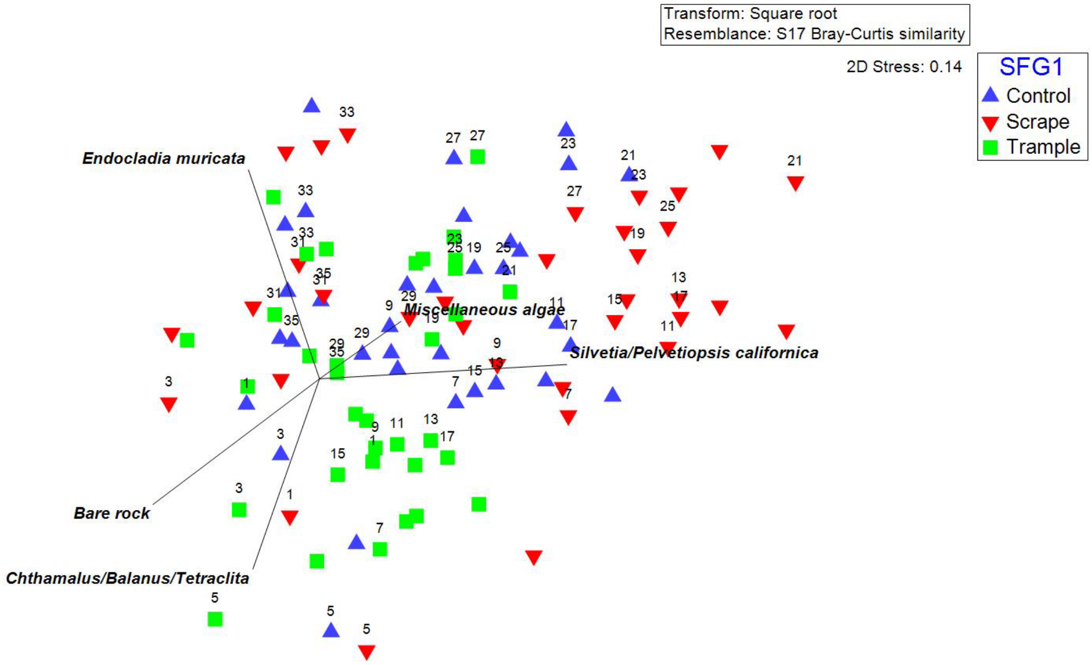

Figure 2.4. Non-metric MDS plot for the sessile species community in the barnacle complex (*Chthamalus* and *Balanus* spp.) from 1981-2014 based on Bray-Curtis dissimilarities.

The overlay vectors represent taxa/substrata driving similarity/dissimilarity between pairs of samples. Numbers for each symbol correspond with survey event order. Note only odd survey events labeled.

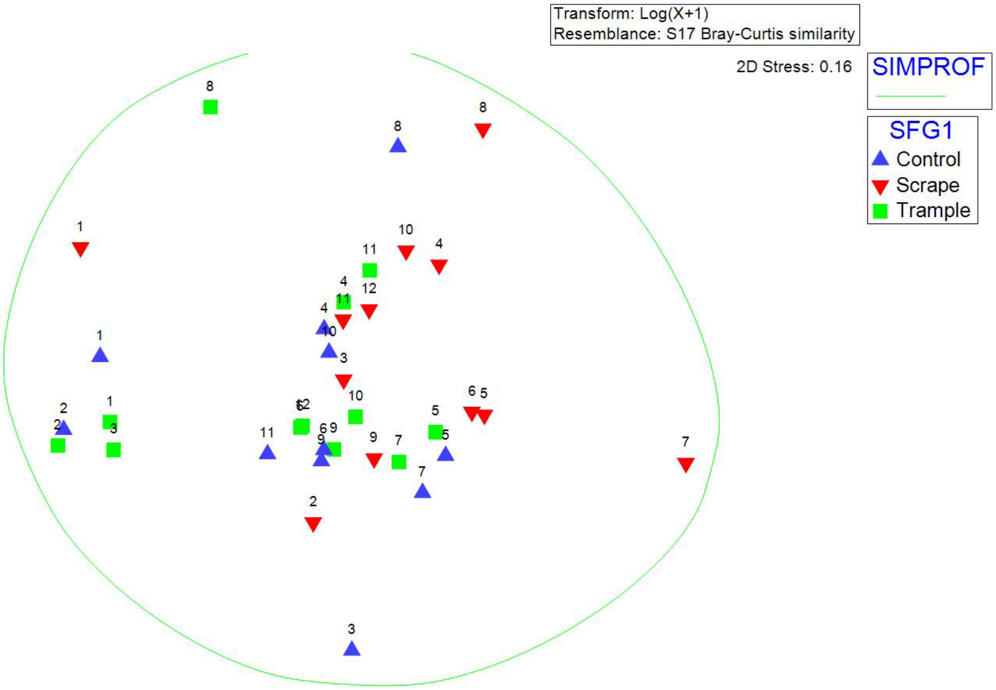

Figure 2.5. Non-metric MDS plot for the motile invertebrate community in the barnacle complex (*Chthamalus* and *Balanus* spp.) from 2001-2010 based on Bray-Curtis dissimilarities.

The overlay clusters represent the similarity levels between pairs of samples. Numbers for each symbol correspond with survey event order.

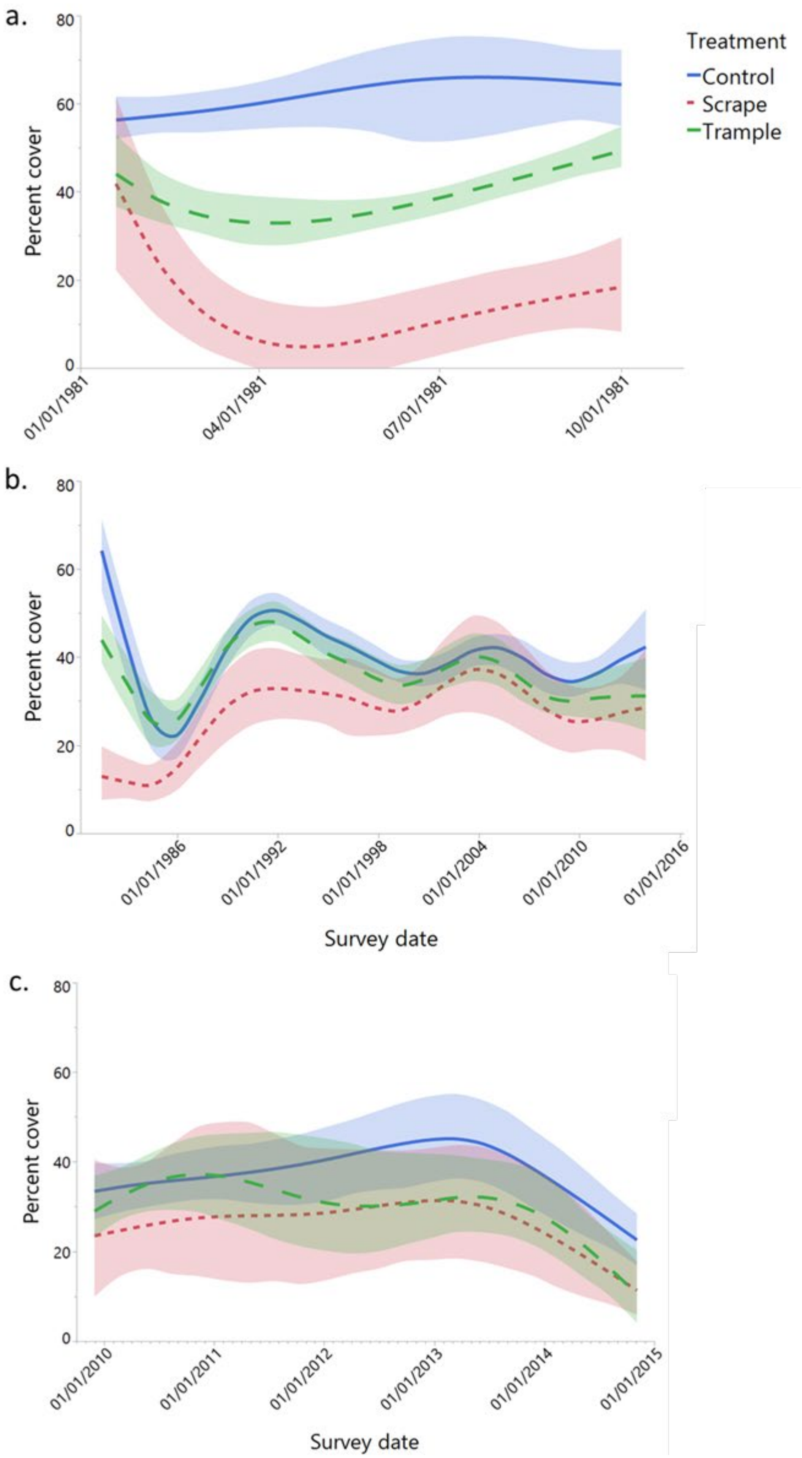

Figure 2.6. Turfweed (*Endocladia muricata*) percent cover.

Cover prior to and one year following the one-time disturbance treatments (a), following the one-time disturbance treatments excluding the pre-treatment (b), and during the last five study years (c). Shaded bands represent the bootstrap confidence region of each fit.

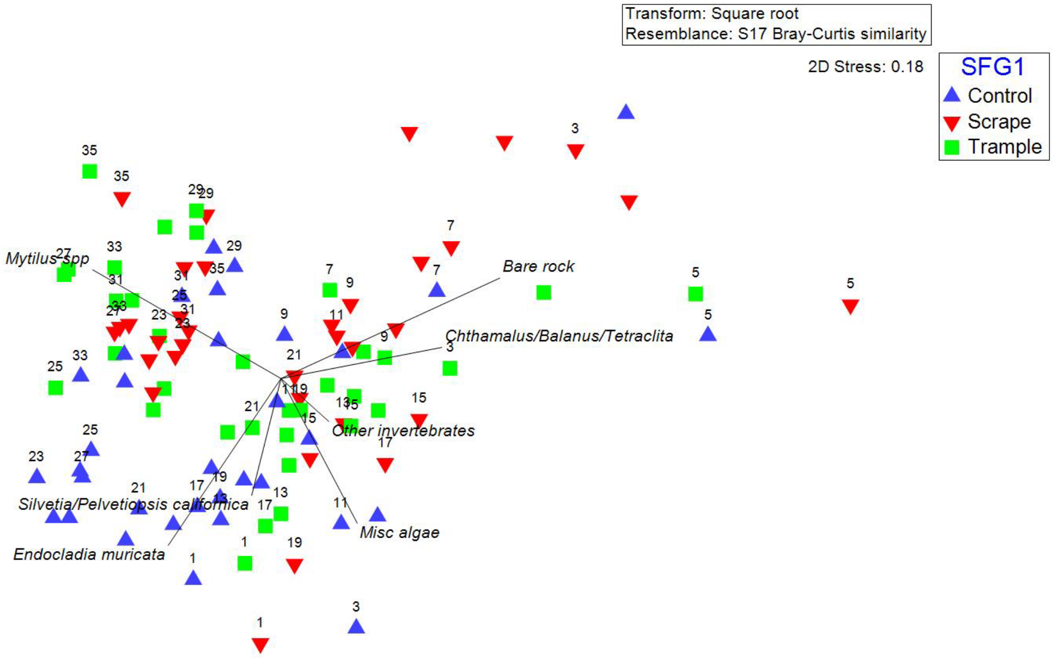

Figure 2.7. Non-metric MDS plot for the sessile species community in the turfweed (*Endocladia muricata*) plots from 1981-2014 based on Bray-Curtis dissimilarities.

The overlay vectors represent taxa/substrata driving similarity/dissimilarity between pairs of samples. Numbers for each symbol correspond with survey event order. Note only odd survey events labeled.

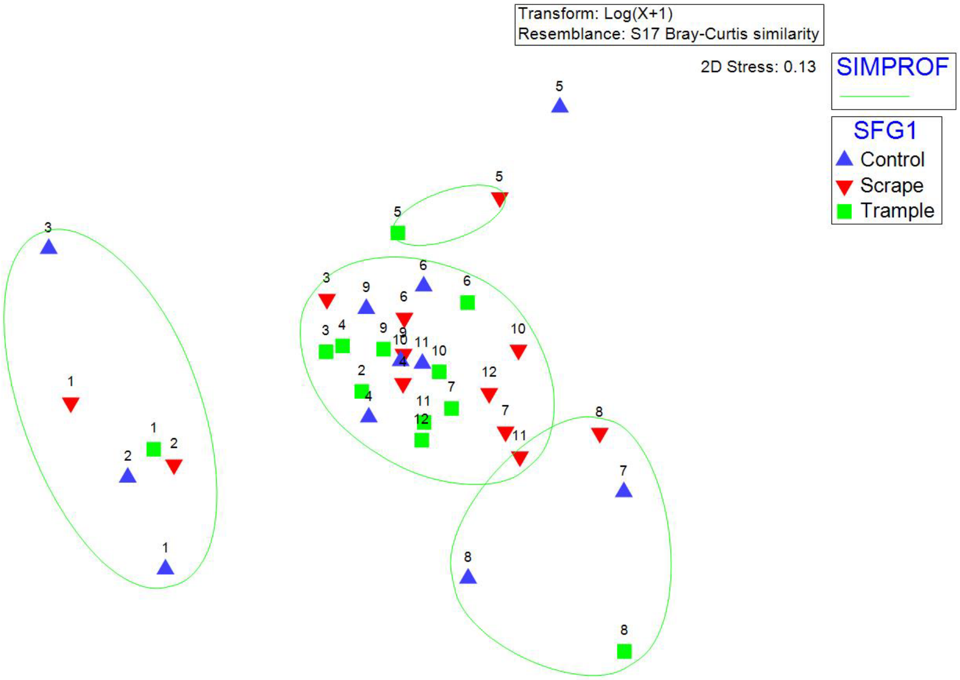

Figure 2.8. Non-metric MDS plot for the motile invertebrate community in the turfweed (*Endocladia muricata*) plots from 2001-2010 based on Bray-Curtis dissimilarities.

The overlay clusters represent the similarity levels between pairs of samples. Numbers for each symbol correspond with survey event order.

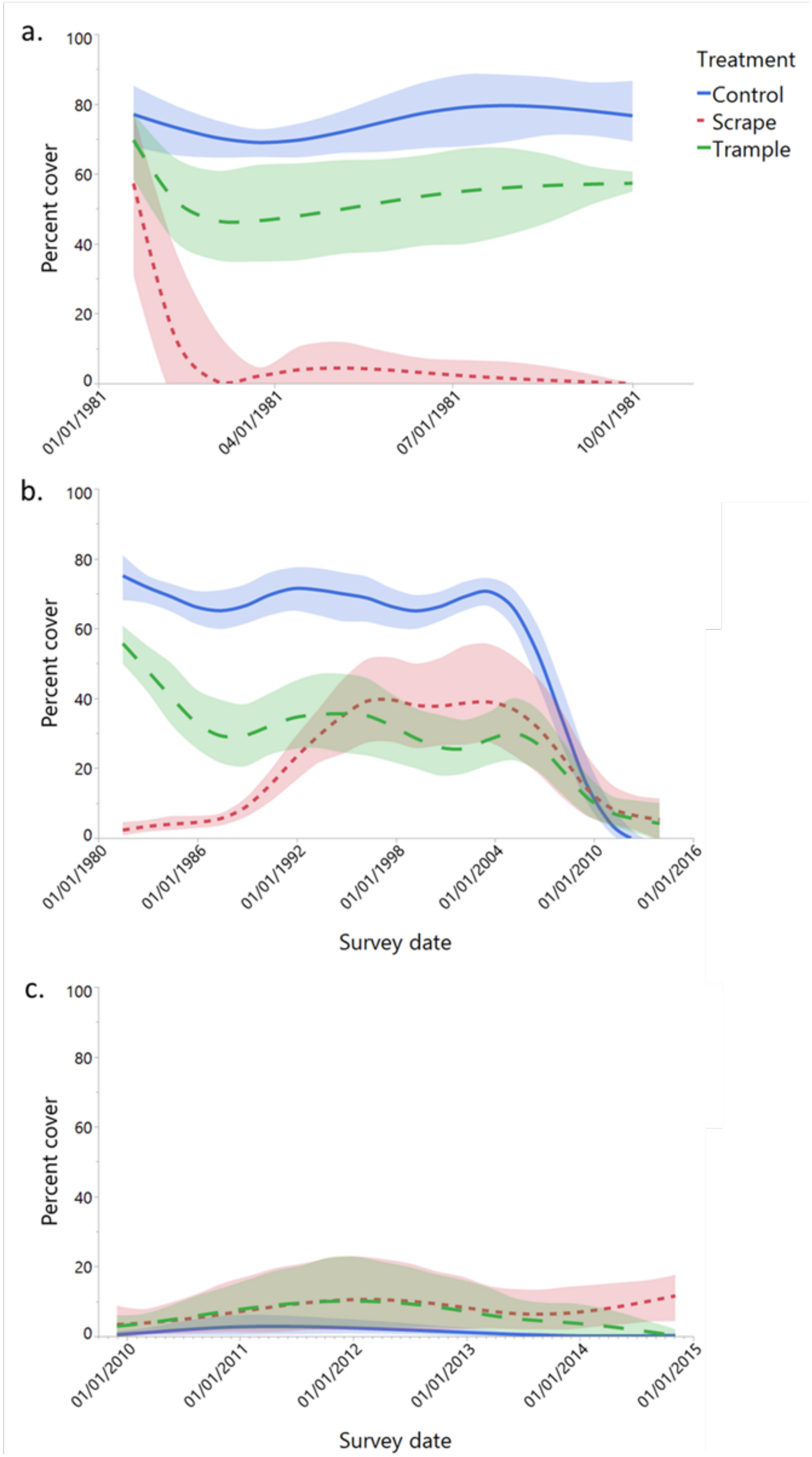

Figure 2.9. Rockweed (*Silvetia compressa* and *Pelvetiopsis californica*) percent cover.

Cover prior to and one year following the one-time disturbance treatments (a), following the one-time disturbance treatments excluding the pre-treatment (b), and during the last five study years (c). Shaded bands represent the bootstrap confidence region of each fit.

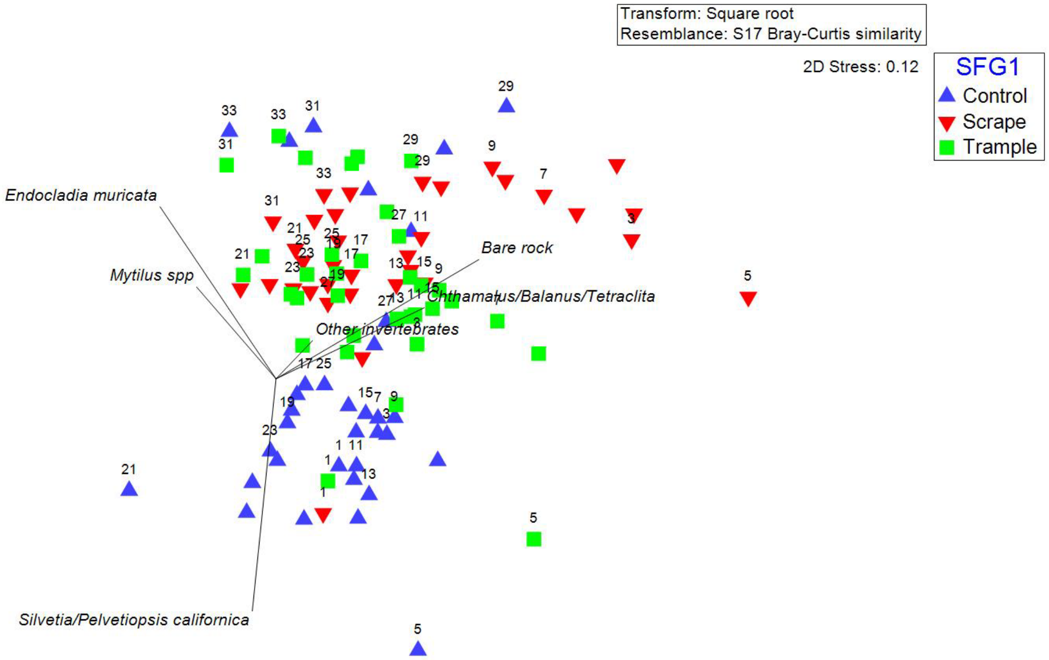

Figure 2.10. Non-metric MDS plot for the sessile species community in the rockweed (*Silvetia compressa* and *Pelvetiopsis californica*) plots from 1981-2014 based on Bray-Curtis dissimilarities.

The overlay vectors represent taxa/substrata driving similarity/dissimilarity between pairs of samples. Numbers for each symbol correspond with survey event order. Note only odd survey events labeled.

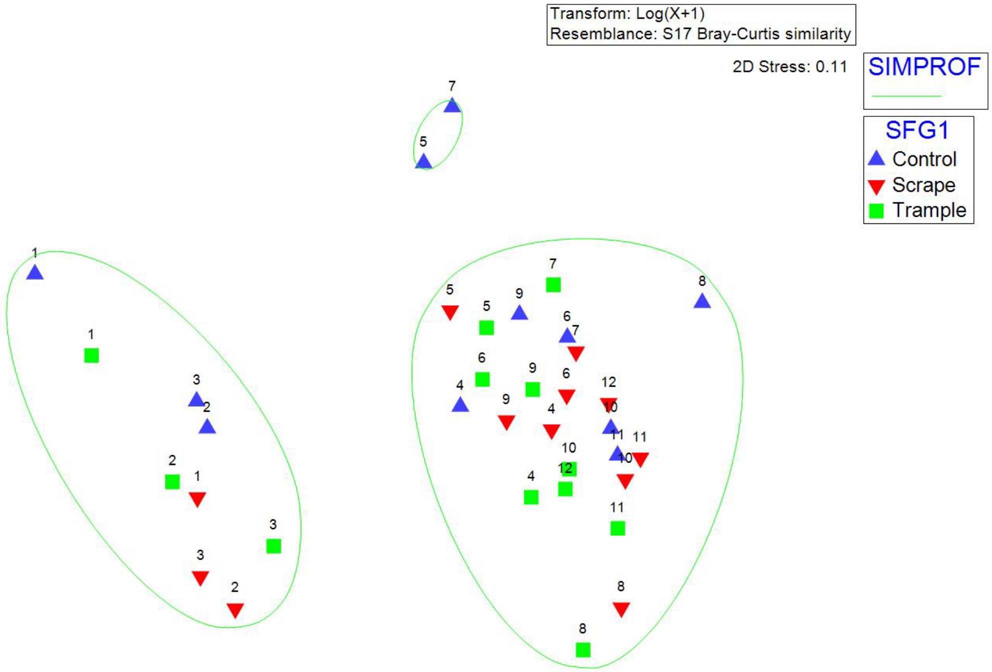

Figure 2.11. Non-metric MDS plot for the motile invertebrate community in the fucoid (*Silvetia compressa* and *Pelvetiopsis californica*) plots from 2001-2010 based on Bray-Curtis dissimilarities.

The overlay clusters represent the similarity levels between pairs of samples. Numbers for each symbol correspond with survey event order.

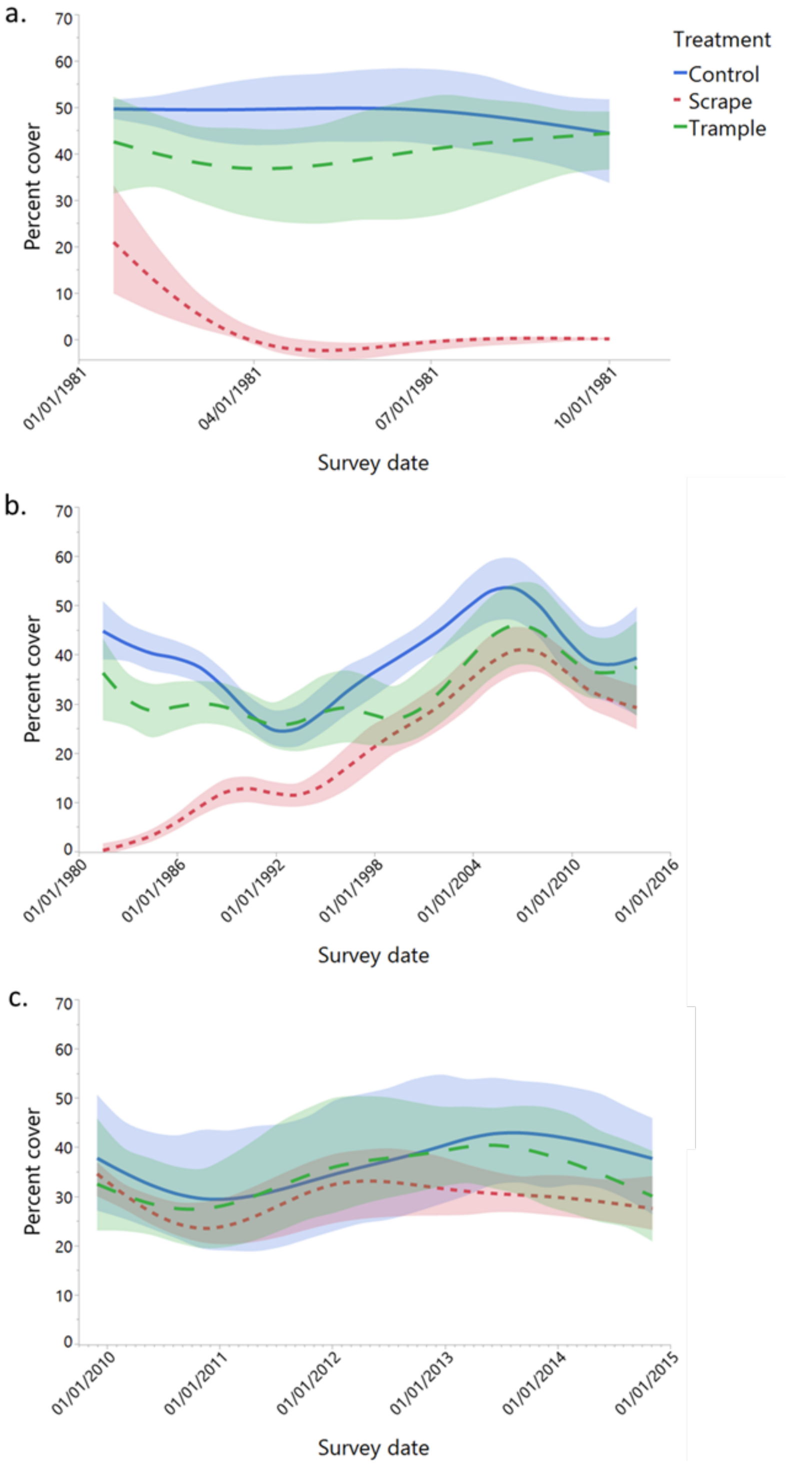

Figure 2.12. California mussel (*Mytilus californianus*) percent cover.

Cover prior to and one year following the one-time disturbance treatments (a), following the one-time disturbance treatments excluding the pre-treatment (b), and during the last five study years (c). Shaded bands represent the bootstrap confidence region of each fit.

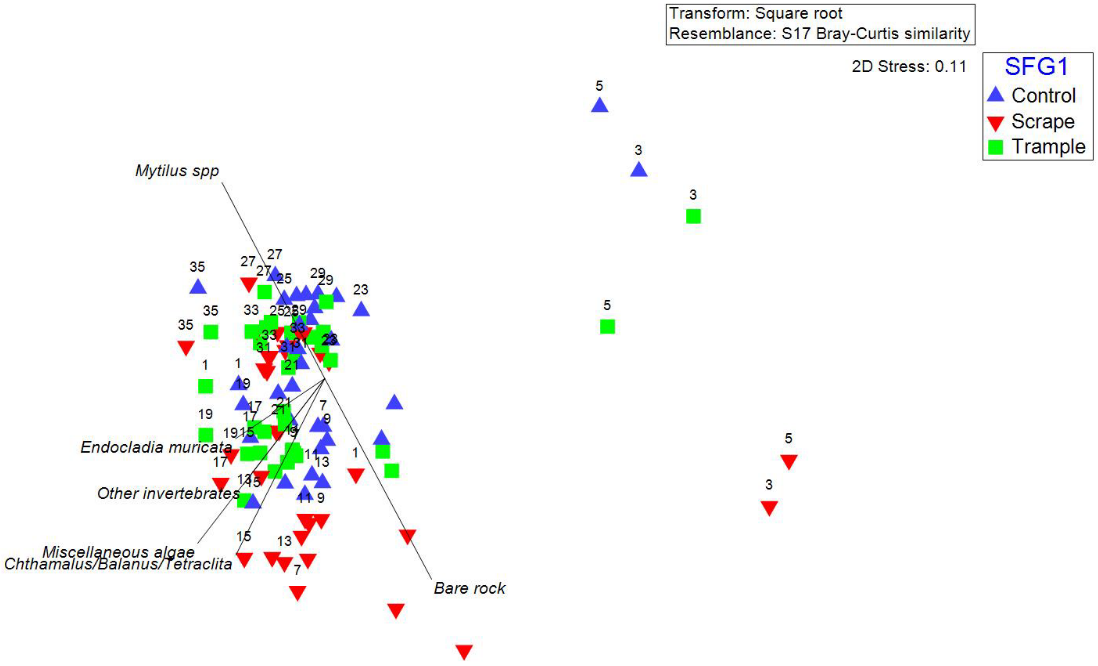

Figure 2.13. Non-metric MDS plot for the sessile species community in the California mussel (*Mytilus californianus*) plots from 1981-2014 based on Bray-Curtis dissimilarities.

The overlay vectors represent taxa/substrata driving similarity/dissimilarity between pairs of samples. Numbers for each symbol correspond with survey event order. Note only odd survey events labeled.

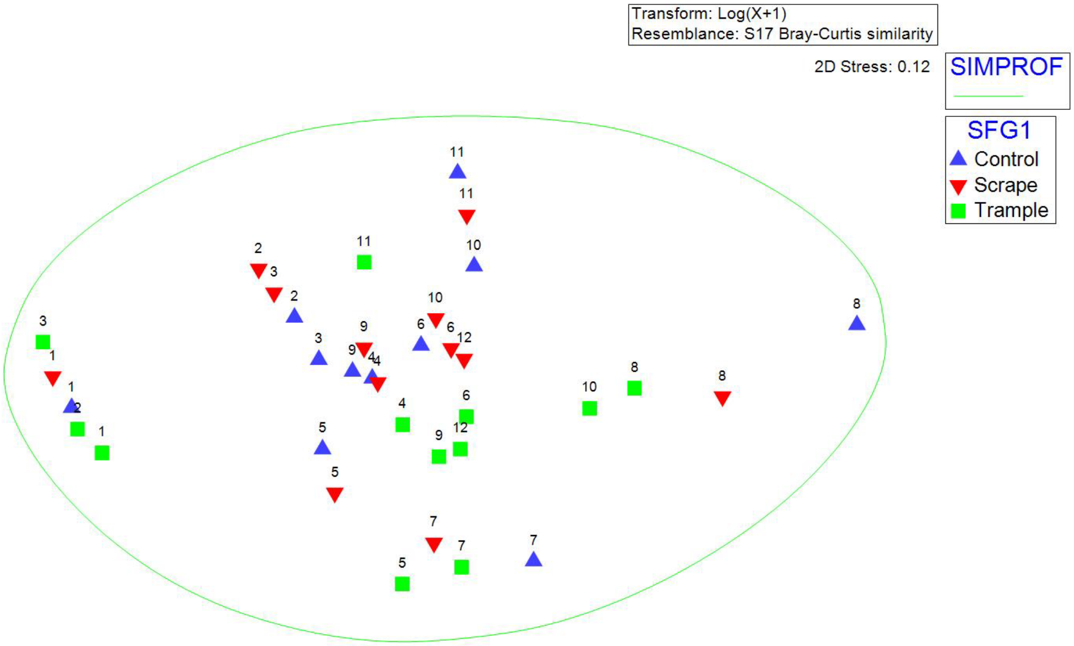

Figure 2.14. Non-metric MDS plot for the motile invertebrate community in the California mussel (*Mytilus californianus*) plots from 2001-2010 based on Bray-Curtis dissimilarities.

The overlay clusters represent the similarity levels between pairs of samples. Numbers for each symbol correspond with survey event order.

Table 2.1. GAMM results for BACI analysis of barnacle (*Chthamalus* & *Balanus* spp.) percent cover prior to and one year following the one-time disturbance treatments

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-0.552	0.147	-3.763	0.0002	**
	Scrape = S	-2.561	0.255	-10.027	0.0000	**
	Trample = T	-0.014	0.207	-0.068	0.9456	
	Before vs. after = B	0.424	0.237	1.784	0.0744	.
	S × B	2.763	0.367	7.533	0.0000	**
	T × B	0.105	0.335	0.314	0.7536	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth	s(Plot)	2.708	6.000	5.411	0.0645	.

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.704, Deviance explained 0.846

-REML : -93.212, Scale est: 1.000, N: 90

Table 2.2. GAMM results for analysis of barnacle complex (*Chthamalus* & *Balanus* spp.) percent cover following the one-time disturbance treatments excluding the pre-treatment

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-1.363	0.287	-4.747	0.0000	***
	Scrape = S	-0.309	0.391	-0.789	0.4305	
	Trample = T	0.706	0.391	1.806	0.0717	.
Component	**Term**	**edf**	**Ref.**	**F-value**	**p-**	
B. smooth terms	s(Event): Control	7.461	8.384	15.653	0.0000	***
	s(Event): S	8.078	8.739	33.552	0.0000	***
	s(Event): T	1.352	1.616	0.274	0.6036	
	s(Plot)	5.865	6.000	5,933.692	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.499, Deviance explained 0.625

fREML : -68.682, Scale est: 1.000, N: 462

Table 2.3. GAMM results for analysis of barnacle complex (*Chthamalus* & *Balanus* spp.) percent cover during the last five study years

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	4.676	1.781	2.626	0.0086	**
	Scrape = S	-0.242	2.552	-0.095	0.9245	
	Trample = T	-2.729	2.548	-1.071	0.2842	
	Event	-0.099	0.033	-3.026	0.0025	**
	S: Event	0.001	0.047	0.031	0.9749	
	T: Event	0.047	0.047	0.995	0.3197	
Component	**Term**	**edf**	**Ref. df**	**F-**	**p-**	
B. smooth terms	s(Plot)	5.447	6.000	55.933	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.453, Deviance explained 0.547

-REML : -57.305, Scale est: 1.000, N: 90

Table 2.4. GAMM results for BACI analysis of turfweed (*Endocladia muricata*) percent cover prior to and one year following the one-time disturbance treatments

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	0.379	0.247	1.537	0.1242	
	Scrape = S	-3.097	0.380	-8.150	0.0000	***
	Trample = T	-0.812	0.348	-2.330	0.0198	*
	Before vs. after = B	-0.134	0.235	-0.571	0.5681	
	S × B	3.357	0.367	9.141	0.0000	***
	T × B	0.606	0.329	1.839	0.0660	.
Component	**Term**	**edf**	**Ref.**	**F-**	**p-**	
B. smooth	s(Plot)	4.682	6.000	19.997	0.0003	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.843, Deviance explained 0.889

-REML : -65.328, Scale est: 1.000, N: 72

Table 2.5. GAMM results for analysis of Turfweed (*Endocladia muricata*) percent cover following the one-time disturbance treatments excluding the pre-treatment

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-0.502	0.416	-1.206	0.2285	
	Scrape = S	-0.717	0.582	-1.231	0.2189	
	Trample = T	-0.096	0.582	-0.165	0.8691	
Component	**Term**	**edf**	**Ref.**	**F-value**	**p-**	
B. smooth terms	s(Event): Control	8.593	8.863	15.633	0.0000	***
	s(Event): S	5.704	6.720	13.972	0.0000	***
	s(Event): T	7.793	8.438	7.295	0.0000	***
	s(Plot)	5.953	6.000	1,599.676	0.0014	**

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.620, Deviance explained 0.683

fREML : -11.546, Scale est: 1.000, N: 466

Table 2.6. GAMM results for analysis of Turfweed (*Endocladia muricata*) percent cover during the last five study years

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-1.528	1.695	-0.901	0.3673	
	Scrape = S	1.552	2.547	0.609	0.5423	
	Trample = T	3.973	2.474	1.606	0.1083	
	Event	0.017	0.031	0.561	0.5745	
	S: Event	-0.041	0.046	-0.884	0.3764	
	T: Event	-0.081	0.045	-1.810	0.0703	.
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-**	
B. smooth terms	s(Plot)	5.708	6.000	109.567	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.592, Deviance explained 0.682

-REML : -65.765, Scale est: 1.000, N: 90

Table 2.7. GAMM results for BACI analysis of rockweed (*Silvetia compressa* and *Pelvetiopsis californica*) percent cover prior to and one year following the one-time disturbance treatments

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	0.978	0.282	3.474	0.0005	***
	Scrape = S	-4.832	0.430	-11.236	0.0000	***
	Trample = T	-0.950	0.396	-2.400	0.0164	*
	Before vs. after = B	0.277	0.227	1.219	0.2228	
	S × B	5.148	0.370	13.904	0.0000	***
	T × B	0.972	0.319	3.048	0.0023	**
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth	s(Plot)	5.164	6.000	47.536	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.936, Deviance explained 0.968

-REML : -132.521, Scale est: 1.000, N: 90

Table 2.8. GAMM results for analysis of rockweed (*Silvetia compressa* and *Pelvetiopsis californica*) percent cover following the one-time disturbance treatments excluding the pre-treatment

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	0.059	0.763	0.077	0.9383	
	Scrape = S	-1.994	1.071	-1.862	0.0632	.
	Trample = T	-1.174	1.070	-1.097	0.2735	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(Event): Control	8.401	8.707	26.845	0.0000	***
	s(Event): S	7.218	8.019	14.586	0.0000	***
	s(Event): T	6.600	7.509	11.541	0.0000	***
	s(Plot)	5.986	6.000	9,019.621	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.838, Deviance explained 0.877

fREML : -325.272, Scale est: 1.000, N: 466

Table 2.9. GAMM results for analysis of rockweed (*Silvetia compressa* and *Pelvetiopsis californica*) percent cover during the last five study years

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	7.671	3.199	2.398	0.0165	*
	Scrape = S	-7.826	4.358	-1.796	0.0726	.
	Trample = T	-2.680	4.435	-0.604	0.5456	
	Event	-0.201	0.059	-3.423	0.0006	***
	S: Event	0.155	0.080	1.941	0.0522	.
	T: Event	0.056	0.081	0.692	0.4888	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(Plot)	5.613	6.000	101.968	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.450, Deviance explained 0.694

-REML : -226.648, Scale est: 1.000, N: 90

Table 2.10. GAMM results for BACI analysis of California mussel (*Mytilus californianus*) percent cover prior to and one year following the one-time disturbance treatments

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-0.173	0.322	-0.538	0.5908	
	Scrape = S	-4.389	0.499	-8.791	0.0000	***
	Trample = T	-0.473	0.456	-1.037	0.2997	
	Before vs. after = B	0.160	0.157	1.018	0.3085	
	S × B	3.593	0.307	11.715	0.0000	***
	T × B	0.217	0.225	0.961	0.3368	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth	s(Plot)	5.538	6.000	78.149	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.902, Deviance explained 0.969

-REML : -118.105, Scale est: 1.000, N: 71

Table 2.11. GAMM results for analysis of California mussel (*Mytilus californianus*) percent cover following the one-time disturbance treatments excluding the pre-treatment

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-0.563	0.383	-1.468	0.1427	
	Scrape = S	-1.154	0.540	-2.138	0.0331	*
	Trample = T	-0.335	0.541	-0.619	0.5363	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(Event): Control	6.054	7.129	9.029	0.0000	***
	s(Event): S	5.912	6.980	37.658	0.0000	***
	s(Event): T	6.017	7.143	9.142	0.0000	***
	s(Plot)	5.966	6.000	25,496.320	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.782, Deviance explained 0.842

fREML : -155.651, Scale est: 1.000, N: 466

Table 2.12. GAMM results for analysis of California mussel (*Mytilus californianus*) percent cover during the last five study years

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	2.282	1.532	1.490	0.1363	
	Scrape = S	0.377	2.163	0.174	0.8618	
	Trample = T	0.652	2.169	0.301	0.7637	
	Event	-0.050	0.028	-1.812	0.0700	.
	S: Event	-0.013	0.039	-0.325	0.7453	
	T: Event	-0.014	0.039	-0.363	0.7166	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(Plot)	5.732	6.000	129.251	0.0000	***

Signif. codes: 0 <= *** < 0.001 < ** < 0.01 < * < 0.05

Adjusted R-squared: 0.654, Deviance explained 0.682

-REML : -65.439, Scale est: 1.000, N: 90

Ecological Restoration Using Intertidal Foundation Species: Considerations and Potential for Rockweed Restoration

Introduction

Ecosystems are often characterized by conspicuous organisms referred to as foundation species (*sensu* Dayton, 1972) that support biodiversity, enhance ecosystem function and stability, and often are culturally valuable. In terrestrial ecosystems, foundation species range in scale from large canopy-forming trees to diminutive grasses. Similarly, marine habitats support a wide spectrum of species that structure communities, including kelps, mangroves, corals, seagrasses, mussels, and oysters. Fundamentally, the influence foundation species have on ecosystems is commensurate with their overall abundance; declines in the abundances of foundation species can have cascading detrimental effects at population and community levels (Ellison et al., 2005, 2019). For example, the precipitous decline of shade-tolerant eastern hemlock trees in North America resulted in significant reductions in aquatic invertebrates as well as declines in sediment retention and productivity in streams (Ellison et al., 2005, Degrassi et al., 2015).

Rocky intertidal foundation species, such as mussels, barnacles, and seaweeds, are common in temperate regions and provide three-dimensional habitat required by other species to survive. Rockweeds, a group of conspicuous brown seaweeds (Phaeophyceae) in the Order Fucales (Fucoids), are often the dominant macroalgae in temperate intertidal and shallow subtidal rocky habitats (Figure 3.1). Ecologically, the importance of these seaweeds in regulating ecosystem functioning and facilitating high biodiversity is well recognized, and rockweeds are increasingly being used as indicator species to assess the status of rocky intertidal ecosystems for management purposes (e.g., Maki, 1991; Orlando-Bonaca et al., 2008; Murray et al., 2016). Economically, rockweeds are valuable as commercially harvested species (Lotze et al., 2019), and they provide important ecological services supporting commercially harvested taxa, including refuge for lobster (Schmidt et al., 2011) and nursery habitat for fish (Gullo, 2002; Vercaemer et al., 2018).

Rockweed populations, like many other species considered foundational to ecosystems, have sustained extensive degeneration and range contractions worldwide (e.g., Wernberg et al., 2011; Nicastro et al., 2013). For example, the southern range edge for the rockweed *Fucus vesiculosus* has shifted northward 1,250 km from Morocco to Portugal (Nicastro et al., 2013), and the species has declined in distribution by more than 95% in the Baltic Sea (Torn et al., 2006). Globally, the causes of population declines are not well known, can result from complex interactions of multiple sources of stressors, and vary greatly among geographic locations and species. Rockweeds are known to be sensitive to both natural and anthropogenic perturbations, including severe storms (Underwood, 1998), ice scour (McCook and Chapman, 1991, 1997), pollution (Bellgrove et al., 1997), trampling (Bertocci et al., 2011), and climate change (Alvarez-Losada et al., 2020).

The decline of rockweed populations, as well as the positive effects that rockweeds have on the biological communities they inhabit, have motivated efforts to conserve remaining populations and to reestablish or enhance depleted ones (e.g., Stekoll and Deysher, 1996; Whitaker, 2009; Whitaker et al., 2010; Coleman and Wernberg, 2017). However, successful reestablishment of depleted populations requires understanding the factors that affect survival of the species along with rigorous scientific testing of outplanting methods. An understanding of community structure, including biotic interactions, is also helpful to ensure restoration is effective (Underwood, 1996). Here, I will (1) explain why rockweeds are prime subjects for restoration, (2) summarize published evidence of changes in rockweed populations, (3) identify and discuss the factors limiting population recovery, and (4) review past restoration activities and provide recommendations for future ecological restoration efforts.

Rockweeds as Foundation Species

Rockweeds play a strong role in the structuring of communities via provision of habitat and modifications to the environment (Bellgrove et al., 2017). The three-dimensional rockweed canopy provides a complex matrix of microhabitats, increasing niche availability for a high diversity of taxa (e.g., Johnson and Scheibling, 1987; Hily and Jean, 1997; Bertness et al., 1999; Fredriksen et al., 2005; Schiel and Lilley, 2011). Different sets of species can be found living in the understory of the rockweed canopy, as epiphytes attached to the rockweeds, along the edge of canopy limits, and as mobile organisms freely moving through a rockweed bed (Figure 3.2). Rockweed canopies modify both abiotic and biotic conditions, either directly, by providing shelter or reducing environmental stress, or indirectly, by altering biotic interactions (e.g., Bertness et al., 1999; Beermann et al., 2013; Watt and Scrosati, 2013a, 2013b; Scrosati, 2017; Scrosati and Ellrich, 2018). Alterations to the environment can have both positive and negative effects on associated species but, generally, rockweed facilitates the presence of long-lived taxa over opportunistic species, thereby increasing community stability, resiliency, and diversity (e.g., Jenkins et al., 1999; Lilley and Schiel, 2006; Eriksson, 2007).

Modifications to the physical environment by rockweed canopies include a reduction in the rate of evaporation and temperature change during emersion periods (Watt and Scrosati, 2013a, 2013b; Scrosati, 2017; Scrosati and Ellrich, 2018; Scrosati et al. 2021), light attenuation, and slowing of water flow. For instance, during warm periods at low tide, air temperature can be 5-16 °C lower under the rockweed canopy compared to exposed rock surfaces (Brawley and Johnson, 1991; Bertness et al., 1999; Beermann et al., 2013). Similarly, evaporation rates underneath the canopy during low tides can be significantly lower than rates on the open rock (Brawley and Johnson, 1991, 1993; Bertness et al., 1999; Beermann et al., 2013). For example, in the high intertidal zone, Bertness et al. (1999) found that water loss during emersion was nearly 60% outside the canopy while only ~5% underneath the canopy. The refuge from thermal stress and desiccation provided by rockweeds is particularly important since these are important factors affecting the ability of organisms to survive in harsh intertidal ecosystems.

Because of the canopy structure and modifications to the environment that rockweed beds provide, they harbor a biologically diverse community of epifaunal and understory species (Colman, 1940; Hawkins and Hartnoll, 1983; Lubchenco, 1983; Gunnill, 1985; Johnson and Scheibling, 1987; Thompson et al., 1996; Hily and Jean, 1997; Bertness et al., 1999; Sapper and Murray, 2003; Jenkins et al., 2004; Fredriksen et al., 2005; Eriksson et al., 2006; Lilley and Schiel, 2006; Schiel and Lilley, 2011). In England, for example, Colman (1940) identified 177 invertebrate species under the canopies provided by three species of *Fucus*. *Silvetia* beds in southern California, USA, had 47 species of algae, 20 sessile invertebrates, and 44 mobile invertebrate species for a total of 107 taxa living under the frond canopy (Sapper and Murray, 2003). In comparison, communities associated with another well-documented ecosystem engineer, the mussel *Mytilus californianus* on the eastern north Pacific coast, harbor a similar level of diversity with a range of 80-120 species found within a mussel bed within a site (Kanter, 1977, 1978, 1979; Straughan and Kanter, 1977).

Rockweeds can also be important for many other taxa, including macroinvertebrates and fish that use the habitat for shorter periods of time, and birds that feed on the invertebrates found within the canopy (Hamilton, 2001; Hamilton and Nudds, 2003). For example, crabs, lobsters (Schmidt et al., 2011; Phillippi et al., 2014; Vercaemer et al., 2018), and many fishes, including some of commercial value (Rangeley and Kramer, 1995; Gullo, 2002; Vercaemer et al., 2018; Gagnon et al., 2019; Mattsson, 2019), utilize rockweed beds as feeding areas or nursery habitat. .

In addition to providing habitat for the organisms that live in the understory, rockweed canopies often facilitate the recruitment of a diversity of taxa (Bertness et al., 1999; Jenkins et al., 2004), including conspecifics (Vadas et al., 1990; Brawley and Johnson, 1991; Bertness and Leonard, 1997; van Tamelen et al., 1997; Moeller, 2002; Philbrick, 2004). Recruitment, a process vital to population maintenance and long-term persistence, is typically enhanced in the presence of rockweed canopy cover because desiccation and thermal stress are reduced during periods of emersion compared to bare rock surfaces (Vadas et al., 2004; Beermann et al., 2013). During periods of immersion, the frond canopy formed by rockweeds slows water flow, which allows for gametes or larvae to settle (Dayton, 1971).

Rockweeds are also large contributors to intertidal and coastal food webs. Productivity of fucoids is considerably higher than many other primary producers, especially in the intertidal zone (Golléty et al., 2008; Tait and Schiel, 2010; Tait et al., 2014; Bordeyne et al., 2015). For example, in France, Bordeyne et al. (2015) found that *Fucus* beds accounted for 77-97% of carbon dioxide flux, with gross primary productivity being 7-9 times higher than that measured in eelgrass (*Zostera nolteii*) communities (Ouisse et al., 2010) and up to 44 times higher than soft bottom habitats (Migné et al., 2004) or sandy beach communities

(Hubas et al., 2006). This fucoid production forms the base of many food webs (Moore, 1977; Bertness and Leonard, 1997; Lubchenco, 1983; Jenkins et al., 2004), providing food for numerous grazers, including amphipods (Moore, 1977), isopods, decapods, littorine snails (Bertness and Leonard, 1997; Lubchenco, 1983), turban snails (Steinberg, 1985), and limpets (Hawkins et al., 2008; Jenkins et al., 2004). Feeding studies confirm that grazers consume rockweeds, including *Fucus* and *Silvetia* (Steinberg, 1985; Kubanek et al., 2004); Steinberg (1985) observed that gastropods, including turban snails and periwinkle snails that commonly seek refuge in rockweed canopies, consistently preferred feeding on brown algae, including *Silvetia*, over red algal species.

Given their high productivity rates and relatively high biomass turnover, 40-70% annually (Vadas et al., 2004; Schmidt et al., 2011), rockweeds are also major contributors to detrital pools (Bishop et al., 2010; Golléty, et al. 2010; Renaud et al., 2015), providing carbon for detrital consumers. Rockweed detrital contributions are not only important within the rockweed habitat, but cross-boundary transport can export production into nearby habitats as well. For example, up to 82% of macrophyte (primarily rockweed) production was exported outside of the intertidal zone in a Canadian Bay (Vadas et al., 2004).

Rockweed declines

Fucoids are declining locally and regionally on temperate rocky shores in the northern hemisphere (Davies et al., 2007; Strain et al., 2014; Wahl et al., 2015). There is also evidence of range contractions (Nicastro et al., 2013; Duarte et al., 2013) and localized extinctions (Viejo et al., 2011; Martinez et al., 2012; Lamela-Silvarrey et al., 2012; Duarte et al., 2013; Fernández, 2016; Fales and Smith, 2022) of rockweeds in multiple regions. Large declines in subtidal fucoids such as *Sargassaceae* have also been documented (reviewed by Falace et al., 2010).

In a thorough literature search on changes in populations of true rockweeds in the family Fucaceae, many examples of local extinctions, range shifts, and population declines were identified (Table 3.1). Multiple searches were conducted across several databases, including Web of Science, ProQuest, and Google Scholar, to find literature pertaining to long-term population declines in the family Fucaceae. Search terms included "rockweed, fucoid, *Ascophyllum, Fucus, Pelvetia, Pelvetiopsis, Silvetia*" AND "change, declines, and population decline", among other key terms. Though targeted searches were performed for studies reporting stability or increases in fucoid populations, fewer examples were found, which in part may be due to publication bias (Table S3.1). Studies that fit the inclusion criteria are included in Table 3.1, categorized by species, region, and the hypothesized driver of change, if described. Most of the studies did not experimentally or quantitatively evaluate the cause of declines or local extinctions but rather qualitatively discussed the likely drivers or causes of change. Nevertheless, these insights may help focus future analyses and experiments.

The causes of declines in rockweed populations varied across regions and time (Table 3.1). Eutrophication or decreased water quality in the Baltic Sea played a role in many subtidal rockweed declines documented in the 1980s, while climate change or extreme climate events and stressors from multiple sources were more frequently associated with declines in the 1990s and onward, particularly in the northeast Pacific and Atlantic. Most of the discussed causes of rockweed declines were anthropogenic in origin, including climate change, water quality, habitat loss, and introduced species, with the exception of increased herbivory documented in the Mediterranean, northeast Atlantic, and the Baltic Sea (Table 3.1). Unfortunately, very few studies evaluated the mechanisms driving these declines, so further work is needed to disentangle the complex causes of declines globally.

Factors Affecting Populations and Limiting Recovery

Fucoid functioning and fitness are influenced by numerous natural and anthropogenic stressors (e.g., Schiel and Foster, 2006; Wahl et al., 2015 and references therein). Natural abiotic stressors include low (Pearson and Davison, 1993, 1994) and high (Bell 1993, Kübler and Davison, 1993) air temperature, decreased humidity (Brawley and Johnson 1991), variations in nutrient supply (Korpinen et al. 2010), irradiance (Schonbeck and Norton, 1980; Martinez et al., 2012) and osmotic shock, and extremes in sea temperature, wave energy and nutrients (Pielou 1981; Vadas et al. 1990). Human-caused stressors include urbanization (Coleman and Wernberg, 2017), eutrophication (Bellgrove et al., 1997), trampling (Keough and Quinn 1998; Schiel and Taylor 1999; Denis, 2003; Irvine, 2005; Araújo et al., 2009; Bertocci et al., 2011), coastal sedimentation (Schiel et al., 2006), petroleum spills (Crowe et al., 2000), harvesting (Boaden and Dring, 1980), invasive species (Sutherland et al., 2014), and climate change (Sagarin et al., 1999; Keser et al., 2005). Individually, each of these abiotic drivers impose serious impacts to fucoids. Collectively, the effects are likely to be synergistically detrimental (Hurd et al., 2014).

Rockweeds lack the ability to reliably disperse long distances, which affects the ability of their populations to recover following declines. Dispersal of rockweeds is mostly limited to the movement of early life stages, including propagules and zygotes (Schiel and Foster, 2006), and is generally low, since the propagules are relatively large, released near the substratum (Johnson and Brawley, 1998; Dudgeon et al., 2001; Hays, 2006), and adhere to the substratum with a polyphenolic adhesive shortly after fertilization (Vreeland et al., 1993). For some species, the distance spores are capable of traveling is further reduced by the thick mucilage that surrounds them and slows their movement (Pearson and Brawley, 1996). Their propensity to time gamete release to periods of calm environmental conditions, such as low tide or low water motion, putatively sensed via carbon acquisition (Pearson et al., 1998), also limits dispersal in fucoids (Pearson and Brawley, 1996). Dispersal distance can vary among different rockweed taxa but is generally less than 30 m (Chapman, 1995), and more often less than 10 m (Serrao et al., 1996; Williams and Di Fiori, 1996). For example, propagules of the rockweed *Ascophyllum nodosum* can disperse up to 6 m from the parent source (Dudgeon et al., 2001) while *Silvetia compressa* recruits typically within <3 m, but mostly less than 1 m from the parent (Williams and Di Fiori, 1996). Longer distance dispersal is possible from drifting of detached reproductive fronds and is common for species in the families Sargassaceae (Fucales) that are neutral or positively buoyant due to floating pneumatocysts (Deysher and Norton, 1981; Norton and Mathieson, 1983; Schiel, 1985; Chapman, 1995; Hawes et al., 2017). The importance of drifting as a dispersal method for other taxa, including rockweeds, has been hypothesized, but strong evidence is lacking (McKenzie and Bellgrove, 2009).

Rockweed recovery can also be inhibited or slowed due to temporal and spatial limitations in settlement and recruitment. Rockweeds typically are reproductive during relatively short periods during specific seasons and, although they tend to be highly reproductive with very high fertilization rates (>95%; Brawley, 1992; Pearson and Brawley, 1996), early post-settlement (EPS) life stages have extremely high mortality rates (e.g., McLachlan, 1974; Gunnill, 1980; Chapman and Johnson, 1990; Brawley and Johnson, 1991;

Vadas et al., 1992; Johnson and Brawley, 1998; Moeller, 2002). For example, Moeller (2002) found that EPS mortality during peak egg production was more than 99.99%. Lamote and Johnson (2008) found the density of recruits from three rockweed species to be exponentially higher under the canopy during all three years of their study while Moeller (2002) found peak egg production for *Silvetia* to be markedly higher underneath the canopy than areas outside the rockweed bed. EPS mortality due to desiccation is particularly high when the rockweed canopy is limited in extent or absent (Johnson and Brawley, 1998; Moeller, 2002; Lamote and Johson, 2008). At the same time, EPS survival is reduced under the rockweed canopy due to mechanical dislodgement caused by the sweeping motion of fronds (Johnson and Brawley, 1998). For example, Johnson and Brawley (1998), observed settlement of EPS *Silvetia* recruits to be 1-2 orders of magnitude greater under the adult canopy, yet juveniles were most abundant outside of the canopy.

As a result of short distance dispersal and temporal and spatial constraints on successful recruitment, recovery of fucoids is highly variable following disturbances (Jenkins et al., 1999, 2004; Underwood, 1998, 1999; Bellgrove et al., 2017). Recovery time can also be affected by numerous other factors, including the intensity and frequency of perturbations, the size of the area disturbed, or proportion of the population removed, and the timing and frequency of disturbance (Sousa, 1979, 1984; Paine and Levin, 1981; Farrell, 1989; Kim and DeWreede, 1996; Foster et al., 2003; Bertocci et al., 2005). Frequent disturbances can inhibit fucoid recovery because a large population with a contiguous canopy can never form as individuals are being repetitively removed over time. The timing of the disturbance can also be important, depending on, for example, whether recovery of a disturbed area occurs during optimal environmental conditions or when fucoids are in peak reproductive periods (Kim and

DeWreede, 1996; Kim et al., 2017). In the Gulf of Maine, disturbance timing has been proposed to determine whether a fucoid-dominated system can recover or shift to an alternative stable state dominated by mussels and barnacles (Petraitis and Dudgeon, 1999, but see Bertness et al., 2002). An alternative stable state can also be induced by the severity of the disturbance, such as a stable *Ascophyllum*-dominated community shifting to a stable *Fucus*-dominated community when a large area of *Ascophyllum* has been manually removed (Menge et al., 2017).

Recovery times for fucoids are further complicated by alterations in biotic interactions as a consequence of the disturbance itself or due to indirect, cascading effects from the removal of the canopy-forming rockweed (e.g., Kim, 1997). For example, canopy removal and resulting decreased whiplash can result in an increase in barnacle recruitment and space occupancy, inhibiting subsequent recruitment of fucoids (Kordas and Dudgeon, 2009). In another study, removal of an *Ascophyllum nodosum* canopy resulted in a cascade of events that inhibited the rockweed from fully recovering more than 12 years after removal (Jenkins et al., 1999, 2004). Without the protection of the *Ascophyllum* frond canopy from desiccation stress, understory turf-forming seaweeds disappeared, which resulted in an increase in limpets that grazed down subsequent rockweed recruits and other seaweeds within which rockweeds settle (Jenkins et al., 1999).

Restoration

Restoration ecology is a relatively new discipline, which may be why it is inherently expensive and associated with somewhat high uncertainty of success and feasibility. This is particularly true for marine restoration which, in comparison to terrestrial systems, is still in its infancy (De Groot et al., 2013; Bayraktarov et al., 2016). Comparably few studies involve marine restoration (Benayas et al., 2009; Blignaut et al., 2013), even though these systems have often been heavily urbanized and degraded (Halpern et al., 2008). For example, in a sample of 224 ecological restoration studies published from 2004-2013, marine habitats were the least represented (~15%) relative to terrestrial and freshwater environments (Kollmann et al., 2016). While restoration can be expensive, the cost of restoration is not necessarily correlated with success. Bayraktarov et al. (2016) found the most successful restoration efforts to be highly contingent upon ecosystem type, site selection, and techniques applied rather than cost. Despite costs and variable levels of success, restoration ecology has strong potential to be a promising tool for repairing degraded ecosystems, particularly as ecological theory evolves and is used more consistently to inform restoration practices (Peterson et al., 2003). Opportunities for practicing restoration will undoubtedly continue through legally mandated responses to impacts on natural resources (e.g., CERCLA, 1980; OPA, 1990).

To date, a substantial amount of marine restoration studies has focused on a few select taxa, such as seagrasses, corals, oysters, and kelp, all considered to be ecosystem engineers. Notably rare, however, are studies on restoration of other ecologically important, canopy-forming macroalgal engineers, such as rockweeds. Certainly, the marked global decline of fucoid algae (Vogt and Schramm, 1991; Wahl et al., 2015; Piñeiro-Corbeira et al., 2016) and their influence on community structure has spurred an increased urgency in developing strategies to halt and reverse their loss. Thus far, fucoid restoration has predominantly focused on non-rockweed, subtidal taxa, such as *Sargassum* and *Cystoseira* (Perkol-Finkel et al., 2012; Campbell et al., 2014; Yoon et al., 2014; de la Fuente et al., 2019; Lardi et al., 2022); only a handful of studies have focused on the restoration of intertidal rockweeds in the family Fucaceae (e.g., Stekoll and Deysher, 1996; Jonsson et al., 2006; Whitaker et al., 2010; Gao et al., 2017; Kautsky et al., 2019; Tronske, 2020).

To reverse losses of fucoids, a wide range of human-mediated actions have been applied with variable levels of success, including passive restoration approaches that involve removing the source of the impact. However, the causes of declines are often unclear or multifactorial (Piñeiro-Corbeira et al., 2016). In cases where the causes of fucoid losses are known, there is some support for the efficacy of passive restoration. For example, in the Baltic Sea, where large declines in subtidal rockweeds were caused by eutrophication (Kautsky et al., 1986; Vogt and Schramm, 1991; Torn et al., 2006), substantial recovery has occurred following reductions in nutrient loads (Eriksson et al., 1998; Nilsson et al., 2004). However, in other regions where water quality has improved, recovery of fucoid populations has failed to occur (Soltan et al., 2001; Coleman et al. 2008; Díez et al., 2009), potentially due to low standing stock or other discussed processes limiting rockweed resilience. In harvested rockweed populations, the implementation of sustainable management strategies, including equipment regulations, harvest limits, maximum cutting heights, and longer periods between harvests, has resulted in reduced impacts (Ugarte and Sharp, 2001; Gendron et al., 2018).

In cases where rockweeds have failed to recover naturally, active restoration techniques have been applied, consisting primarily of transplantation of individuals from the wild, cultivating outplants, constructing artificial habitat or substrate, and seeding with fertile branches or propagules (Campbell et al., 2014; de la Fuente et al., 2019; Kautsky et al., 2019). Transplantation of whole individuals or thalli, in particular, has been relatively successful (Figure 3.3). For example, Gao et al. (2017) attributed the recruitment of ~1000 rockweed individuals to a transplant method they applied involving the attachment of fertile rockweed thalli to polyethylene rope which, in turn, was affixed to the substratum. Experimental transplantation of *Silvetia compressa* by chipping off rock pieces with rockweeds attached from donor sites and affixing the rock to the substrate at restoration sites using marine epoxy resulted in survival as high as ~60% (Whitaker et al. 2010, Tronske 2020). Success was particularly high when transplants were placed on sloped surfaces protected from direct sunlight and trampling by visitors. More than a decade later, at a site where rockweed had become locally extinct for well over two decades, and despite only <70 rockweed thalli being transplanted (Whitaker et al., 2010), the small population has expanded in 2022 to include well over a thousand individuals (Figure 3.4). More recent efforts by the authors to outplant *Silvetia* at several locations have shown early success with high survivorship (>75% after ~4 months) and subsequent recruitment of new individuals.

Some rockweed restoration studies have utilized seeding, construction of artificial substrates, or a combination of these techniques to stimulate or enhance recruitment of rockweeds. Whitaker (2009) collected fertile receptacles of *Silvetia* and affixed them to the substrate in mesh containers, while Stekoll and Deysher (1996) attached entire fertile *Fucus gardneri* individuals to erosion control netting and inoculated the plots with a solution of zygotes. More recently, the authors have preliminarily tested attaching fertile branches to the substrate, stimulating gamete release in the field, and outplanting of discs with germlings from laboratory gamete release. Though these studies found that seeding techniques were unsuccessful, similar approaches have been found to be successful for other Fucales that are predominantly subtidal, such as *Cystoseira* (Verdura et al., 2018) and *Sargassum* (Yu et al., 2012). Although Stekoll and Deysher (1996) were unable to enhance recruitment via seeding erosion control netting, they observed that moisture retention facilitated by the netting may have enhanced recruitment of zygotes from the surrounding *Fucus* population. In a factorial field experiment, Whitaker et al. (2010) found that the presence of artificial canopy significantly enhanced survival of *Silvetia* transplants.

The deployment of artificial substrates or structures that mimic the positive effect of a rockweed canopy by reducing desiccation and facilitating natural recruitment warrants further exploration. Studies employing the use of artificial substrate for restoration of fucoids have primarily been conducted on subtidal species, but the techniques utilized may also be applicable to rockweed restoration. These studies have largely focused on cultivating germlings onto artificial substrates *in vitro*, then outplanting the substrate into the wild. For instance, Chai et al. (2014) cultured *Sargassum* germlings *in vitro* onto “breeding boards” that were then mounted on concrete blocks and placed at the restoration site. The germlings survived and, after one year, had grown to an average length of ~15 cm. Growth of *Gongolaria* germlings in laboratory conditions also showed promise for use in restoration efforts (Lardi et al., 2022), though outplanting of germlings has not been tested. A similar technique could potentially be utilized in rockweed restoration by cultivating rockweed germlings *in vitro* onto artificial substrates such as ceramic tiles or epoxy discs, which may then be affixed to the reef with bolts or marine epoxy. Early efforts by the authors show that *Silvetia* can be stimulated to release gametes with germlings settling on discs in the laboratory but germlings on outplanted discs have not survived. Several additional studies have utilized *in vitro* propagation of fucoids onto artificial substrates with varying levels of success (Yoon et al. 2014, Yatsuya 2010, Terawaki et al., 2003 and references therein, Leung et al., 2014, De La Fuente et al, 2019, Choi et al., 2003, Falace et al., 2006, Verdura et al., 2018, Kautsky et al., 2019).

Continued exploration of restoration techniques for rockweeds is needed, particularly with the use of seeding and lab cultivations. Though, as previously discussed, transplanting entire thalli has been one of the more successful techniques implemented in rockweed restoration, it also has a potential impact on the donor population. This is a particularly important consideration for those species that have experienced steep population declines and have limited distribution. Seeding and outplanting techniques limit the amount of material harvested from the donor population, as fertile receptacles (Whitaker, 2009), branches (Verdura et al., 2018), or even drift material (Yatsuya, 2010) can be collected and used to propagate individuals *in vitro* or be placed at a restoration site to establish a source of propagules that may facilitate natural recruitment.

Conclusions and Recommendations

Fucoid declines are predicted to increase in frequency and intensity in the future, with rising temperatures accompanying climate change (Keser et al., 2005; Wilson et al., 2015; Kay et al., 2016; Takolander et al., 2017; Rugiu et al., 2018). Recovery of damaged rockweed populations is slow and unpredictable (Hill 1980, Vesco and Gillard 1980) since dispersal is limited and early life stages experience extreme mortality (Moeller 2002). Recovery is particularly limited when perturbations result in low abundances or local extirpations because of insufficient adult sources for recruitment and reestablishment. Assisted recovery can facilitate a return to stable populations, particularly for those populations with low abundances whose inhibited recovery may otherwise result in continued declines and eventual extirpation. Because they are foundational species, rockweed recovery can increase the biodiversity of the entire rocky intertidal ecosystem dependent on them. For these reasons, rockweeds are optimal candidates for restoration. While restoration in rocky intertidal habitats is in its infancy, with very few examples of tested approaches, some methods for successfully restoring rockweeds have been identified through rigorous empirical testing (Whitaker et al. 2010, Gao et al. 2017).

Scaling up rockweed restoration remains a central challenge. While some work has been done in support of this goal (e.g., seeding and cultivation), these studies were largely unsuccessful (e.g., Stekoll and Deysher 1996, Whitaker et al. 2010). Cultivation techniques for rockweeds have been developed (e.g., Pearson et al., 1998), but extremely high levels of mortality for early life stages of rockweed species requires vast numbers of propagules or cultivation to larger sizes to enable successful restoration. More research and development are needed to effectively cultivate rockweed to stages that are resistant to mortality, in large enough numbers to use in restoration projects.

In the face of climate change, relying on historical reference states as a target for restoration may be ineffective, if the changing climate is a major factor contributing to habitat degradation and species decline. Current regulatory frameworks understandably emphasize conserving essential species within their indigenous range, and the concept of assisted migration, also known as managed relocation (Richardson et al., 2009) or assisted colonization (Hällfors et al., 2014), is controversial. For restoration to be successful in a rapidly changing climate, nevertheless, the specific environmental requirements of individual species and the possible impacts of such management actions should be seriously considered (Harris et al., 2006).

Rocky intertidal ecosystems have tremendous value through the provision of significant economic benefits for tourism, fisheries, and real estate, vital ecosystem services, such as shoreline stabilization and protection, and a rich environment for education, research, and recreation. As a result, rocky shores have long had great cultural and historical significance, including for tribal nations. However, rocky intertidal ecosystems are vulnerable to impacts of human activities, such as urbanization (Vogt and Schramm 1991), overexploitation (Harley and Rogers-Bennet, 2004), pollution (Kangas et al. 1982, Mäkinen et al. 1984, Kautsky et al. 1986, Kukk and Martin 1992, Eriksson et al. 1998, Middelboe and Sand-Jensen 2000, Eriksson et al. 2002, Nilsson et al. 2004, Torn et al. 2006), and climate change (e.g., Barry et al. 1995, Sagarin et al. 1999). Many rocky shore ecosystems, particularly near urban centers, are already degraded, and that trend will continue as coastal development progresses. Thus, effective and quantifiable restoration is needed to maintain habitat health and resilience, as well as the valuable services that rocky intertidal ecosystems provide. Restoring key foundation species, such as rockweeds, is an efficient way to achieve broader benefits to ecosystem integrity. It is critically necessary to identify effective methods for restoring rocky intertidal communities at meaningful spatial scales to counter future large- and small-scale impacts to this ecologically important and valuable marine ecosystem. Restoring foundational rockweeds and their associated communities is one of them and will help buffer against the impacts of climate change and other catastrophic events in the future as well as prevent larger-scale losses of intertidal communities.

Table 3.1. Studies observing population changes of multiple species of rockweed from four regions and the discussed causes of change. The discussed causes of changes are indicated by: I. Herbivory, II. Climate change, III. Water quality, pollution, oil spill, IV. Habitat loss, V. Introduced species, VI. Other impacts

Species	Type of change	Discussed causes of change						Studies
		I	II	III	IV	V	VI	
Northeast Pacific								
Silvetia compressa	Decline		X	X				Barry et al. 1995, Gerrard 2005, Goodson 2003, Graham et al. 2018, Sagarin et al. 1999, Whitaker et al. *in prep*, Widdowson 1971
Pelvetiopsis californica	Decline Local extinctions		X				X	Fales and Smith 2022, Thom and Widdowson 1978
Fucus distichus	Decline		X	X				Barry et al. 1995, Driskell et al. 2001, Weitzman et al. 2021
Northeast Atlantic								
Ascophyllum nodosum	Decline	X	X					Davies et al. 2007
Fucus guiryi	Decline Local extinctions Range change		X					Riera et al. 2015
Fucus serratus	Decline Range change	X	X					Álvarez-Losada et al. 2020, Duarte et al. 2013, Fernández 2016, Reichert and Buchholz 2006
Fucus spiralis	Decline Local extinctions	X	X					Lamela-Silvarrey et al. 2012
Fucus vesiculosus	Decline	X	X					Fernández 2016, Lamela-Silvarrey et al. 2012, Piñeiro-Corbeira et al. 2016
Pelvetia canaliculata	Decline Local extinctions	X	X					Lamela-Silvarrey et al. 2012
Baltic Sea								
Fucus serratus/spp.	Decline	X		X	X			Eriksson et al. 2002, Nilsson et al. 2004, Vogt and Schramm 1991
Fucus vesiculosus	Decline			X				Eriksson et al. 1998, Kangas et al. 1982, Kautsky et al. 1986, Kukk and Martin 1992, Mäkinen et al. 1984, Middelboe and Sand-Jensen 2000, Torn et al. 2006
Mediterranean								
Fucus virsoides	Decline	X		X	X	X		Battelli 2016, Munda 1982, Munda 1993, Rindi et al. 2020

Figure 3.1. Rockweeds are often the dominant seaweed in temperate rocky intertidal ecosystems.

Left, the rockweed *Silvetia compressa* in the upper intertidal zone on the Channel Islands, California (photo S. Whitaker 2021). Right, *Fucus distichus* covers most of the mid and upper intertidal gradient on Calvert Island in British Columbia, Canada (photo L. Anderson 2012)

Figure 3.2. The canopy provided by rockweed supports a diverse assemblage of rocky intertidal taxa at the California Channel Islands.
(photo M. Ready 2022)

Figure 3.3. Rockweed transplant being attached via marine epoxy. (photo M. Ready 2022)

Figure 3.4. ***Silvetia compressa*** **at Little Corona del Mar in Newport Beach, CA 14 years after restoration.**
(photo J. Smith 2021)

Table S3.1. Results of literature search on population declines, range shifts, and stability in the Fucales, including methods and the suggested drivers of change

Author, Year	Title	Fucoid Species	Methods	Initial Timeframe	Study Timeframe	Type of Change	Suggested Specific Drivers	Region
Álvarez-Losada et al. 2020	A regime shift in intertidal assemblages triggered by loss of algal canopies: A multidecadal survey	*Fucus serratus*	surveyed percent cover of algae and sessile invertebrates	n/a	1990's-2018	decline	climate change: increased air temperatures, reduced nutrient availability, increased grazing	Europe Atlantic
Barry et al. 1995	Climate-Related, Long-Term Faunal Changes in a California Rocky Intertidal Community	*Fucus distichus, Silvetia compressa*	compared to historical data	1930	1990s	decline	climate change	US West Coast
Battelli 2016	Disappearance of *Fucus virsoides* J. Agardh from the Slovenian coast (Gulf of Trieste, Northern Adriatic)	*Fucus virsoides*	compared current surveys to historical literature and herbarium specimens	1856	2010-2015	decline	increase in density of limpet grazers	Mediterranean
Benedetti-Cecchi et al. 2001	Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores	*Cystoseira spp.*	compared Cystoseira abundance in pristine and urbanized areas	n/a	1996-1999	local extinction	anthropogenic disturbance/urbanization	Mediterranean

Bianchi et al. 2014	Thirty years after: dramatic change in the coastal marine habitats of Kos Island (Greece), 1981-2013	*Cystoseira brachycarpa, C. corniculata, C. crinita, C. foeniculacea, Sargassum vulgare*	conducted diving surveys of sites studied in 1981 using the same methods and personnel	1981	2013	*Cystoseira* spp.: decline and local extinction, *Sargassum* spp.: local extinction	increasing SST's, anthropogenic impacts, invasive species	Mediterranean
Bianchi et al. 2014	Thirty years after: dramatic change in the coastal marine habitats of Kos Island (Greece), 1981-2013	*Cystoseira barbata*	conducted diving surveys of sites studied in 1981 using the same methods and personnel	1981	2013	increase	none given	Mediterranean
Blanfuné et al. 2016	The fate of *Cystoseira crinita,* a forest-forming Fucale (Phaeophyceae, Stramenopiles), in France (North Western Mediterranean Sea)	*Cystoseira crinita*	Compared field surveys to historical literature, reports, and herbarium specimens	1700	2010-2016	decline and local extinction	primarily grazing and/or habitat destruction	Mediterranean
Blanfuné et al. 2019	The ups and downs of a canopy-forming seaweed over a span of more than one century	*Cystoseira mediterranea*	compared current abundances observed in the field to published and unpublished data, as well as herbarium vouchers	1817	2007, 2012	southern pop.: decline followed by partial recovery; northern pop.: local extinction	multiple factors: habitat destruction, pollution, an invasive mussel, heat waves, and a severe storm. The increase in severe storms after 2007 cleared space in the invasive mussel bed, allowing the southern *Cystoseira* population to partially recover.	Mediterranean

Catra et al. 2019	Degradation of a photophilic algal community and its associated fauna from eastern Sicily (Mediterranean Sea)	*Cystoseira brachycarpa*	compared SCUBA surveys to historical abundances, analyzed algal and invertebrate community structure, as well as invertebrate associations with algae	1994	2015-2016	local extinction	increased water turbidity and overgrazing	Mediterranean
Cecere et al. 1991	The marine algae of Mar Piccolo, Taranto (Southern-Italy): a re-assessment	*Cystoseira ercegovicii, C. sauvageauana, C. spinosa*	compared field samples to historical studies and herbarium specimens	1923, 1959, and 1960	1987-1988	local extinction	pollution	Mediterranean
Cecere et al. 1991	The marine algae of Mar Piccolo, Taranto (Southern-Italy): a re-assessment	*Cystoseira barbata, C. compressa*	collected field samples and compared them to historical studies and herbarium specimens	1923, 1959, and 1960	1987-1988	these species still present at site	none given	Mediterranean
Cecere et al. 2001	Changes in seaweed biodiversity of the Gargano Coast (Adriatic Sea, Mediterranean Sea)	*Cystoseira corniculata, C. schiffneri f. tenuiramosa, C. spinosa v. spinosa, Sargassum acinarium, S. hornschuchii*	compared floristic samples to previous floristic lists	1960's	1997	local extinction	sedimentation/lowered light penetration	Mediterranean
Coleman et al. 2008	Absence of a Large Brown Macroalga on Urbanized Rocky Reefs Around Sydney, Australia, and	*Phyllospora comosa*	compared field surveys to herbarium collections and anecdotal reports	1940's	2007	local extinction (but was later restored, see Vergés et al. 2020)	most likely occurred due to the populations' proximity to sewage outfalls	Oceania

	Evidence for Historical Decline		from marine scientists					
Cormaci and Furnari 1999	Changes in the benthic algal flora of the Tremiti Islands (southern Adriatic) Italy	*Cystoseira crinita, C. humilis, C. schiffneri, C. spinosa, Sargassum acinarium, S. hornschuchii*	compared floristic surveys to historical data	1960's-1970's	1997	local extinction	pollution: reduced water clarity	Mediterranean
D'Archino et al. 2019	New Zealand Macroalgae: Distribution and Potential as National Scale Ecological Indicators	*Durvillaea antarctica*	field surveys of macroalgal community	n/a	2009, 2017	decline	not given	Oceania
Davies et al. 2007	Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales	*Ascophyllum nodosum*	compared historical and current aerial photographs of the *Ascophyllum* canopy, historical and current limpet abundance data, data on physical site characteristics, and performed manipulative experiments	1962	2001-2003	decline	increased limpet densities possibly linked to climate change	Europe Atlantic
Driskell et al 2001	Long-term signal of disturbance: *Fucus gardneri* after the	*Fucus gardneri*	compared oil spill sites to reference sites	n/a	1989-1996	lack of recovery after pulse disturbance	oil spill	US West Coast

	Exxon Valdez oil spill							
Duarte et al. 2013	Recent and historical range shifts of two canopy-forming seaweeds in North Spain and the link with trends in sea surface temperature	*Fucus serratus, Himanthalia elongata*	reviewed large-scale studies, reports, and publications, and conducted field surveys to compare current and historical distributions	late 1800's	2009	decline	climate change: warming SST's	Europe Atlantic
Elsberry 2019	Population demographic characteristics of two foundation species in the centers and at the edges of their biogeographic ranges	*Pelvetiopsis limitata, Silvetia compressa*	100 ind. tagged at 4 sites, collected receptacles, counted zygotes, outplanted tiles for juv. survival rate	n/a	2018	decline	none given	US West Coast
Eriksson et al. 1998	Long-term changes in the sublittoral zonation of brown algae in the southern Bothnian Sea	*Fucus vesiculosus*	Resurveyed historical diving profiles with SCUBA	1940's	1996	upward tidal shift/decreased depth	attributed primarily to eutrophication: sedimentation, epiphyte overgrowth, and shading by plankton	Baltic Sea
Eriksson et al. 2002	Long-term changes in the macroalgal vegetation of the inner Gullmar Fjord, Swedish Skagerrak coast	*Fucus vesiculosus, F. serratus, Halidrys siliquosa*	resurveyed historical transects; grouped species into thallus shape and life history categories	1941	1998	decline	eutrophication	Baltic Sea

Fales and Smith 2022	Long-term change in a high-intertidal rockweed (Pelvetiopsis californica) and community-level consequences	*Pelvetiopsis californica*	MARINe long term plots, photo quads	1980s	1980-2010s	decline	unknown	US West Coast
Fales and Smith 2022	Long-term change in a high-intertidal rockweed (*Pelvetiopsis californica)* and community-level consequences	*Pelvetiopsis californica*	revisit historical sites	varies	2017-2018	local extinction	unknown	US West Coast
Fernández 2016	Current status and multidecadal biogeographical changes in rocky intertidal algal assemblages: The northern Spanish coast	*Fucus serratus, F. vesiculosus, Himanthalia elongata*	resurveyed historical transects	1977-1978	2007-2008	decline	climate change: warming SST's	Europe Atlantic
Fernández 2016	Current status and multidecadal biogeographical changes in rocky intertidal algal assemblages: The northern Spanish coast	*Bifurcaria bifurcata, Cystoseira baccata, C. tamariscifolia*	resurveyed historical transects	1977-1978	2007-2008	increase	warming climate/SST's favor these warm-temperate fucoid species	Europe Atlantic
Fraschetti et al. 2011	Effects of unplanned development on marine biodiversity: a lesson from Albania (central Mediterranean Sea)	*Cystoseira spp.*	field surveys	no baseline data available at the time of the study	2007	decline	urbanization, aquaculture	Mediterranean

Gerrard 2005	Changes in the rocky intertidal floras along the Palos Verdes peninsula (Los Angeles County) since E.Y. Dawson’s surveys in the late 1950s	*Halidrys dioica, Cystoseira osmundacea, Silvetia compressa*	resurveyed 5 of Dawson's sites in Palos Verdes, also compared to Widdowsons resurveys	1950s, 1970s	2000	*H. dioica* and *C. osmundacea*: local extinction; *S. compressa*: decline	pollution, changes in ocean temperature	US West Coast
Goodson 2003	Long-term changes in rocky intertidal populations and communities at Little Corona del Mar, California: A synthesis using traditional and non-traditional data	*Silvetia compressa*	resurvery of Dawson's transect	1950s	1999	decline	unknown	US West Coast
Gorman et al. 2020	Decadal losses of canopy-forming algae along the warm temperate coastline of Brazil	*Sargassum spp.*	meta-analysis	1969	2017	decline	a combination of climate change and the increase in human population along the coast	South America
Graham et al. 2018	Changes in Abundance of *Silvetia compressa* at San Clemente Island before and during the 2015–2016 El Niño	*Silvetia compressa*	MARINe	2012	2016	decline	associated with high SST	US West Coast

Hoffmann et al. 1988	Evolution of the populations of *Cystoseira balearica* (Phaeophyceae) and epiphytic Bangiophyceae in the Bay of Calvi (Corsica) in the last eight years	*Cystoseira belearica*	compared field surveys with previous surveys	1980-1982	1987-1988	decline	sewage effluent	Mediterranean
Johansson et al. 1998	Long-term changes of macroalgal vegetation in the Skagerrak area	*Fucus spp., Halidrys spp. Ascophyllum nodosum*	compared to historical data	1960's	1997	stable overall	none given	Baltic Sea
Jueterbock et al. 2018	Decadal stability in genetic variation and structure in the intertidal seaweed *Fucus serratus* (Heterokontophyta: Fucaceae)	*Fucus serratus*	assessed genetic diversity over 5-10 generations	n/a	2000 and 2010	genetic diversity was stable across latitudes; declining heterozygosity at range edges	climate change	Europe Atlantic
Kangas et al. 1982	A general model of the decline of *Fucus vesiculosus* at Tvärminne, south coast of Finland in 1977-81	*Fucus vesiculosus*	field surveys	n/a	1977-1981	decline	eutrophication	Baltic Sea
Kangas and Niemi 1985	Observations of recolonization by the bladder-wrack, *Fucus vesiculosus*, on the southern coast of Finland	*Fucus vesiculosus*	resurveyed previously studied sites	1968-1971	1980-1984	recovered	inconclusive: potentially due to fluctuations in hydrographic conditions, or reduced nutrient load	Baltic Sea
Kautsky et al. 1986	Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940's indicates	*Fucus vesiculosus*	re-sampled historical transects	1940's	1984	upward tidal shift/decreased depth	nutrient enrichment	Baltic Sea

	eutrophication of the Baltic Sea							
Kautsky et al. 1992	Studies on the *Fucus vesiculosus* community in the Baltic Sea	*Fucus vesiculosus*	measured biomass at previously sampled sites	1974-1975	1989-1990	decline in areas near pulp mills	decreased water quality	Europe
Kukk and Martin 1992	Long-term dynamics of the phytobenthos in Parnu Bay, the Baltic Sea	*Fucus vesiculosus*	compared field surveys to previously published checklist	early 1980's	1987-1991	decline	sewage effluent	Baltic Sea
Lamela-Silvarrey et al. 2012	Fucoid assemblages on the north coast of Spain: past and present (1977-2007)	*Fucus spiralis, F. vesiculosus, Pelvetia canaliculata*	compared current biomass, net primary productivity, and grazer abundance in fucoid populations to a study done in 1977	1977	2007	*F. spiralis* and *P. canaliculata*: decline; *F. vesiculosus*: local extinction (author's pers. obs. post-study)	climate change: increased air and water temperatures; reduced nutrient availability from lowered frequency of upwelling; increase in herbivore density	Europe Atlantic
Lamela-Silvarrey et al. 2012	Fucoid assemblages on the north coast of Spain: past and present (1977-2007)	*Ascophyllum nodosum*	compared current biomass, net primary productivity, and grazer abundance in fucoid populations to a study done in 1977	1977	2007	increase in annual average biomass	none given	Europe Atlantic
Lima et al. 2007	Do distributional shifts of northern and southern species of algae match the warming pattern?	*Ascophyllum nodosum, Cystoseira baccata, C. tamariscifolia, Fucus serratus*	compared field surveys to historical data	1950's and 60's	2001-2006	no significant shift	inconclusive, these species may be more resilient to higher SST's	Europe Atlantic

Lima et al. 2007	Do distributional shifts of northern and southern species of algae match the warming pattern?	*Bifurcaria bifurcata, Fucus vesiculosus, Halidrys siliquosa*	compared field surveys to historical data	1950's and 60's	2001-2006	southward shift	for cold-water species: inconclusive, may be due to indirect effects of upwelling, or may be due to chance	Europe Atlantic
Lima et al. 2007	Do distributional shifts of northern and southern species of algae match the warming pattern?	*Himanthalia elongata, Pelvetia canaliculata, Sargassum flavifolium*	compared field surveys to historical data	1950's and 60's	2001-2006	northward shift	for warm and cold-water species: increasing SST's, for cold-water species: may also be due to chance	Europe Atlantic
Lourenço et al. 2016	Upwelling areas as climate change refugia for the distribution and genetic diversity of a marine macroalga	*Fucus guiryi*	compared field surveys with previously published literature and herbarium specimens	not given	2012-2014	range contraction at southern edge of distribution, but persistent (though reduced) populations were found in upwelling areas	climate change/climatic events	Europe Atlantic, Africa
Lundälv et al. 1986	Long-term trends in algal-dominated rocky subtidal communities on the Swedish west coast - a transitional system?	*Halidrys siliquosa*	stereo photography surveys	n/a	1970-1985	decline (followed by some recovery at 5-m depth)	eutrophication, temperature fluctuations, or *Halidrys* population dynamics	Europe Atlantic
Mäkinen et al. 1984	Changes in the littoral rocky shore vegetation of the Seili area, SW archipelago of Finland	*Fucus vesiculosus*	resurveyed historical transects	1968-1969	1981-1982	decline	eutrophication/sedimentation	Baltic Sea
Mangialajo et al. 2008	Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages	*Cystoseira amentacea var. stricta*	sampled fucoid abundances along an urbanization gradient	n/a	n/a	decline	urbanization	Mediterranean

Mangialajo et al. 2008	Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages	*Cystoseira compressa*	sampled fucoid abundances along an urbanization gradient	n/a	n/a	increase	reduced competition with *C. amentacea*	Europe
Martínez et al. 2018	Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming	13 fucoid species	analyzed herbarium records to create predictive models of seaweed distribution changes due to ocean warming	n/a	predictions for 2100	declines, range shifts, and local extinctions	climate change	Oceania
Méndez-Sandín and Fernández 2016	Changes in the structure and dynamics of marine assemblages dominated by *Bifurcaria bifurcata* and *Cystoseira* species over three decades (1977–2007)	*Bifurcaria bifurcata*	compared field surveys to historical data	1977	2007	decline	Increased SST's, reduced upwelling	Europe Atlantic
Méndez-Sandín and Fernández 2016	Changes in the structure and dynamics of marine assemblages dominated by *Bifurcaria bifurcata* and *Cystoseira* species over three decades (1977–2007)	*Cystoseira baccata, C. tamariscifolia*	compared field surveys to historical data	1977	2007	increase	*Cystoseira* spp. may be more resilient to higher SST's due to being warm-temperate species	Europe Atlantic
Middelboe and Sand-Jensen 2000	Long-term changes in macroalgal communities in a Danish estuary	*Fucus spp*. and *Halidrys siliquosa*	compared field surveys to historical data	1941-1943	1982-1994	decline	eutrophication	Baltic Sea

Munda 1974	Changes and succession in the benthic algal associations of slightly polluted habitats	*Ascophyllum nodosum, Cystoseira spp., Fucus spiralis, F. serratus, F. vesiculosus, F. virsoides, Pelvetia canaliculata, Sargassum Hornschuchii, S. linifolium*	field surveys	n/a	1967-1972	*A. nodosum* and *Cystoseira spp.*: decline; *Fucus spp*: decline and local extinction; *P. canaliculata*: local extinction, *Sargassum spp.*: decline and local extinction	sewage effluent; reduced tidal movement and salinity in land-locked fjord	Europe
Munda 1982	The effect of organic pollution on the distribution of fucoid algae from the Istrian coast (vicinity of Rovinj)	*Cystoseira spicata, C. crinita, C. adriatica, C. barbata, C. compressa, C. discors, C. fucoides, Fucus virsoides, Sargassum acinarium, S. hornschuchii*	compared field surveys to historical distribution data	1967-1969	1978-1980	*Cystoseira spp.*: decline and local extinction; *Fucus virsoides*: decline followed by recovery; *Sargassum spp.*: local extinction	organic pollution	Mediterranean
Munda 1993	Changes and degradation of seaweed stands in the Northern Adriatic	*Cystoseira compressa, C. barbata, C. crinita, C. corniculata, C. ercegovichii, Fucus virsoides, Sargassum acinarium, S. hornschuchii*	compared surveys to historical data/observations	1970's	1990's	*Cystoseira spp.*: decline and local extinction; *Fucus virsoides*: decline; *Sargassum spp.*: local extinction	pollution/eutrophication	Mediterranean

Munda 2000	Long-term marine floristic changes around Rovinj (Istrian coast, North Adriatic) estimated on the basis of historical data from Paul Kuckuck's field diaries from the end of the 19th century	*Cystoseira spp., Sargassum spp.*	compared recent floristic surveys to historical field diaries	1894-1899	1967-1970 and 1978-1983	decline	pollution/eutrophication	Mediterranean
Neiva et al. 2015	Genes left behind: climate change threatens cryptic genetic diversity in the canopy-forming seaweed *Bifurcaria bifurcata*	*Bifurcaria bifurcata*	used Ecological Niche Models and molecular data to predict future genetic diversity changes	n/a	predictions for 2040-2050 and 2090-2100	predicted northward range shift; potential threat of losing one of the endemic lineages at the southern range edge	climate change	Europe Atlantic, Africa Atlantic
Nicastro et al. 2013	Shift happens: trailing edge contraction associated with recent warming trends threatens a distinct genetic lineage in the marine macroalga *Fucus vesiculosus*	*Fucus vesiculosus*	compared field surveys to published literature and herbarium specimens; analyzed genetic data from extant and extinct populations	1982	2009-2011	range contraction at southern limit of distribution, loss of genetic diversity	climate change	Europe Atlantic
Nilsson et al. 2004	Long-term decline and recent recovery of *Fucus* populations along the rocky shores of southeast Sweden, Baltic Sea	*Fucus vesiculosus, Fucus serratus*	long-term monitoring	1984	2001	decline; decline followed by recovery	eutrophication, increased grazer activity	Baltic Sea

Oliveira and Qi 2003	Decadal changes in a polluted bay as seen from its seaweed flora: the case of Santos Bay in Brazil	brown algae, including *Sargassum spp.*	compared current and historical floristic surveys	1957	1998-1999	increase	improvement of water quality	South America
Perkol-Finkel and Airoldi 2010	Loss and Recovery Potential of Marine Habitats: An Experimental Study of Factors Maintaining Resilience in Subtidal Algal Forests at the Adriatic Sea	*Cystoseira spp.* and *Sargassum spp.*	compared field surveys to historical data, grey literature, and first-hand accounts	1941-2001	2006-2010	*Cystoseira* spp.: decline; *Sargassum* spp.: local extinction	habitat loss/destruction due to natural (hydrodynamic) and anthropogenic causes	Mediterranean
Phillips and Blackshaw 2011	Extirpation of macroalgae (*Sargassum* spp.) on the subtropical east Australian coast	*Sargassum amaliae, S. aquifolium, S. carpophyllum, S. polycystum, S. spinifex*	compared field surveys to previously published literature and herbarium specimens	pre-1960s	2004-2006	local extinction	inconclusive: probably related to decreased water quality from eutrophication and urbanization	Oceania
Piñeiro-Corbeira et al. 2016	Decadal changes in the distribution of common intertidal seaweeds in Galicia (NW Iberia)	*Cystoseira nodicaulis, Fucus vesiculosus, Himanthalia elongata*	compared presence/absence data to historical survey	1998-1999	2014	*C. nodicaulis*: local extinction; *F. vesiculosus*: decline; *H. elongata*: decline	climate change	Europe Atlantic
Piñeiro-Corbeira et al. 2016	Decadal changes in the distribution of common intertidal seaweeds in Galicia (NW Iberia)	*Bifurcaria bifurcata*	compared presence/absence data to historical survey	1998-1999	2014	increase	may be more resilient to warming	Europe Atlantic
Ramos et al. 2020	Changes in the distribution of intertidal macroalgae along a	*Himanthalia elongata*	re-survey of previously sampled transects	2011	2017	decline	climate change: increasing SST's	Europe Atlantic

	longitudinal gradient in the northern coast of Spain							
Ramos et al. 2020	Changes in the distribution of intertidal macroalgae along a longitudinal gradient in the northern coast of Spain	*Bifurcaria bifurcata, Cystoseira baccata*	re-survey of previously sampled transects	2011	2017	increase in distribution of warm-temperate fucoids	climate change: increasing SST's	Europe Atlantic
Reichert and Buchholz 2006	Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002	*Fucus serratus, Halidrys siliquosa*	re-surveyed plots from previous study	1984	2002	decline	*F. serratus*: a series of cold winters combined with increased herbivory; *H. siliquosa*: competition with invasive *S. muticum*	Europe Atlantic
Riera et al. 2015	Long-term herbarium data reveal the decline of a temperate-water algae at its southern range	*Fucus guiryi*	compared newly and historically sampled *Fucus* populations; used herbarium specimens to analyze morphological changes over time	1972	2012	decline and local extinctions	climate change: increasing SST's	Africa
Rindi et al. 2020	Long-term changes in the benthic macroalgal flora of a coastal area affected by urban impacts (Conero	*Cystoseira foeniculacea, C. humilis, Fucus virsoides, Sargassum acinarium*	compared current and historical floristic surveys	1941-1946	2011-2019	local extinction	urbanization: habitat destruction, reduced water quality, introduction of new species	Mediterranean

	Riviera, Mediterranean Sea)							
Sagarin et al. 1999	Climate-Related Change in an Intertidal Community over Short and Long Time Scales	*Silvetia compressa*	resurvery of Hewett's 1931-1933 transect, counted all inverts, only percent cover of *Silvetia* (no other algae studied)	1930s	1993-1996	decline	attributed to temperature	US West Coast
Sales and Ballestros 2009	Shallow *Cystoseira* (Fucales: Ochrophyta) assemblages thriving in sheltered areas from Menorca (NW Mediterranean): relationships with environmental factors and anthropogenic pressures.	*Cystoseira spp.*	field surveys	1912 (for some study areas, no historical data available for others)	2005	decline and local extinction	eutrophication combined with unfavorable geomorphology and wave exposure of some sites	Mediterranean
Sales and Ballestros 2009	Shallow *Cystoseira* (Fucales: Ochrophyta) assemblages thriving in sheltered areas from Menorca (NW Mediterranean): relationships with environmental factors and	*Cystoseira spp.*	field surveys	1912 (for some study areas, no historical data available for others)	2005	stable	less anthropogenic pressure at some sites, more beneficial geomorphology	Europe

	anthropogenic pressures.							
Schiel 2011	Biogeographic patterns and long-term changes on New Zealand coastal reefs: Non-trophic cascades from diffuse and local impacts	*Cystophora torulosa, Hormosira banksii*	long-term (17 years) monitoring of permanent transects and physical conditions	n/a	1993-2010	fluctuation	*C. torulosa:* declined when *H. banksii* cover increased; *H. banksii*: declines occurred when the Southern Oscillation Index (SOI) was high	Oceania
Serio et al. 2006	Changes in the benthic algal flora of Linosa Island (Straits of Sicily, Mediterranean Sea)	*Cystoseira brachycarpa v. brachycarpa, C. brachycarpa v. claudiae, C. crinitophylla, C. elegans, C. foeniculacea f latiramosa, C. foeniculacea f. tenuiramosa, C. sauvageauana, C. zosteroides, Sargassum acinarium, S. trichocarpum*	sampled along the same transects as 1973 study, compared number of species found	1973	1999	local extinction	climate change and changes in the deep circulation of the Mediterranean basin	Mediterranean
Sfriso 1987	Flora and vertical distribution of macroalgae in the lagoon of Venice: a	*Cystoseira spp.* (Cystoseira "association")	compared results of field sampling to historical surveys	1938, 1962	1979-1984	local extinction	eutrophication	Mediterranean

	comparison with previous studies							
Shepherd et al. 2009	Long-term changes in macroalgal assemblages after increased sedimentation and turbidity in Western Port, Victoria, Australia	Fucoid/laminarian canopy: including *Cystophora spp.*, *Scaberia spp.*, *Sargassum spp.*, *Hormosira spp.*	floristic surveys; surveys of vertical distribution	1967-1971	2002-2006	decrease in maximum depth limit of fucalean/laminarian canopy; loss of 3 fucoid species	reduced water quality associated with massive decline of seagrass	Oceania
Smale and Wernberg 2013	Extreme climatic event drives range contraction of a habitat-forming species	*Scytothalia dorycarpa*	compared cover of *S. dorycarpa* before and after marine heat wave in 2011	2000-2010	2011-2012	local extinction	climate change: marine heat wave	Oceania
Soltan et al. 2001	Changes in Macroalgal Communities in the Vicinity of a Mediterranean Sewage Outfall After the Setting Up of a Treatment Plant	*Cystoseira amantacea*	assessed changes in algal community 8 years after wastewater treatment plant was put in place	1972-1974	1995-1996	decline	Pollution/eutrophication was most likely responsible for the initial decline of *Cystoseira*; the short dispersal distance of *Cystoseira* may be inhibiting its recovery, and the water quality may not have improved enough	Mediterranean
Tanaka et al. 2012	Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds	*Sargassum spp.*	compared field surveys to previous distribution data as well as long-term SST data	1970's	2006-2010	range shifts: temperate *Sargassum* species contracted/declined, tropical *Sargassum* species expanded	increasing sea surface temperatures	Asia

Thibaut et al. 2005	Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean)	*Cystoseira crinita, C. barbata, C. foeniculacea f. tenuiramosa, C. spinosa, C. spinosa var. compressa, C. caespitosa, C. zosteroides, C. elegans, C. mediterranea, Sargassum hornschuchii, S. vulgare*	compared current populations to historical data, herbarium specimens, and historical field diaries	Early 1900's	2003	*Cystoseira spp.:* decline and local extinction, *Sargassum spp.:* local extinction	inconclusive: may be a result of several factors, including eutrophication/pollution, herbivory/competition from other species, human trampling, scientific collecting, and habitat loss	Mediterranean
Thibaut et al. 2005	Long-term decline of the populations of Fucales (*Cystoseira* spp. and *Sargassum* spp.) in the Albères coast (France, North-western Mediterranean)	*Cystoseira compressa*	compared current populations to historical data, herbarium specimens, and historical field diaries	Early 1900's	2003	stable	none given	Mediterranean

Thibaut et al. 2014	Decline and local extinction of Fucales in French Riviera: the harbinger of future extinctions?	*Cystoseira elegans, C. foeniculacea f. latiramosa, C. squarrosa, C. spinosa var. spinosa, C. amentacea, C. barbata f. barbata, C. brachycarpa, C. crinita, C. sauvageauana, C. foeniculacea f.tenuiramosa, C. spinosa var. compressa, Sargassum hornschuchii, S. vulgare, S. acinarium*	compared present distribution to historical data (literature and herbarium vouchers)	early 1800's	2007-2013	decline and local extinction	habitat destruction, overgrazing, competition from invasive algae, scientific collecting, and damage from fishing nets	Mediterranean
Thibaut et al. 2014	Decline and local extinction of Fucales in French Riviera: the harbinger of future extinctions?	*Cystoseira jabukae*	compared present distribution to historical data (literature and herbarium vouchers)	early 1800's	2007-2013	previously not found at study sites	none given	Mediterranean
Thibaut et al. 2016 a	Unexpected temporal stability of *Cystoseira* and *Sargassum* forests in Port-Cros, one of the oldest Mediterranean marine National Parks	*Cystoseira spp.* and *Sargassum spp.*	compared field surveys with historical data (herbarium vouchers, peer reviewed and grey literature, and maps)	1963	2005-2007	populations at Port-Cros were healthy; only one *Cystoseira* spp. had declined	lack of habitat destruction, high water quality, and regulation of human activities	Mediterranean

Thibaut et al. 2016 b	The *Sargassum* conundrum: very rare, threatened, or locally extinct in the NW Mediterranean and still lacking protection	*Sargassum acinarium, S. hornschuchii, S. vulgare, S. trichocarpum, S. flavifolium*	compared field surveys to previously published literature, unpublished data, and herbarium specimens	1950	2003-2014	decline and local extinction	inconclusive: probably a combination of factors, including habitat loss, overgrazing, trawling, fishing nets, and water turbidity	Mediterranean
Thom and Widdowson 1978	A resurvey of E. Yale Dawson's 42 intertidal algal transects on the southern California mainland after 15 years	*Pelvetiopsis californica*	resurveyed 42 of Dawson's southern CA transects	1950s	1973-1975	local extinction	discussed human impacts and urbanization	US West Coast
Thomsen et al. 2019	Local extinctinon of Bull Kelp (*Durvillaea* spp.) Due to a Marine Heatwave	*Durvillaea antarctica, D. poha, D. willana*	field surveys were conducted before and after a marine heatwave event	n/a	2017-2018	decline and local extinction	marine heat wave	Oceania
Torn et al. 2006	Present and past depth distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic Sea	*Fucus vesiculosus*	analyzed published and unpublished current and historical data and reports	~1900	2001	upward tidal shift/decreased depth	eutrophication	Baltic Sea
Tsiamis et al. 2013	Macroalgal community response to re-oligotrophication in Saronikos Gulf	*Cystoseira spp., Sargassum spp.*	Collected samples of the algal flora at increasing distances from a waste water treatment plant, and monitored water quality over the course of the study	Cite some studies discussing decrease in Cystoseira from 1918 to 1987	1998-2010	decline	reduced water quality, habitat destruction, overgrazing	Mediterranean

Vergés et al. 2014 b	Tropical rabbitfish and the deforestation of a warming temperate sea	*Cystoseira spp., Sargassum spp.*	sampled fish, algal, and invertebrate communities, and conducted feeding experiments	n/a	2008	decline	increasing SST's, which facilitated the range expansion of tropical herbivorous fish	Mediterranean
Vogt and Schramm 1991	Conspicuous decline of *Fucus* in Kiel Bay (western Baltic): what are the causes?	*Fucus serratus, Fucus vesiculosus*	estimated population density and total Fucus biomass in area	1950-51	1987-1988	decline	eutrophication and substrate loss	Baltic Sea
Weitzman et al. 2021	Changes in Rocky Intertidal Community Structure During a Marine Heatwave in the Northern Gulf of Alaska	*Fucus distichus*	field surveys of community composition and species abundance	n/a	2012-2019	decline	climate change: marine heat wave	US West Coast
Wernberg et al. 2013	An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot	kelp and large fucoids	ecological surveys conducted before and after the 2011 marine heat wave	n/a	2006-2011	decrease in cover of canopy-forming algae	climate change: marine heat wave	Oceania
Whitaker et al. in prep	Decline of a North American rocky intertidal foundation species	*Silvetia compressa*	data from MARINe long-term monitoring plots	1980s	1983-2017	decline south of Pt. Conception at ~20 sites	unknown	US West Coast
Whitaker et al. in prep	Decline of a North American rocky intertidal foundation species	*Silvetia compressa*	data from MARINe long-term monitoring plots	1980s	1983-2017	stable north of Pt. Conception	unknown	US West Coast
Widdowson 1971	Changes in the intertidal algal flora of the Los Angeles area since the survey by E. Yale	*Silvetia compressa*	resurveyed 15 of Dawson's transects	1950s	1968-1970	decline	collecting, air pollution	US West Coast

	Dawson in 1956-1959							
Yesson et al. 2015	Large brown seaweeds of the British Isles: Evidence of changes in abundance over four decades	*Fucus spp., Ascophyllum nodosum,* and other fucoids	meta-analysis comparing historical abundance data with SST data	1974	2010	*F. vesiculosus, F. serratus*, and *A. nodosum* increased in abundance; other fucoids experienced no change or insignificant declines	increase in *A. nodosum* and *F. vesiculosus* related in part to increasing SST's; no relation between *F. serratus* increase and temperature change	Europe Atlantic
Zavodnik et al. 2002	Note on recolonisation by fucoid algae *Cystoseira* spp. and *Fucus virsoides* in the North Adriatic Sea	*Cystoseira spp., Fucus virsoides*	measured fucoid biomass and compared it to previous studies where historical data was available	1960's-1970's for Rovinj; no data for Haludovo Beach	1998-1999	recovery	cycle of decline and recovery driven by natural causes rather than anthropogenic impacts	Mediterranean

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