Climate-related changes in rocky intertidal species distribution on the Farallon Islands in Northern California

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In

Interdisciplinary Marine and Estuarine Sciences

By

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Certification of Approval

I certify that I have read Climate-related changes in rocky intertidal species distribution on the

Farallon Islands in Northern California by Elizabeth Max, and that in my opinion this work meets

the criteria for approving a thesis submitted in partial fulfillment of the requirement for the

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Abstract

This thesis investigates long-term ecological changes in the rocky intertidal communities on the Farallon Islands, an island refuge in the Greater Farallones National Marine Sanctuary (GFNMS). Using data from the GFNMS rocky intertidal monitoring program (1993 – 2011), this study examines trends in species cover in response to local environmental and large-scale oceanic conditions. Previous analysis by Roletto et al. (2014) documented a decline in upright species cover alongside an increase in crustose species, highlighting the need to explore potential drivers behind these shifts. To this end, three research questions guided this study: (1) Are variations in air temperature, sea surface temperature (SST), and sea surface salinity (SSS) associated with changes in cover?; (2) Does cover respond to ocean climate patterns (NPGO, PDO, SOI, CUTI, BEUTI)?; (3) Are the biogeographical poleward range shifts that are seen on the mainland exhibited on the Farallones?

The results from this paper indicated that while certain models of local environmental and oceanic indices ranked the highest when compared amongst each other, they provided limited explanatory power, with R^2 values across models remaining low. These findings suggest that additional ecological factors may influence the observed trends. Regarding biogeographical range shifts, some southern species showed some expansion; however, no significant poleward shifts were observed. This study underscores the importance of long-term datasets to understand island ecosystem responses to climate change and advocates for continued monitoring and a broader assessment of ecological drivers to inform conservation strategies.

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Table of Contents

List of Figures

List of Tables

Introduction

Understanding the factors that drive species distribution, abundance, and diversity over space and time remains a key focus of marine ecology, particularly in relation to how these patterns respond to climate change (Barry et al., 1995; Gaines & Roughgarden, 1985; Iles et al., 2012; Menge et al., 1997; Paine & Levin, 1981; Raimondi et al., 2019; Sagarin et al., 1999; Sanford et al., 2019). Efforts to characterize large-scale spatial patterns of species distributions and the mechanisms driving them have been a primary focus of ecology for decades, informing predictions of how species distributions may respond to climate change (Gaines & Lubchenco, 1982; Helmuth et al., 2002; Sanders, 1968). Studies increasingly document changes in the distribution and abundance of organisms, consistent with ecological predictions of species responses to climate shifts (Barry et al., 1995; Blanchette et al., 2008; Harley et al., 2006; Helmuth et al., 2006; Henson et al., 2017; Kroeker et al., 2016; Sagarin et al., 1999). While mainland coastal habitats in the Northeast Pacific have been well-studied in the context of climate change (Harley et al., 2006; Hawkins et al., 2003; Helmuth et al., 2006; Mieszkowska et al., 2005; Sagarin et al., 1999), questions remain about whether these are occurring in island habitats. This research analyzed long-term rocky intertidal survey data from the United States Fish and Wildlife Services Farallon Island National Wildlife Refuge (Farallon Islands or Farallones), 30 miles west of San Francisco, California within the Greater Farallones National Marine Sanctuary (GFNMS) and about 5 miles east from the continental shelf (Cooper, 1973), investigating trends in species cover and distribution in response to oceanic conditions.

Rocky intertidal habitats are ideal for studying climate impacts because they exist at the land-sea boundary, making them highly responsive to environmental changes and potentially serving as early indicators of climate effects (Barry et al., 1995; Connell, 1972; Harley et al., 2006; Hawkins et al., 2003; Joh & Di Lorenzo, 2017; Mieszkowska et al., 2005; Sagarin et al., 1999; Thompson et al., 2004). The rocky intertidal supports diverse marine algal and invertebrate species due to structural habitat complexity and exposure to both terrestrial and marine conditions (Schoch & Dethier, 1996). Thermal stress has been closely linked to declines in species cover within these systems (Barry et al., 1995; Helmuth et al., 2002; Sanford et al., 2019), while additional factors – such as ocean currents, reproductive dispersal, and larval behavior – affect native species' abilities to repopulate lost habitat (Menge et al., 2009; Paine & Levin, 1981; Thomsen et al., 2015).

Much research has focused on how intertidal communities respond to thermal and desiccation stress as primary indicators of community structure (Bertness et al., 1999; Gedan et al., 2011; Helmuth et al., 2006; Maharana et al., 2015). With climate change, the distribution of intertidal organisms is expected to shift in response to these stressors, potentially altering biogeographic range limits (Helmuth et al., 2002). A landmark study by Barry et al. (1995) documented northward shifts in the range limits of rocky intertidal invertebrates and macroalgae by resampling plots from the 1930s to the 1990s in Monterey Bay, California, correlating rising sea surface temperature (SST) with increased abundance of southern species and decrease in northern species while cosmopolitan species persisted. A more recent study observed similar trends in recruitment of southern species like *Lottia gigantea* and *Tetraclita rubescens* between Point Reyes and Point Arena, suggesting shifts in response to extreme

marine heatwaves (Sanford et al., 2019). Thermal acclimation of *Kelletia kelletii*, a marine welk,

extended its range northward from Baja California, Mexico to Monterey Bay, California (Díaz et

al., 2021). *Anthopleura sola*, another species moving northward, extended its northern

boundary from Monterey Bay to Bodega Bay, California (Cornwell et al., 2022). Although *Lottia*

gigantea has been observed on the Farallon Islands, it was not recorded in the 1993 – 2011

dataset central to this study, while *Tetraclita rubescens* was present. The new survey methods

post-2011 include a *Lottia gigantea* survey site. So far, *Kelletia kelletii* and *Anthopleura sola*

have not been seen on the Farallones. These findings illustrate consistent biogeographical

range shifts on the mainland, but similar patterns remain under-investigated in island

ecosystems within the Northeast Pacific (Blanchette et al., 2008; Fenberg et al., 2015; Kroeker

et al., 2016).

Biogeographical range shifts are well-documented in mainland intertidal communities,

but island studies in the Northeast Pacific are scarce. It remains unclear whether island habitats

like the Farallones are experiencing similar declines in northern species cover or expansions of

southern species. Barriers to colonization, particularly for sessile species, may affect island

habitats differently than mainland environments, potentially limiting the reach of species

dispersal due to the islands' isolation (Martins et al., 2008; Miner et al., 2021). The Farallones'

proximity to mainland populations and habitat limitations may ultimately shape which species

successfully establish and persist on the islands (Davenport & Stevenson, 1998; MacArthur &

Wilson, 1967; Menge et al., 2003).

However, the dynamics of range shifts on islands, where recruitment may be limited by

geographic isolation, remain underexplored on the Farallones. Studies from protected islands in

Southern California, particularly within the Channel Islands National Park (Channel Islands), provide valuable insights into these dynamics (Engle, 2008; Miner et al., 2021; Richards et al., 1997). Long-term monitoring programs of the intertidal and subtidal communities on the Channel Islands demonstrates that the islands' isolation, combined with distinctive oceanographic conditions, leads to species compositions and community dynamics unique from what is seen on the mainland (Engle, 1994; Richards et al., 1997). For example, research on the Channel Islands has documented both the persistence and gradual shifts of species that are closely linked to upwelling-driven nutrient availability and episodic warming events, including El Niño oscillations, which often lead to temporary reductions in cold-water species (Engle, 2008). The isolation of the Channel Islands has also resulted in reduced recruitment rates for some species, likely due to limited larval dispersal between mainland and island habitats (Miner et al., 2021). The GFNMS long-term dataset analyzed in this research offers an opportunity to investigate these trends within a protected island habitat, contributing to our understanding of climate impacts on intertidal ecosystems and the dynamics of range shifts in island environments.

Rocky intertidal algae and sessile invertebrates are exposed to the air during low tide and ocean water during high tide (Harley et al., 2006; Helmuth et al., 2006). As temperatures rise in both the atmosphere and the sea, variability in these conditions is observed on a climatic scale and extreme events are becoming more frequent and severe (Cai et al., 2015; Ragno et al., 2018). Increased air temperature can lead to desiccation and damage from UV radiation to intertidal species (Huang et al., 2021; Martone et al., 2010; Roberts & Bracken, 2021). High tide historically provides a reprieve from higher-than-normal low tide temperatures. But when SST

is also high, intertidal organisms lose their opportunity to recover. An additional layer to thermal stress is the longevity and severity of said stress, and the increased wave action that occurs during extreme events (Church et al., 2013; Haring et al., 2002; Nielsen, 1999; Seapy & Littler, 1978). The climate crisis has already raised global temperatures making desiccation and thermal stress of intertidal organisms an ever-increasing determinant for species cover (Haring et al., 2002; Steinbeck et al., 2005). When combined with temperature, sea surface salinity (SSS) can be a primary factor for predicting intertidal species cover, especially when considering the vulnerable planktonic stages of algae and invertebrates (Fenberg et al., 2015; Saha et al., 2020; Zacharias et al., 1999).

Extreme oceanographic and environmental events, intensified by climate change, are having notable impacts on nearshore and intertidal species and their habitats. During a "warm" Pacific Decadal Oscillation (PDO) phase in 1997-1998 a historically strong El Niño occurred, second only to the most severe El Niño on record in 2015/2016 (Anderson et al., 2016; Baxter & Nigam, 2015; Di Lorenzo & Mantua, 2016; Joh & Di Lorenzo, 2017; Menge et al., 2011). The oceanographic indices, the North Pacific Gyre Oscillation (NPGO) and the PDO exhibited persistent (about 2 years) abnormal trends that led to a prolonged marine heatwave in the Northeast Pacific in 2014/2015, the largest in scale and longest ever recorded (Anderson et al., 2016; Baxter & Nigam, 2015; Joh & Di Lorenzo, 2017). This marine heatwave manifested into a historically severe El Niño event, measured in part by the Southern Oscillation Index (SOI) at the end of 2015 that lasted through 2016 (Di Lorenzo & Mantua, 2016). During these extreme, and especially prolonged, events, recruitment of new individuals in rocky intertidal habitats of the Northeast Pacific is severely impacted (Connolly & Roughgarden, 1999; Gouhier et al., 2010;

Menge, 2000; Menge et al., 2011). An increase of upwelling in the Northeast Pacific, as measured by the Coastal Upwelling Transport Index (CUTI) and Biological Effective Upwelling Transport Index (BEUTI), has been linked to difficulties in settlement for the planktonic stage of invertebrates and algae to establish in rocky intertidal habitats (Connolly & Roughgarden, 1999; Jacox et al., 2018). It is with this context that my research is prepared to investigate long-term change and biogeographical range shifts in the rocky intertidal environment of an island refuge and marine sanctuary.

Marine sanctuaries play a key role in long-term ecological monitoring. GFNMS has conducted yearly surveys of the rocky intertidal on the Farallon Islands since 1993, with this study focusing on data from 1993 – 2011 due to methodological changes in later surveys (Roletto et al., 2014). This research uses an existing rocky intertidal dataset from the GFNMS on the Farallon Islands. Roletto et al. (2014) identified three trends in this dataset: (1) decrease of mean percent cover of non-crustose algal species; (2) increase in mean percent cover of crustose algal species; (3) increase in mean percent cover of uncolonized area. These changes suggest a shift toward habitat simplification, with formerly upright species being replaced by crustose species or bare rock. Given the rarity of long-term intertidal surveys on islands with this level of protection from anthropogenic influences, this dataset is uniquely positioned to inform ongoing analyses of climate impacts on California's intertidal zones, particularly on islands protected from human disturbance like the Farallones.

The species found on the Farallones's rocky intertidal exhibit diverse dispersal methods, yet it remains unclear whether the same mechanisms that are occurring on the mainland are happening on the islands. Mainland populations often rely on extensive coastal habitats and

connected larval pathways, facilitating recruitment through ocean currents and direct dispersal (Shanks, 2009). However, island habitats like the Farallones are geographically isolated, potentially limiting larval influx and making successful recruitment more sporadic and dependent on unique oceanographic conditions, such as rare, favorable current patterns or high larval output from nearby populations (Gaines et al., 2015; Siegel et al., 2003). This study investigates the possible drivers behind this observed decline in intertidal cover in upright species, examining thermal stress due to climate change and potential poleward migration trends as seen on the mainland. By analyzing the GFNMS long-term dataset in conjunction with environmental and oceanographic data, this research aims to elucidate the ecological responses of Farallon Island rocky intertidal communities and contribute valuable insights for understanding climate impacts in protected island ecosystems.

By revealing the environmental drivers that may explain the ecological responses in the rocky intertidal on the Farallon Islands through in-depth analysis of the GFNMS long-term dataset, we can use these results to evaluate possible climate change impacts in the rocky intertidal during 1993 to 2011. The frequent semi-annual sampling of the GFNMS rocky intertidal team's data serves as a useful tool to explain the persistent decline of rocky intertidal species on the Farallon Islands and add to the scant body of rocky intertidal species trend research for island refuges in marine sanctuaries in the Northeast Pacific.

My research is poised to analyze the observed trends in cover of algae and sessile invertebrates in this habitat by asking: (1) Are variations in air temperature, SST, and SSS associated with changes in cover?; (2) Does cover respond to ocean climate patterns (NPGO,

PDO, SOI, CUTI, BEUTI)?; (3) Are the biogeographical poleward range shifts that are seen on the mainland exhibited on the Farallones?

Methods

Study Area – USFW Farallon Island Refuge in the GFNMS

This study uses a long-term dataset from the GFNMS to analyze intertidal species cover. Established in 1981, the GFNMS encompasses the Farallon Islands, located approximately 30 miles (48 km) west of San Francisco, California (Figure 1) (Office of National Marine Sanctuaries, 2017). These granite islands host diverse marine and terrestrial species and are influenced by upwelling in the California Current, one of the world's most productive regions (Capitolo, 2009). The California Current is characterized by cold, nutrient-rich current flowing southward along the coast (Checkley & Barth, 2009). This current originates from the North Pacific and plays a critical role in the upwelling process along the coast, bringing nutrients from deeper waters to the surface (Huyer, 1983). The Farallon Islands are situated to the north of the strongest flow of the California Current but still experiences its effects, particularly in colder months when the current is more prominent. Point Blue Conservation Science (Point Blue) has managed scientific monitoring on the islands since the designation of the USFWS Farallon Island Refuge in 1968 (Capitolo, 2009). The relative inaccessibility and protection of the Farallones make their rocky intertidal habitats suitable for studying ecological changes with minimal direct human disturbance (Lucas & Smith, 2016; White, 1995).

I surveyed the 1993 – 2011 GFNMS survey sites in February 2020. The winter season on the Farallones is characterized by intense pinniped use, especially northern elephant seals

(*Mirounga angustirostris*) during this time (Hastings & Sydeman, 2002; Lee et al., 2018; Nur et al., 2022). Each site varied in terms of exposure to wave action, habitat use by marine mammals and birds, slope, and habitat rugosity – a measure of surface complexity that affects habitat suitability for intertidal organisms (Connell, 2007). Most of the original epoxy markers used to demarcate the permanent survey quadrats were challenging to locate due to wear and site accessibility issues. Given the presence of vulnerable Northern fur seals (*Callorhinus ursinus*) and their pups, Maintop Island sites were not accessible during the February 2020 ground-truthing.

GFNMS Intertidal Survey Methods and Dataset

Since 1993, GFNMS biologists have conducted annual rocky intertidal surveys on the two South Farallon Islands: Maintop and Southeast Farallon Island (SEFI) (Figure 2) (Roletto et al., 2014). Each site includes several long-term study plots, with sampling conducted during the lowest annual tides in accessible locations, marked by permanent epoxy quadrats (Figure 4 – 6). Sampling involved point-intercept counts of species in a grid within quadrats, recording species cover at 50 sampling points per quadrat.

Six long-term study areas exist on the two largest South Farallon Islands (Figure 2). Four sites are on the larger SEFI and two are on Maintop. Sites were chosen to represent the various rocky intertidal habitats on the islands, considering factors like cardinal direction and habitat substrate, such as areas with and without sand, to capture the range of environmental conditions. Site accessibility was also an important factor, ensuring consistent and safe monitoring over time. The sampling season is determined by accessibility of the sites during the

lowest tides of the year during daylight hours, limiting sampling to the end of fall, winter, and summer seasons. As seabird populations rebounded, sampling was discontinued in the summer to accommodate nesting colonies. Each site had three to four permanent quadrats, placed in the middle and high intertidal zones. Due to the steep terrain of most rocky intertidal sites on the Farallones, these zones are narrow at most locations. A random number system was used to choose the direction and distance from each permanent quadrat resulting in about 1 to 3 randomly placed quadrats. All quadrats were 30 x 50 cm ($0.15m^2$) and underwent point-intercept sampling of 50 points each, one point for each equal-sized rectangle in a grid. Permanent quadrat locations were chosen based on accessibility within each site, with corners marked by epoxy. Tidepools, all sea stars, mobile invertebrates, and highly rugose areas were avoided in both the permanent and random quadrats. While these exclusions simplify data collection and focus on specific community components, they could potentially overlook important aspects of intertidal biodiversity and ecological interactions.

Both environmental and survey data were processed in R (R Core Team, 2023), with GFNMS intertidal survey data from Microsoft Access and transposed in Excel to align species cover with environmental conditions over time. Monthly averages of air temperature, SST, and SSS were calculated, and survey data was aligned with environmental data lagged by three months to reflect the timescale of environmental and climatic impacts on species cover (Menge et al., 2009).

Ocean-Climate Conditions and Oceanographic Indices

Ocean-climate conditions at the Farallones are measured daily, with air temperature recorded on SEFI while SST and SSS are sampled from Dead Sea Lion Flat (Figure 2). Air temperature is recorded from a thermometer, SST is measured with a submersible thermometer, and SSS is sampled into vials to be determined in a lab on the mainland. The GFNMS endures a distinct combination of influences from surrounding water masses such as nutrient-rich cold water from the depths cycled through seasonal upwelling and downwelling, water from the ocean at large, and outflow of differently salinized water from San Francisco Bay (Wing et al., 1998).

There are several oceanographic indices that represent climatic forces in this region of the Northeast Pacific. I used the NPGO, PDO, SOI, CUTI, and BEUTI to see if these large-scale climate conditions had correlations with species cover. Each large-scale ocean-climate pattern is indexed on a monthly scale and came from multiple sources, BEUTI and CUTI are specific to 37°N latitude (Di Lorenzo et al., 2008; Jacox et al., 2018; *Pacific Decadal Oscillation (PDO)*, 2017; *Southern Oscillation Index*, 2020). NPGO describes currents that influence sea surface height (SSH) anomalies in my study region which can be used to explain variations in salinity, nutrients, and chlorophyll-a concentrations (Fisheries, 2022). PDO characterizes anomalies of SST in the North Pacific (Mantua, N. J., 1999; *Pacific Decadal Oscillation (PDO)*, 2017). SOI describes variation in SST obtained from measurements of sea level pressures over Tahiti, French Polynesia and Darwin, Australia (*Southern Oscillation Index*, 2020). For this reason, SOI is key when gauging the severity of El Niño and La Niña events. SOI standardizes fluctuations in SST on a year-by-year basis in contrast to PDO and NPGO that describe SST and SSH, respectively, on

an interdecadal timespan (http://www.cgd.ucar.edu/cas/catalog/climind/soi.html,

http://jisao.washington.edu/pdo/, http://eros.eas.gatech.edu/npgo/). Changes in water

temperature and salinity are tied into these indices, which are factors in the impact of species

cover in the rocky intertidal. CUTI describes the volume of nutrient export of upwelling in the

water column while BEUTI is focused on nitrate flux of upwelling in the area (Jacox et al., 2018).

BEUTI and CUTI are important to consider for this analysis because they describe the amount

and type of nutrients that are available to the rocky intertidal organisms on the Farallones from

the important upwelling that occurs in the summer (Barth et al., 2007; Fenberg et al., 2015; Iles

et al., 2012; Menge et al., 2003; Reddin et al., 2015).

Data were evaluated on a monthly timescale, accounting for season lags between

climate changes and species responses (Menge et al., 2008). To understand the decline in non-

crustose species documented by Roletto et al. (2014), species cover data was separated into

three groups: (1) upright algae; (2) non-crustose sessile invertebrates and (3) combined cover.

Crustose species were excluded to focus on changes of upright species cover (Connell & Russell,

2010). This choice reflects findings by Roletto et al. (2014), which showed an increase in

crusting species alongside a decrease in upright species across all study sites. By concentrating

on upright species, this research focuses on identifying the drivers behind these declines,

specifically investigating whether environmental and oceanographic factors disproportionately

impact non-crusting organisms. Excluding crustose species allows for a targeted analysis of

changes relevant to structural complexity and habitat functionality in this rocky intertidal

habitat. Crustose species include bryozoans, crusting algae, and sponges which make up

approximately 10% of the total species counts in the dataset. These groups were identified broadly, with few instances of genus- or species-level identification.

Research Questions and Analysis

1. **Are variations in air temperature, SST, and SSS associated with changes in cover?** The focus of this question is on three main environmental drivers that have quantitative effects on algal and sessile invertebrate physiology and ecology on a weather-scale: (1) low-tide air temperature; (2) SST and (3) SSS. These datasets from the Farallones provide a localized resolution that allows for direct comparisons with intertidal survey data. Monthly averages for air temperature, SST, and SSS from 1983 to 2020 were analyzed, with species cover calculated as a percent based on point-intercept counts per quadrat. Cover data were divided into three main categories based on ecological characteristics: (1) upright algae; (2) non-crustose sessile invertebrates and; (3) all upright species (1 and 2 combined) to examine the observed declines in upright cover noted by Roletto et al. (2014). A set of 45 candidate models was constructed to evaluate all combinations of air temperature, SST, SSS, and the interactive qualities of SST and SSS across each cover category, with AIC model ranking used to identify the best-fitting models in R (Mazerolle, 2020). AIC stands for Akaike Information Criterion which is a technique for ordering models by best fit. The purpose of AIC is to estimate the quality of each model, relative to each of the other models. After the best model(s) were determined, I took a closer look at the respective top linear mixed models to determine the extent that the given model answers my research question, assessing the strength of the associations.

2. **Does cover respond to ocean climate patterns (NPGO, PDO, SOI, BEUTI, CUTI)?** To assess whether large-scale oceanographic indices influence species cover, this question focuses on five key indices: (1) NPGO; (2) PDO; (3) SOI; (4) CUTI and (5) BEUTI that provide a climate-scale perspective on this region of the Northeast Pacific. Given the different growth and survival rates of intertidal organisms in response to long-term shifts, these indices offer a broader context for understanding community dynamics. Species from the survey data were again divided into three groups: (1) upright algae; (2) non-crustose sessile invertebrates and; (3) all upright species (1 and 2 combined) creating 96 candidate linear mixed models to test index combinations across each cover group. These models were ranked by AIC for fit and evaluated to determine if large-scale climate indices had a measurable effect on intertidal cover (Menge et al., 2008).

3. **Are the biogeographical poleward range shifts that are seen on the mainland exhibited on the Farallones?** Climate warming has shifted marine species ranges poleward globally, with some intertidal species in California moving up to 50 km per decade (Kennedy et al., 2019; Yalcin & Leroux, 2017). Range shifts depend on species' persistence, dispersal, and establishment, with studies on mainland habitats revealing a consistent northward trend for southern species and declines for northern species (Parmesan & Yohe, 2003; Sanford et al., 2019; Sorte et al., 2010; Sunday et al., 2012), although there is at least one example of species shifting southward (Chang, 2009). This analysis aimed to utilize the GFNMS 1993 – 2011 dataset to test for similar shifts on the Farallones by examining long-term cover data to identify increases in southern species and decreases in northern species. Following Barry et al. (1995) and Yalcin & Leroux (2017), the species were classified into Northern, Southern,

and Cosmopolitan groups based on geographic range definitions drawn from multiple sources (Figure 3) (Abbott & Hollenberg, 1976; Blanchette et al., 2008; Ricketts & Calvin, Jack, 1968). Northern species are classified by having a historical southern limit of Point Conception. Southern species have a northern limit of Cape Mendocino. Cosmopolitan species range limits exceed Point Conception and Cape Mendocino. Northern species included *Anthopleura xanthogrammica*, *Callithamnion pikeanum*, and *Microcladia borealis*; Southern species included *Cladophora graminea, Myriogramme variegata*, and *Tetraclita rubescens*; and Cosmopolitan species included *Balanus spp.*, *Corallina vancouveriensis*, and others with broad geographic ranges. *Myriogramme variegata* is plucked from the dataset because it is considered rare, typically hyperlocal to Pacific Grove, California (Abbott & Hollenberg, 1976).

The objective here was to classify species as experiencing expansion, contraction, or stability over time based on significant changes in percent cover by geographic category. Mann-Kendall tests, applied using the "Kendall" package in R, were employed to detect trends across cover categories (Abe et al., 2021; McLeod, 2022). This approach provided insights into whether range shifts observed on the mainland were mirrored in the isolated Farallon Island ecosystem, revealing response potentially driven by climatic and ecological constraints.

Results

GFNMS Intertidal Survey Methods and Dataset

With guidance from members of the original 1993 – 2011 GFNMS survey team, all permanent quadrat locations on the SEFI survey sites were found. The SEFI sites (Blowhole Peninsula, Dead Sea Lion Flat, Low Arch, and Mussel Flat) had been surveyed more consistently than those on Maintop Island (Drunk Uncle Islet and Raven's Cliff), with survey gaps in 2004, 2005, 2008, 2009, and 2010. Consistent with the patterns published in Roletto et al. (2014), we observed an overall increase in crusting species and a decline in upright species across all sites.

Local environmental properties and large-scale ocean-climate indices

Environmental data from 1983 to 2020 were analyzed, showing that air temperature was warmer than average from 1992 to 1999 and cooler from 1999 to 2011. SST reflected similar trends, while SSS dropped below average in 1995 and then remained relatively constant throughout the study period. Large-scale climate indices – NPGO, PDO, and SOI – correlated with local environmental trends.

While the AIC model ranking analysis identified the best-performing models relative to each other, none of these models provided a strong explanatory power for species cover, as indicated by consistently low R^2 values across all groups. This means that, although certain combinations of the local environmental properties and large-scale ocean-climate indices rated higher in model comparisons, these variables alone do not adequately explain the trends observed in species cover and likely point to additional factors not analyzed in this research.

Associations Between Environmental Variables and Species Cover

1. **Are variations in local air temperature and water properties (like SST and SSS) associated
   with changes in cover?** The AIC model ranking analysis yielded three top-ranking models
   based on species cover categories: (1) all upright sessile non-crusting species, (2) upright
   non-crusting algae, (3) upright non-crustose sessile invertebrates. Top models show
   significant ecological associations between air temperature, SST, SSS, and the interaction of
   SST and SSS with upright species cover, whether all species groups were examined together
   or separately as algae and invertebrates.

   The top influencing factor for all upright species was air temperature and SSS (Table 1). The
   model showed significant positive association between air temperature and cover, and a
   significant positive association between salinity and cover. However, the explanatory power
   of the model was low (R^2 = 0.035) suggesting additional ecological factors also influenced
   species distribution and abundance (Table 2).

   For the upright non-crusting algae group, the SSS model ranked highest (Table 1). This
   model suggested a significant positive ecological association between SSS and upright algal
   species. The linear model for SSS had a low R^2 value of 0.0007, suggesting other drivers of
   algal cover beyond the scope of this study are also at play (Table 3).

   Among the upright non-crustose invertebrate group, the top model was the interaction of
   SSS and SST (Table 1), suggesting a negative ecological association between the interaction
   of SST and SSS on upright sessile invertebrates, but the overall model also had a low R^2
   value of 0.008 indicating other ecological drivers were also at play (Table 4).

Response of Species Cover to Large-Scale Ocean-Climate Patterns

2. **Does cover respond to large-scale ocean-climate patterns (NPGO, PDO, SOI, CUTI, BEUTI)?**

   The AIC model ranking results for this question were separated into the same three groups: (1) all upright sessile non-crustose species, (2) upright non-crustose algae, (3) upright non-crustose sessile invertebrates. Responses to large-scale ocean-climate patterns indicated significant ecological associations between the large-scale climate patterns and the intertidal species.

   For the upright species group, the AIC model ranking identified two top models: (1) NPGO + SOI + CUTI + BEUTI; and (2) NPGO + SOI + BEUTI (Table 5). The top models were 30% and 28% more likely to explain response in cover of all upright species, respectively. The top model indicated a significant negative ecological association between NPGO and SOI with cover for all upright species, a significant positive ecological association between BEUTI and cover for all upright species, and non-significant association with CUTI. The overall explanatory power for this model was low (R^2 0.101) suggesting other ecological drivers were also at play (Table 6).

   In the algal species group, the top ranked AIC model included NPGO + PDO + CUTI + BEUTI. This model indicated significant negative ecological associations between NPGO, PDO, and CUTI with cover of non-crustose upright species, and a significant positive ecological association between BEUTI and cover of upright algae species. The overall explanatory value of the model was low, (R^2 0.037) suggesting other environmental drivers were also at play (Table 7).

For the invertebrate group, SOI ranked highest (Table 5), indicating a significant positive ecological association between SOI and cover of upright sessile invertebrate species, but with low R^2 value of 0.003 (Table 8), emphasizing that large-scale indices, while potentially influential, do not wholly account for changes in intertidal cover in this analysis.

Biogeographical Range Shifts

3. **Are the biogeographical poleward range shifts that are seen on the mainland exhibited on the Farallon Islands?** The Mann-Kendall test showed that of the Southern species group, *Cladophora graminea* had a positive z-score and significant p-value indicating an increasing trend. In contrast, all Northern species showed declining trends without significant p-values (Figure 8).

When species were grouped by geographic range in analysis, all groups yielded negative z-scores, with only the Cosmopolitan group displaying a significant decline (Figure 9).

Discussion

This analysis reveals that shifts in community composition of rocky intertidal organisms on the Farallon Islands are more complex than anticipated. We found ecological associations with local oceanographic variables and with large-scale climate patterns, but the overall explanatory power of the variables included in our analysis was low, indicating that other processes and environmental drivers were also at play.

Most research on biogeographical range shifts in rocky intertidal habitats has focused on mainland populations, leaving a knowledge gap in understanding island communities such as

those on the Farallon Islands. This study aimed to explore the relationships between intertidal species cover and both local and large-scale oceanic conditions. The correlation of local environmental trends with large-scale climate indices supports the idea that regional oceanographic patterns are linked to changes observed in the intertidal community (Menge, Daley, Wheeler, Dahlhoff, et al., 1997). My findings reflect similar trends to those reported by Roletto et al. (2014), with a marked decline in upright species and an increase in crustose species over the study period. This trend aligns with findings from other intertidal studies suggesting these changes may be related to shifts in environmental or physical conditions (Connell & Russell, 2010). For example, warming temperatures in the northeastern Pacific have been associated with similar shifts in species composition in rocky intertidal communities, as species more tolerant to desiccation and thermal such, such as crustose algae, tend to increase, while upright species decline (Harley et al., 2006; Helmuth et al., 2002). Such patterns are not isolated to the Pacific, as studies from coastal regions around the world also show comparable changes in community composition as temperatures rise, further indicating that intertidal communities on the Farallon Islands may be responding to similar environmental stressors (Amstutz et al., 2021; Marion & Bergerot, 2018; Rivadeneira & Fernández, 2005; Thompson et al., 2002). However, based on my analysis, these stressors cannot be fully explained by local environmental or large-scale oceanographic conditions alone.

1. **Local Environmental Variables and Species Cover**

In answering my first research question, "Are variations in air temperature, SST, and SSS associated with changes in cover?" the results indicated that these variables while significantly associated with changes in cover, are not the main environmental drivers of rocky intertidal

cover on the Farallon Islands. While the model that considered air temperature and SSS together ranked the highest, their low R^2 values suggest these variables alone are insufficient to account for observed declines. Variability across sites is important to point out here, as the sea surface data is recorded only at a north-facing site. This finding points to other potential ecological or environmental factors that could drive these patterns, such as nutrient availability, biotic interactions (e.g., competition, predation, or trampling), or habitat-specific variables that were not measured. This supports the suggestion in Roletto et al. (2014) that the trends can be explained by pinniped trampling.

The impact of pinniped trampling on the rocky intertidal is worth investigating. Future studies that examine the correlation between pinniped presence and species cover would help validate this hypothesis, potentially revealing more about the mechanisms behind declining upright species (Boersma & Parrish, 1999). Site accessibility for pinnipeds can be assessed by observation records and the slope of the intertidal combined with its relation to tidal height.

2. Large-Scale Ocean-Climate Patterns and Species Cover

My second research question asked, "Does cover respond to ocean climate patterns (NPGO, PDO, SOI, CUT, BEUTI)?". Higher values of the CUTI and BEUTI indices during this period suggest strong upwelling, which likely influences nutrient availability and habitat conditions (Checkley & Barth, 2009). This analysis yielded inconclusive results, with low explanatory power for these oceanic indices in predicting intertidal cover changes. While indices like BEUTI, which indicates upwelling, showed some positive effects, most indices negatively impacted species cover but with minimal explanatory strength (low R^2 values). This suggests that, although

ocean-climate patterns may influence intertidal communities, they are likely not the sole

drivers of observed trends on the Farallon Islands perhaps due to the resolution disparity of the

indices (large) with the rocky intertidal sites (small). This finding suggests that island

communities like those on the Farallon Islands may have unique ecological dynamics compared

to mainland ecosystems (Graham & Largier, 1997).

3. Biogeographical Range Shifts

In addressing the third research question, "Are the biogeographical poleward range

shifts seen on the mainland exhibited on the Farallon Islands?" the results do not suggest

strong evidence of a range shift. While *Cladophora graminea*, a southern species, displayed a

positive z-score in the Mann-Kendall test results, indicating an increase, no significant patterns

were observed for the Northern species group. This suggests that the range shift dynamics

commonly observed on the mainland are not seen on the Farallon Islands. This may be due to

the isolation of the Islands, and that the Islands' distance from the mainland can act as a barrier

to colonization or limit recruitment, affecting the likelihood of range shifts (Helmuth et al.,

2002).

The significant decrease in the Cosmopolitan group's cover further supports the idea

that other ecological or environmental factors, possibly unrelated to climate change, are driving

the observed patterns. Given that the bulk of the rocky intertidal species surveyed on the

Farallon Islands have broad geographic distributions, such as spanning from Baja California to

British Columbia, barriers to successful colonization may be due to the distance and isolation of

the islands relative to mainland populations (Abe et al., 2021; Davenport & Stevenson, 1998; Engle, 1994; MacArthur & Wilson, 1967; Sotka & Palumbi, 2006).

Implications of Community Composition Shifts

The shift from upright species to encrusting species observed in this research mirrors global trends where encrusting organisms often replace upright species under conditions of increased disturbance or environmental stress (Airoldi, 2003; Connell & Russell, 2010). This could imply that local temperature changes on the Farallon Islands or altered oceanographic conditions in the California Current are favoring species with traits more resilient to physical stressors (Dudgeon et al., 2010). Encrusting species are typically more tolerant of variable or extreme environmental conditions, whereas upright species might be more vulnerable to fluctuations, such as temperature instability or nutrient limitation (Barry et al., 1995). Future studies could benefit from investigating localized physical stressors, such as pinniped trampling, that may contribute to this community shift.

Limitations and Recommendations for Future Research

One notable limitation of this study was the absence of data on what life stage the algae and invertebrates were in when they were being counted. This could be significant since juveniles are more vulnerable to climatic stressors than adults, potentially able to tell a story about the success and failure of recruitment in the surveyed sites (Hughes et al., 2000; Menge, 2000; Porri et al., 2006). The rapid lifecycle of macroalgae, for example, suggests that findings related to low-tide air temperature, SST, and SSS might be more directly relevant to algal cover than invertebrates, which often respond over longer timescales (Steneck & Dethier, 1994).

Similarly, SOI, PDO, and NPGO may be better indicators for invertebrate responses, whose responses to climate variation could manifest over extended periods (Menge et al., 2002).

A more comprehensive understanding of these changes could be achieved by incorporating data from additional environmental variables, particularly those affecting intertidal juveniles and early life stages. Long-term studies and datasets remain crucial for this purpose. Not only do they allow us to observe ecological changes and predict future trends, but they also offer insight into ecosystem resilience and adaptability (Ducklow et al., 2009; Hughes et al., 2017; Lindenmayer et al., 2010; Magnuson, 1990). Without such data, snapshots may miss the broader impacts of climate change and yield incomplete assessments of ecosystem health.

Not being able to survey the rocky intertidal on the Farallon Islands during the summer season hinders us from seeing the full picture of cover in this habitat. The summer is the most productive time for photosynthesis. Perhaps remote sensing techniques could provide valuable data during this season without disturbing the nesting seabird populations.

The Value of Long-Term Monitoring and Holistic Climate Analysis

There is an increasing need to view climate impacts not solely as temperature increases but as patterns of climatic instability. Fletcher et al. (2016) describes this as a "pendulum swing", where temperatures increasingly reach and remain at extremes, causing stress on vulnerable ecosystems. Long-term datasets are invaluable in capturing such dynamics and are instrumental for developing predictive models and guiding conservation efforts. Ducklow et al. (2009) and Lindenmayer et al. (2012) underscore the importance of such datasets, which can

detect ecological responses to climate change, inform models, and aid in the sustainable management of ecosystems.

Conclusion

While this project found that local environmental and large-scale oceanographic factors had limited explanatory power for species cover changes, the observed trends highlight the need for continued monitoring and research. The unique conditions on the Farallon Islands, coupled with trampling by pinnipeds and other unexplored factors, likely contribute to the intertidal community dynamics observed here. A continued focus on long-term datasets and interdisciplinary approaches will be essential for understanding and conserving complex and dynamic island ecosystems.

Figures
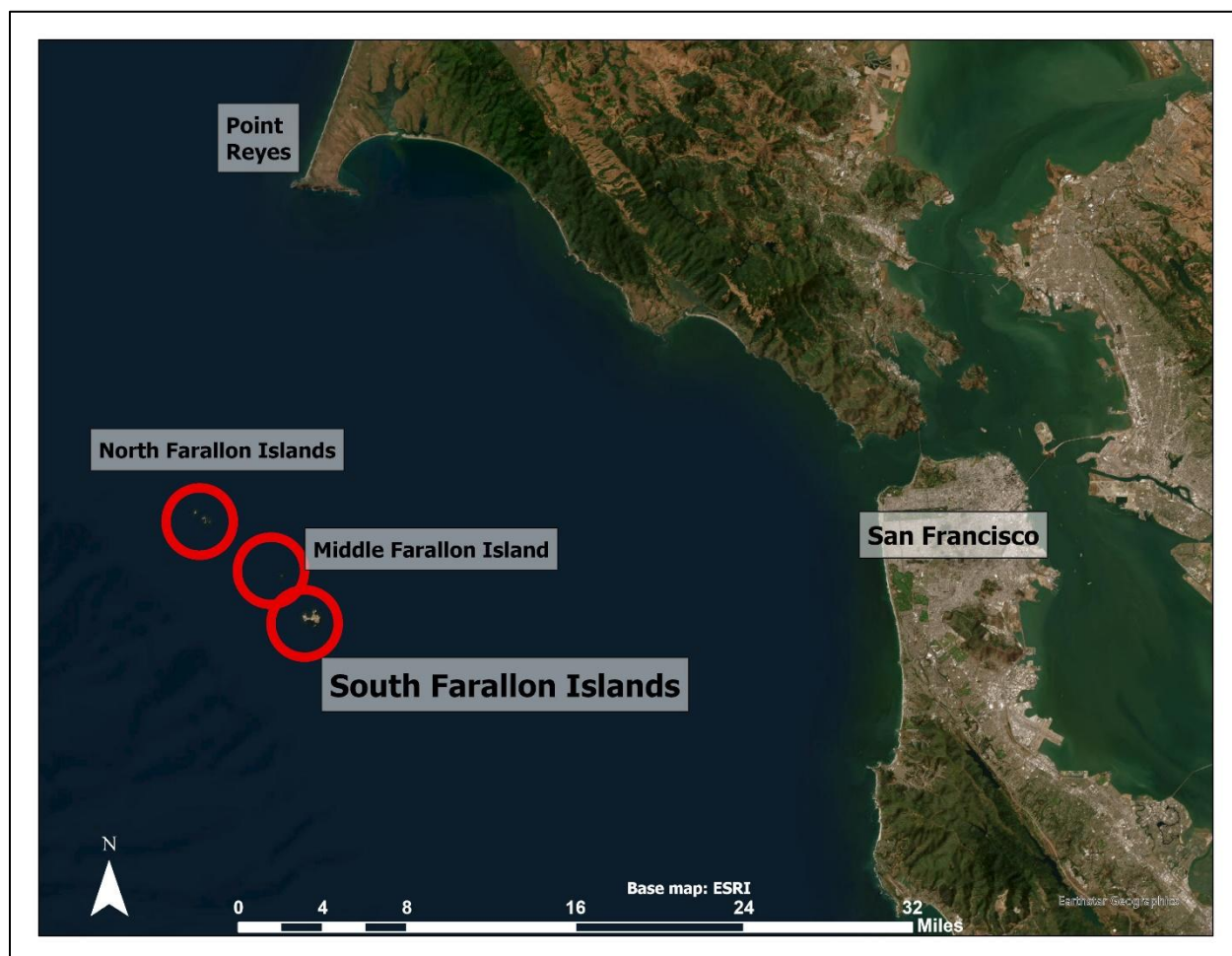
Figure 1. The Farallon Islands.
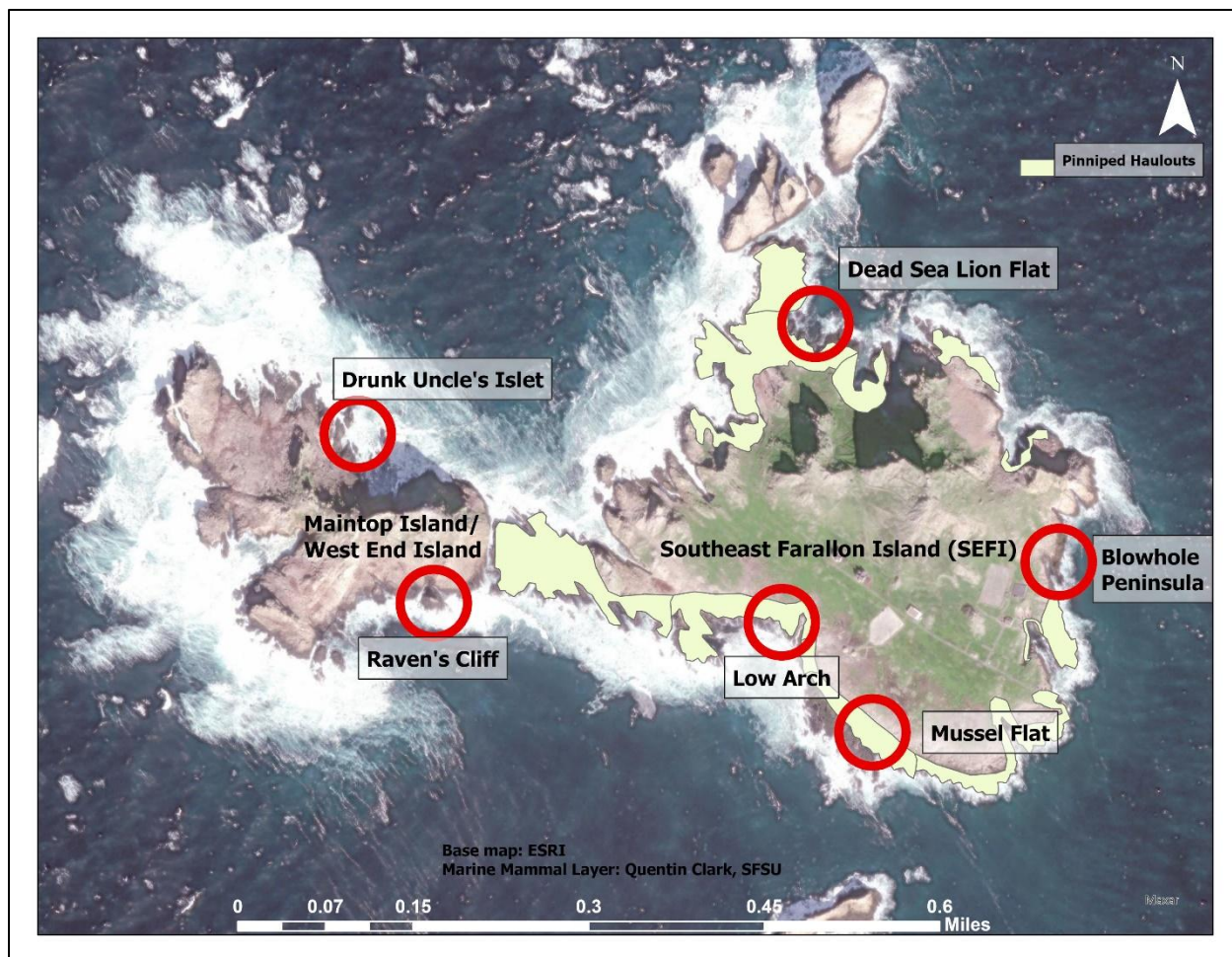
Figure 2. Greater Farallones National Marine Sanctuary Rocky Intertidal Survey Site map on the two south Farallon Islands. Red circles represent study areas. Pinniped haulouts are in yellow, data source Quentin Clark, San Francisco State University.
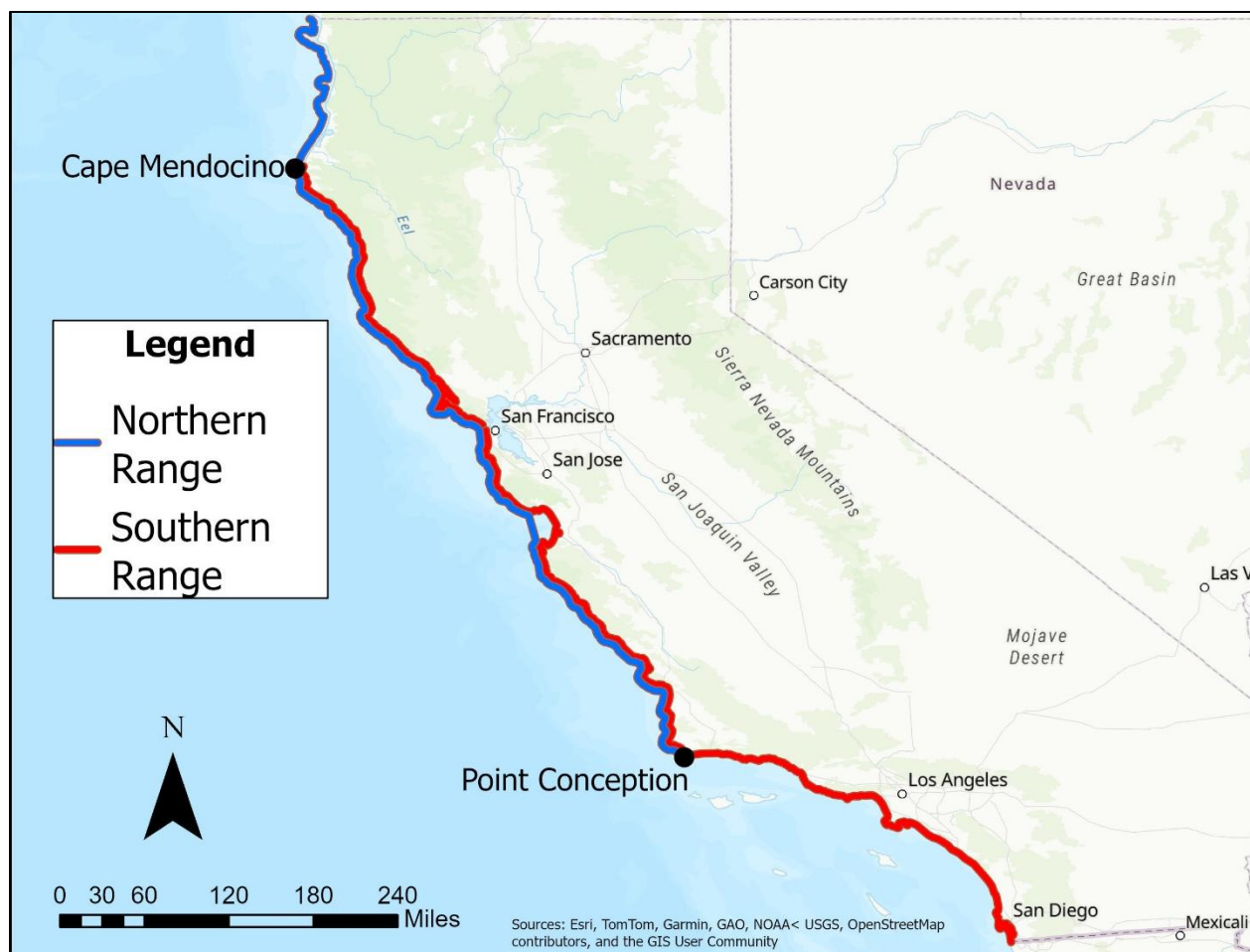
Figure 3. Biogeographic range boundaries for rocky intertidal species in California (Barry et al., 1995).
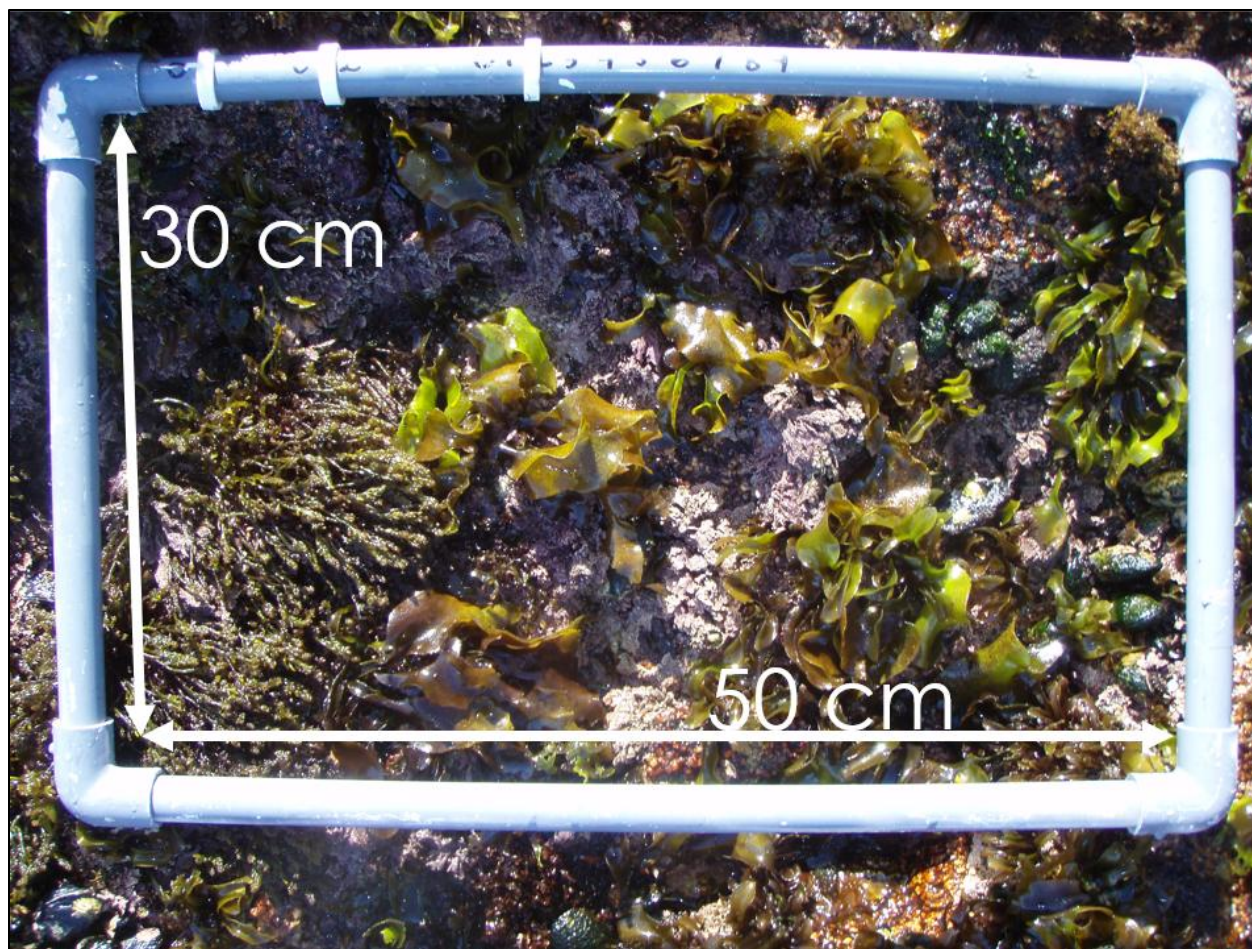
Figure 4. Quadrat 1 from Blowhole Peninsula, February 2020.

Figure 5. Quadrat 4 from Dead Sea Lion Flat, February 2020.

Figure 6. Quadrat 17 from Low Arch in February 2020.

Figure 7. Quadrat 19 from Mussel Flat in February 2020.
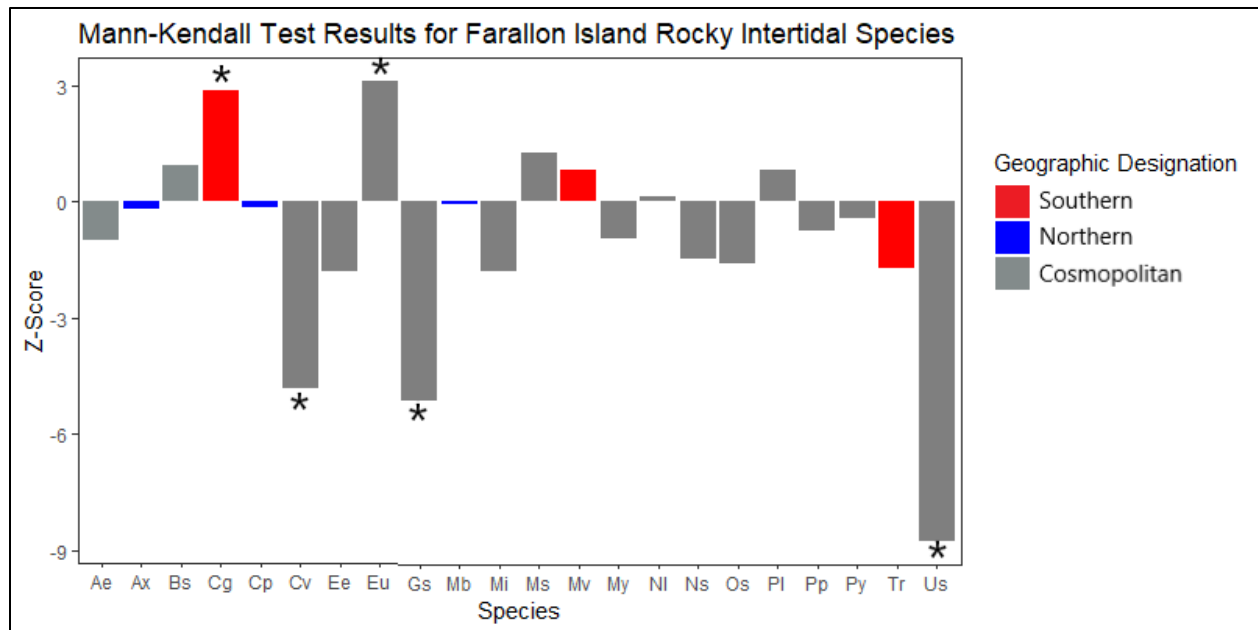
Figure 8. Z-scores from the Mann-Kendall Test by species to determine range shifts (Question 3). Positive z-scores indicate an increasing trend, negative z-scores indicate a decreasing trend. An asterisk indicates a significant p-value (less than 0.05).

Ae = *Anthopleura elegantissima*, Ax = *Anthopleura xanthogrammica*, Bs = *Balanus* spp., Cg = *Cladophora graminea*, Cp = *Callithamnion pikeanum*, Cv = *Corallina vancouveriensis*, Ee = *Egregia menziesii*, Eu = *Endocladia muricata*, Gs = *Gelidium* spp., Mb = *Microcladia borealis*, Mi = *Microcladia coulteri*, Ms = *Mastocarpus* spp., Mv = *Myriogramme variegata*, My = *Mytilus californianus*, Nl = *Neorhodomela larix*, Ns = *Neogastroclonium subarticulatum*, Os = *Osmundea spectabilis*, Pl = *Polysiphonia savatieri*, Pp = *Pollicipes polymerus*, Py = *Porphyra* spp., Tr = *Tetraclita rubescens*, Us = *Ulva* spp.
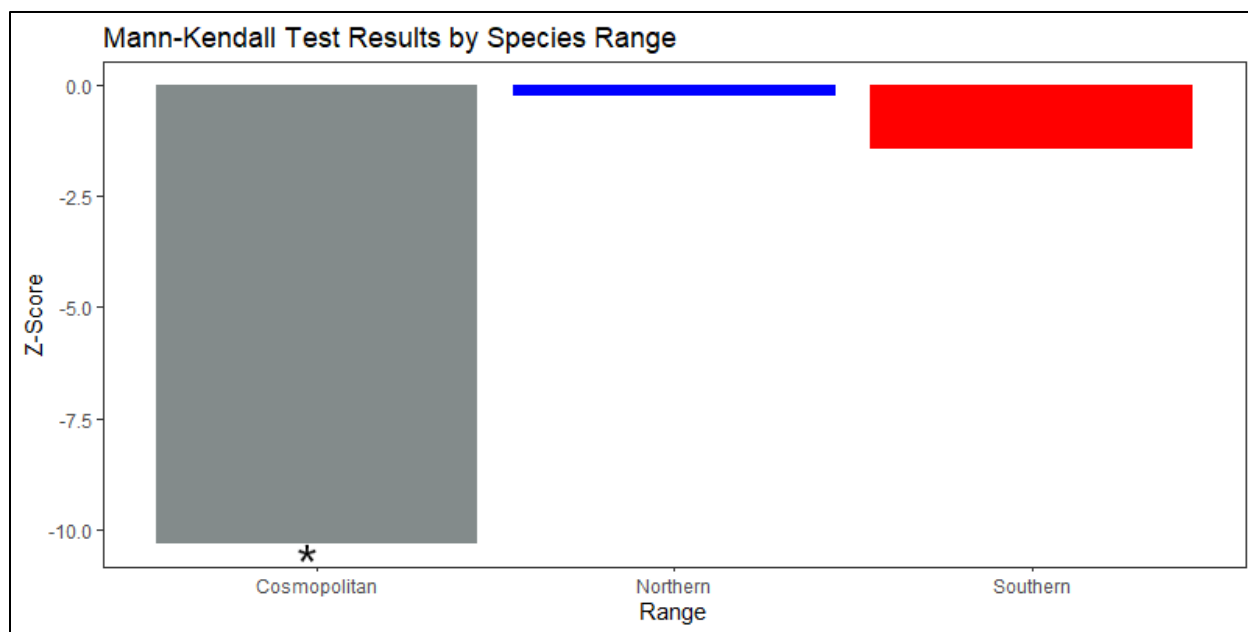
Figure 9. Z-scores from the Mann-Kendall Test by species range groups to determine species range shifts (Question 3). Positive z-scores indicate an increasing trend, negative z-scores indicate a decreasing trend. An asterisk indicates a significant p-value (less than 0.05).

Tables

Table 1. AIC ranked top models for all categories in Question 1. The plus sign "+" indicates additive variables, the colon ":" represents the interaction between variables.

Category of Upright Species Cover	Top Model	K	AIC	AIC Wt.	LL
All	Air temp. + SSS	4	7055.60	0.32	-3523.77
Algae (upright, non-crusting)	SSS	3	6847.81	0.13	-3420.89
Invertebrates	SST:SSS	3	6346.19	0.21	-3170.08
K = multiplier penalty term depending on the number of terms in the model. AIC = Aikaki Information Criterion (AIC); models with lower AIC values contain more information. $AIC Wt$ = weight of evidence for given model. LL = log-likelihood of given model.					

Table 2. Results for the top ranked model for the effects of heat stress and salinity on upright species cover on the Farallon Islands. The top ranked model for species cover was: mean air temperature + mean sea surface salinity (SSS). *Estimates* = slope of model; sign (-/+) indicates the effect of each explanatory factor.

Top ranked linear model for local air temperature and water properties on all upright species.				
			Cover	
Predictors	*Estimates*	*std. Error*	*CI*	*p*
Intercept	-74.97	41.06	-155.57 – 5.63	0.068
Air temperature	2.29**	0.75	0.82 – 3.77	0.002
SSS	3.65**	1.32	1.07 – 6.24	0.0006
Observations			753	
R^2/ R^2 adjusted			0.035 / 0.033	
			*p<0.05 **p<0.01 ***p<0.0001*	
CI = 95% confidence intervals p = p-value R^2 = variation explained by the model. Low R^2 implies that the model does not fit the data. R^2 adjusted = modified version of R^2 adjusted for predictors that are not significant in the model; lower R^2 means that not-significant input variables are not contributing value to the model.				

Table 3. Results for the top ranked model for the effects of heat stress and salinity on upright (non-crustose) algae species cover on the Farallon Islands. The top ranked model for species cover was: SSS. See Table 2 for abbreviations.

Top ranked linear model for local air temperature and water properties on upright algal species.				
		Cover		
Predictors	*Estimates*	*std. Error*	*CI*	*p*
Intercept	-37.38	35.30	-106.67 – 31.91	0.290
SSS	2.46*	1.06	0.38 – 4.54	0.021
Observations		753		
R^2/ R^2 adjusted		0.007 / 0.006		
			*p<0.05 **p<0.01 ***p<0.0001	

Table 4. Results for the top ranked model for the effects of heat stress and salinity on upright (non-crustose) invertebrate species cover on the Farallon Islands. The top ranked model for species cover was: SST:SSS. The R^2 value of 0.008 indicates that other ecological factors are affecting cover of upright (non-crustose) invertebrate species. See Table 2 for abbreviations.

Top ranked linear model for local air temperature and water properties on upright sessile invertebrates.				
		Cover		
Predictors	*Estimates*	*std. Error*	*CI*	*p*
Intercept	38.72 ***	8.36	22.31 – 55.12	<0.001
Interaction between SST and SSS	-0.05*	0.02	-0.09 – -0.01	0.012
Observations		753		
R^2/ R^2 adjusted		0.008 / 0.007		
			*p<0.05 **p<0.01 ***p<0.0001	

Table 5. AIC ranked top models for all categories in Question 2. The plus sign "+" indicates additive variables, the colon ":" represents the interaction between variables. See Table 1 for abbreviations.

Category of Upright Species Cover	Top Model	K	AIC	AIC Wt.	LL
All	NPGO + SOI + CUTI + BEUTI	6	7006.48	0.30	-3497.18
	NPGO + SOI + BEUTI	5	7006.59	0.28	-3498.25
Algae	NPGO + PDO + CUTI + BEUTI	6	6831.04	0.30	-3409.46
Invertebrates	SOI	3	6350.64	0.16	-3172.30

Table 6. Results for the top ranked models for the response of large-scale ocean-climate patterns on upright species cover on the Farallon Islands. The top ranked model for species cover was: NPGO + SOI + CUTI + BEUTI. See Table 2 for abbreviations.

Top ranked linear model for large-scale ocean-climate patterns on cover of all upright species.				
		Cover		
Predictors	*Estimates*	*std. Error*	*CI*	*p*
Intercept	75.43 ***	1.31	72.85 – 78.01	<0.001
NPGO	-5.15 ***	0.68	-6.49 – -3.81	<0.001
SOI	-1.34**	0.50	-2.33 – -0.35	0.008
CUTI	-7.24	4.96	-16.98 – 2.50	0.145
BEUTI	2.09**	0.65	0.82 – 3.35	0.001
Observations		753		
R^2/ R^2 adjusted		0.101 / 0.096		
			*p<0.05 **p<0.01 ***p<0.0001*	

Table 7. Results for the top ranked models for the response of large-scale ocean-climate patterns on upright algal species cover on the Farallon Islands. The top ranked model for species cover was: NPGO + PDO + CUTI + BEUTI. See Table 2 for abbreviations.

Top ranked linear model for large-scale ocean-climate patterns on cover of upright (non-crustose) algae species.				
		Cover		
Predictors	*Estimates*	*std. Error*	*CI*	*p*
Intercept	45.73***	1.21	43.36 – 48.10	<0.001
NPGO	-3.27***	0.64	-4.53 – -2.02	<0.001
PDO	-1.90*	0.77	-3.41 – -0.39	0.014
CUTI	-10.25*	4.50	-19.08 – -1.42	0.023
BEUTI	1.24*	0.56	0.14 – 2.33	0.027
Observations		753		
R^2/ R^2 adjusted		0.037 / 0.032		
			*p<0.05 **p<0.01 ***p<0.0001*	

Table 8. The top ranked models for the response of large-scale ocean-climate patterns on upright sessile invertebrate species cover on the Farallon Islands. The top ranked model for species cover was: SOI. See Table 2 for abbreviations.

Top ranked linear model for large-scale ocean-climate patterns on cover of upright sessile invertebrate species.				
			Cover	
Predictors	*Estimates*	*std. Error*	*CI*	*p*
Intercept	17.43***	0.61	16.23 – 18.62	<0.001
SOI	0.43	0.30	-0.17 – 1.02	0.163
Observations			753	
R^2/ R^2 adjusted			0.003 / 0.001	
			*p<0.05 **p<0.01 ***p<0.0001*	

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