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Decline of a North American rocky intertidal foundation species linked to extreme dry, downslope Santa Ana winds

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Foundation species are essential to ecosystem function, but their role as habitat providers is predicated on their spatial dominance. Worldwide, kelps, seagrasses, corals, and other marine foundation species have declined. This is true also for rockweeds, the canopy-forming analog of subtidal kelp forests in temperate rocky intertidal ecosystems. On the west coast of North America, dense beds of the rockweed *Silvetia compressa* occur across large biogeographic regions, benefitting numerous species by ameliorating physical stress caused by sun exposure, desiccation, heat, and wave disturbance. Like many rockweed species, *Silvetia* is long-lived, slow-growing, and short-dispersing – characteristics that reduce its resilience to disturbance. Using a generalized additive mixed-effects model with explicit spatial effects, we analyzed canopy cover data from 30 sites spanning 18 years, and we tested the hypothesis that *Silvetia* population trends are tightly linked to atmospheric climate conditions, particularly Santa Ana wind events (SAWs): strong, hot, and dry downslope winds that originate inland and move offshore. We 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, and 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. Our results suggest that 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.

KEYWORDS

ecosystem engineer, desiccation, rockweed, fucoid, offshore winds, prolonged desiccation events

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1 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 (Agardh, 1824) (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; Skamarock and Klemp, 2008). *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) 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 et al., 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

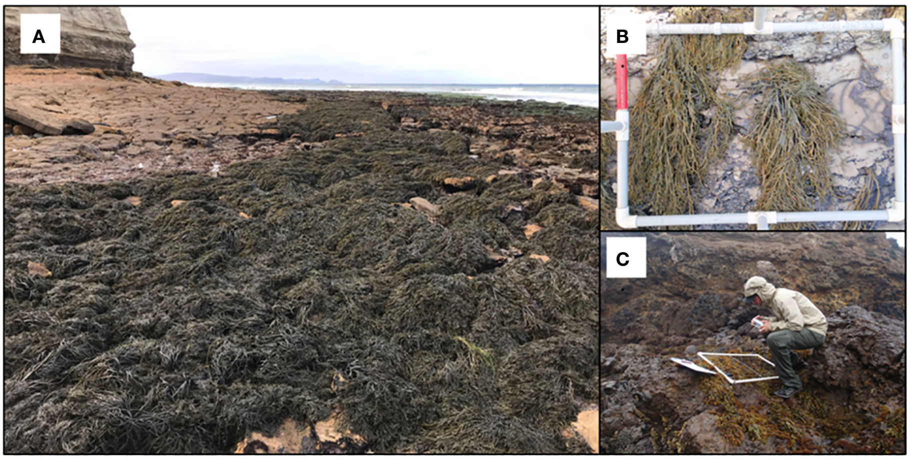

FIGURE 1
Rockweed, *Silvetia compressa*, forming large beds in the middle intertidal zone on the northwest side of Santa Rosa Island **(A)**; fixed plot established to document the percent cover of the rockweed, *Silvetia compressa* **(B)** (photos, S. Whitaker); lead author S. Whitaker scoring a fixed plot for rockweed **(C)** (photo, K. Chan).

frequency gradually increased beginning in 2000 (Li et al., 2016; see Figure 17 in Rolinski et al., 2019). 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.

2 Materials and methods

2.1 Study sites

Thirty long-term monitoring sites (Figure 2; Supplementary Table S1) 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

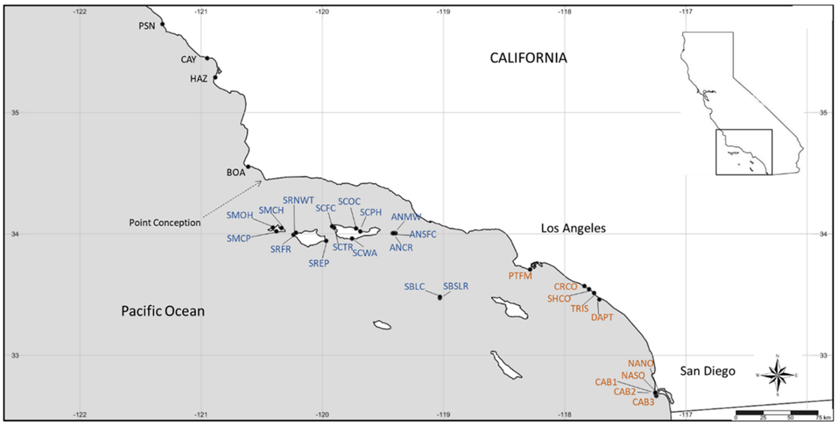

FIGURE 2
Map of long-term monitoring sites for *Silvetia compressa* used in this study. See Supplementary Table S1 for full site names and positions. Site abbreviations are color-coded by region (black = central California, blue = Channel Islands, orange = southern California).

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.

2.2 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). 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.

2.3 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.

2.4 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). *Site* (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., $meanD_d \times Region$) 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) (Supplementary Table S2). 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)]. To account for the extremes 0 and 1, response variable data were transformed using $(y \cdot (n-1) + 0.5)/n$ where n is the sample size (Smithson and Verkuilen, 2006).

Using GAMM, we analyzed the following equation:

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

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

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

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

$$Site_i \sim N(0, \sigma^2_{Site}) \qquad (1)$$

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*D_d using JMP Ver. 14.2.0 (SAS Institute Inc., 2018).

3 Results

3.1 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 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 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 (Figures 3, 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.

3.2 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; Supplementary Table S2). 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

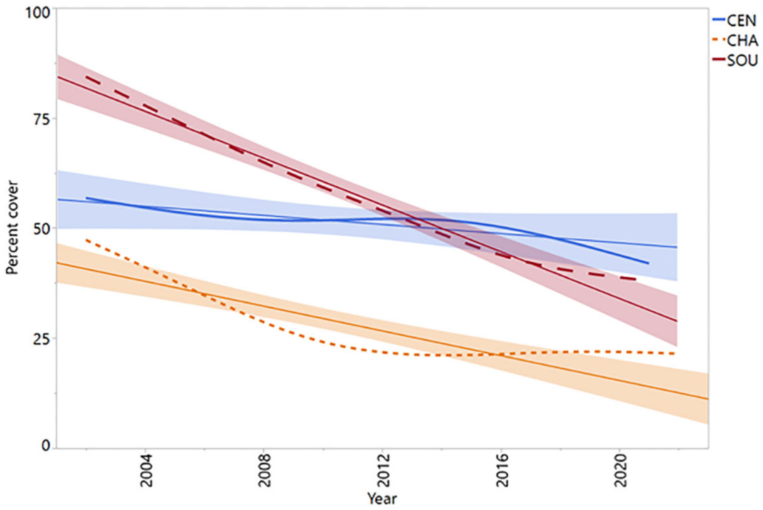

FIGURE 3
Mean annual percent cover data for *Silvetia* by region. Shade lines represent approximate linear fit. CEN, Central California region (P = 0.0982); CHA, Channel Islands region (P < 0.0001); SOU, Southern California region (P < 0.0001).

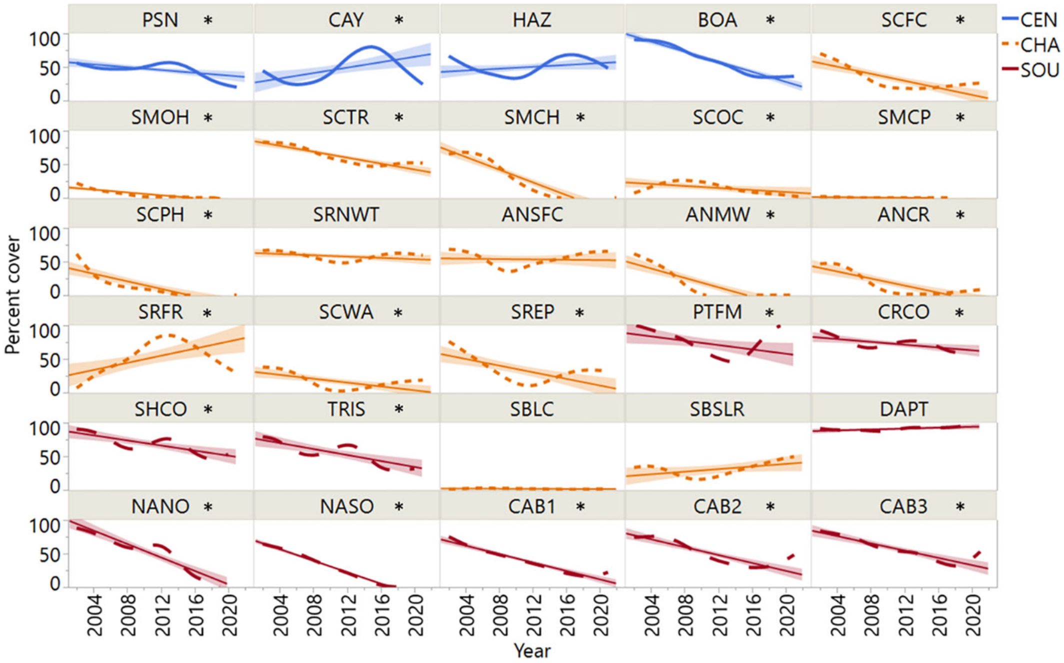

FIGURE 4
Mean annual percent cover data for *Silvetia* at each of the thirty sites arranged by latitude. Site codes are defined in Table 1. Asterisk denotes significance of the linear regression slope (P = <0.05). CEN, Central California region; CHA, Channel Islands region; SOU, Southern California region.

model. Based on Δ*BIC*, 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 (Supplementary Figure S1). Residuals for the spatial coordinates represented variation in *Silvetia* cover not captured by covariates modeled with the GAMM (Supplementary Figure S2). 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.

3.3 Dewpoint depression

Maximum dewpoint depression (maxD_d) was negatively correlated with *Silvetia* cover in all three regions (Table 1; Figures 5, 6). The relationship between *Silvetia* cover and maxD_d appeared nonlinear for the three regions (Figures 5, 6). Model selection indicated that an

TABLE 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 <= '***'.
Adjusted R-squared: 0.739, Deviance explained 0.835.
fREML : -57.440, Scale est: 1.000, N: 841.

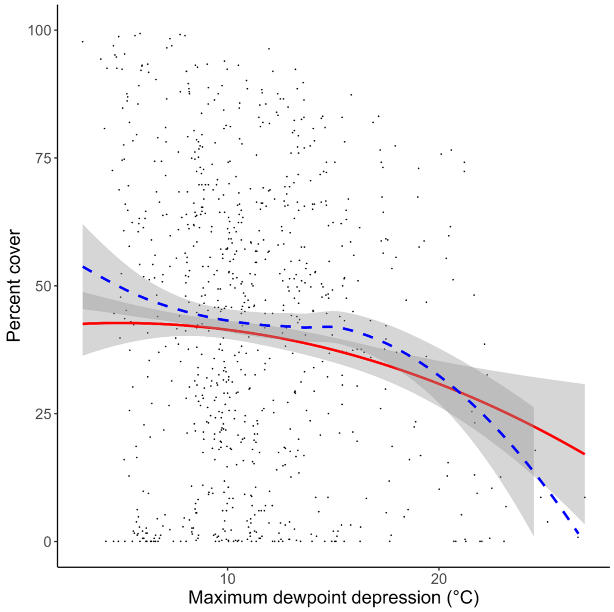

FIGURE 5
Effect of max dewpoint depression (maxD$_d$) on *Silvetia* cover at an average site and year plotted on the original scale. The blue dashed line represents a smoothed fit using the actual data. The red line represents a smoothed fit using the model (predicted data). The grey areas indicate the 95% confidence interval for the actual data and the modeled fit. Points denote measured data.

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 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 6). At the CHA region, *Silvetia* cover remained relatively stable until around 20°C before declining as $maxD_d$increased (Figure 6).

3.4 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 (Supplementary Table S2). Collinearity between D_d and W$_s$ was low (Supplementary Figure S3). Model selection indicated that neither meanW$_s$ nor maxW$_s$ should be included in the preferred model based on AIC and BIC (Supplementary Table S2).

4 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 3, 4). This pattern mirrors worldwide declines and range shifts in rockweeds and other fucoids (Bokn and Lein, 1978; Kautsky 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 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

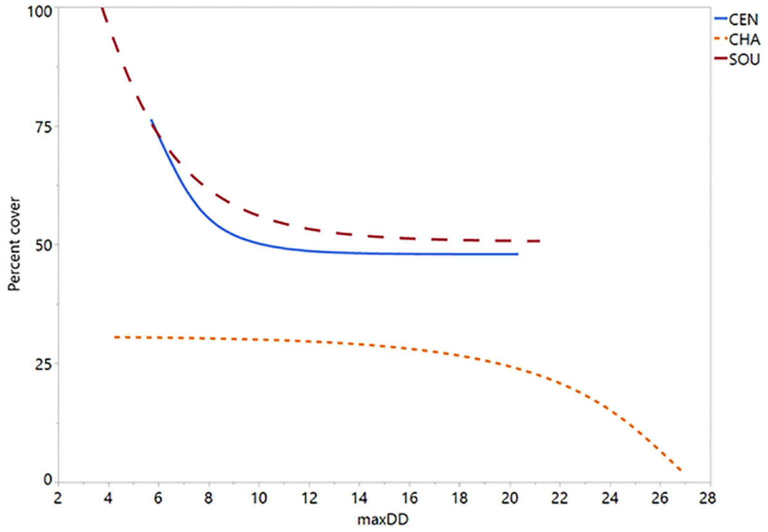

FIGURE 6
Silvetia percent cover plotted on scale of maximum dewpoint depression (°C). Regression slopes are all significant (P = 0). CEN, Central California; CHA, Channel Islands; SOU, Southern California.

California steadily increased from 1950 to 2010 (Gonzalez, 2020). Macroalgae including *Silvetia* can be stressed by oceanographic parameters including seawater temperature (Breeman, 1988; Wernberg et al., 2011; Hurd et al., 2014; 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 (see Figure 17 in Rolinski et al., 2019). 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 3, 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 et al. (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; Hughes et al., 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.

5 Implications

Population dynamics are influenced by local- to regional-scale variability in environmental conditions across a broad range of temporal scales (Oro, 2013; Dallas and Kramer, 2022). Variations in environmental conditions arise from extensive habitat heterogeneity common in ecosystems (Tilman and Kareiva, 1997), including the rocky intertidal, where climatic variables range widely across regions to individual plots (Helmuth and Hofmann, 2001). Extreme variability in atmospheric factors such as air temperature, humidity, and wind, results from both continental scale differences in topographical landscapes composed of mountains, valleys, and plains (Keeley et al., 2004; Cao and Fovell, 2013), and microtopographical differences in substratum orientation, aspect, hue, and rugosity (Helmuth and Hofmann, 2001; Helmuth et al., 2006; Harley, 2008; Choi et al., 2019). Similarly, variance in oceanographic conditions such as temperature, pH, and wave energy, occurs across the large spatial scales of regional ocean currents and prominent land features such as headlands, to local offshore reefs and kelp forests (Harley and Helmuth, 2003). Temporally, rocky intertidal ecosystems vary as atmospheric and oceanographic conditions change on short- and long-term timescales due to tides, local weather patterns, season, and interannual and decadal climatological cycles such as the El Niño Southern Oscillation and the Pacific Decadal Oscillation (Wootton et al., 1996; Thompson et al., 2002; Menge et al., 2008). This variability presents complex challenges for ecologists testing broad-scale ecological hypotheses and forecasting population dynamics.

To account for high levels of spatial and temporal variability in environmental conditions in our study, we used long-term observational data at multiple spatial scales to test the simple hypothesis that canopy cover of the foundational rockweed *Silvetia* is reduced by dry air events associated with offshore Santa Ana winds. We found extensive spatial and temporal variability in *Silvetia* cover driven by a combination of large- and small-scale processes. Rockweed cover in all three regions of our study was significantly and often dramatically reduced by dry air events associated with Santa Ana winds, but the response of rockweed varied markedly by region. Rockweed in the southern and central study regions responded very differently depending on site, whereas the rockweed in the northern region was more stable and homogeneous across sites. Including 'site' as a random effect increased the deviance explained by approximately 10%, suggesting that local processes influence the dynamics of *Silvetia* cover, reducing or overriding the effects of regional scale factors including Santa Anas. Our results underscore the need for continued long-term monitoring of ecosystems across regions to capture both local and large-scale variation and effectively inform the conservation and restoration of important foundation species.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SW: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. PR: Formal analysis, Writing – review & editing. JS: Writing – review & editing. HL: Writing – review & editing. SG: Writing – review & editing. RM: Funding acquisition, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2024.1291310/full#supplementary-material

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