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ARTICLE

Persistent kelp forests during a massive decline reveal the importance of land–sea connectivity

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Abstract

A fundamental goal in ecology is to understand the drivers of stability in natural ecosystems in the face of disturbances. However, this is challenging when biotic and abiotic stressors operate simultaneously across multiple spatial scales. Such is the case for bull kelp forests (*Nereocystis luetkeana*) in northern California, where losses of predators combined with marine heatwaves have led to shifts from kelp forest to sea urchin barren states. However, despite the >90% loss of bull kelp forests since 2014, some patches remain. Here, we investigate the bull kelp community assemblage in these remnant patches as well as the drivers of bull kelp forest resistance. We used a combination of in situ field surveys (years 2020–2022), remote sensing data (years 2016–2022), and a laboratory grazing experiment with urchins (*Strongylocentrotus purpuratus*). We found that, in addition to the two dominant states (kelp forest vs. urchin barren), there is a third community state dominated by understory canopy-forming macroalgae that stays subsurface. Moreover, bull kelp abundance and cover were positively associated with freshwater flow and proximity to freshwater sources, and bull kelp persistence was positively associated with sand cover, all of which seem to diminish sea urchin abundance and the negative effects of sea urchin herbivory on bull kelp. This was also shown in the laboratory experiment where sea urchin herbivory rates on bull kelp decreased with decreasing salinity. Overall, these results suggest that freshwater influence in shallow coastal environments could prevent loss of bull kelp and show that land–sea connections should be considered for species-specific management and conservation actions.

KEYWORDS

coastal interface, ecosystem stability, freshwater, herbivory, macroalgae, macrophyte, marine forest, resilience, resistance, river mouth

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INTRODUCTION

Ecologists have long been interested in the factors driving ecosystem stability in the face of disturbance. These research goals have become even more imperative in the Anthropocene as climate change and other human-caused stressors have fundamentally changed ecosystems, with some heading toward collapse, often resulting in a regime shift to a different ecological state (Duarte et al., 2009; Wernberg et al., 2016). After a disturbance, understanding the causes of ecosystem resilience as the combination of both resistance—the ability of a system to maintain its state by withstanding disturbance—and recovery, the ability to rapidly go back to pre-disturbance conditions (see Capdevila et al., 2021; Hodgson et al., 2015), is crucial to implement effective conservation and management actions. There might be clues in instances when a disturbance does not yield complete habitat loss. In this sense, drivers of ecological resistance can be explored by studying the lack of structural change in communities after a disturbance to identify processes operating to maintain stability (Connell & Ghedini, 2015; Ghedini et al., 2015), for instance, by focusing research efforts on persistent habitat patches of a particular ecosystem (i.e., present in a certain reference condition through time) (Grimm, 1996; Pimm, 1984; Van Meerbeek et al., 2021). Furthermore, persistent patches could also provide critical resources for propagules needed for ecosystem recovery (Gaylord et al., 2004; Reed et al., 2004), while at the same time could act as refugia for ecologically important species and species of concern (Millar et al., 2007).

Historically, kelp forests have displayed a high level of resistance to, and ability to recover from, natural and anthropogenic disturbances (Edwards, 2004; Foster & Schiel, 2010). However, in the last decade, climate change and other anthropogenic pressures led to unprecedented kelp forest declines in many regions across temperate oceans, where shifts from kelp forests to algal turfs or sea urchin barrens are increasing (Butler et al., 2020; Filbee-Dexter & Wernberg, 2018; Krumhansl et al., 2016). These losses have triggered scientists and managers to address the local, regional, and global causes of these declines, yet many are left without a playbook for recovery-oriented management (Eger et al., 2022), further highlighting the importance of remaining persistent kelp beds as centers for inquiry and protection.

In northern California (USA), extensive forests of the bull kelp, *Nereocystis luetkeana*, are a conspicuous component of rocky reef bottoms. Bull kelp, an annual species, is the main canopy-forming species in the region, and it represents one of the most important ecological, economical, and cultural coastal habitats as it provides

critical ecosystem services (e.g., carbon sequestration, coastal protection, biodiversity enhancement, and habitat and food provisioning for important life stages of fishes, invertebrates, and marine mammals; Rogers-Bennett & Catton, 2019; Springer et al., 2010). However, a record-breaking marine heatwave struck the Pacific NW coast during 2014–2016, which eventually led to a >90% decline of bull kelp cover along more than 350 km of coastline that has not yet recovered (García-Reyes et al., 2022; McPherson et al., 2021; Rogers-Bennett & Catton, 2019). Several episodic events occurred almost simultaneously and generated a perfect storm that affected bull kelp, including the loss of the predatory sunflower sea star *Pycnopodia helianthoides* through wasting disease (Galloway et al., 2023; Hewson et al., 2014), and temperatures that exceeded the thermal threshold for bull kelp (Muth et al., 2019; Rogers-Bennett & Catton, 2019). The historical decimation of sea otter populations *Enhydra lutris* through hunting (Estes & Palmisano, 1974) and overfishing of top predators (Springer et al., 2010), together with the loss of sunflower sea stars *P. helianthoides*, eventually led to the proliferation of the purple sea urchin *Strongylocentrotus purpuratus* (Rogers-Bennett & Catton, 2019). This, when coupled with heat stress, led to the near-complete collapse of northern California bull kelp forests (Rogers-Bennett & Catton, 2019). However, despite the widespread loss, certain habitat patches of bull kelp (<10%) remained (Cavanaugh et al., 2023; García-Reyes et al., 2022; Rogers-Bennett & Catton, 2019), presenting an opportunity to better understand the key factors driving its ecological resistance.

Several biotic and abiotic factors acting at different spatial and temporal scales are known to influence the natural distribution and abundance of bull kelp. Abiotic factors include irradiance, substrate type, pollution, sedimentation, nutrient levels, temperature, water motion, and salinity; while biotic factors include grazing and habitat competition among macrophytes, and epiphytes (Deiman et al., 2012; Hollarsmith et al., 2022; Lind & Konar, 2017; Schroeder et al., 2020). Annual fluctuations in bull kelp abundance have been generally associated with prior winter and even >1 year oceanographic conditions such as the Pacific Decadal Oscillation, the El Niño Southern Oscillation, and the North Pacific Gyre Oscillation, indicating that greater abundance in rocky bottoms is associated with large-scale processes bringing colder seawater temperatures and nutrient inputs through upwelling events (García-Reyes et al., 2022; Hamilton et al., 2020; Pfister et al., 2018); and also local scale impacts such as low water quality and increased herbivory (Schroeder et al., 2020). However, none of these factors explain spatial distribution patterns following the decline

(García-Reyes et al., 2022). In fact, the most recent records of remaining patches are detected near the mouths of small rivers (B. Hughes, personal observation, Cavanaugh et al., 2023), and therefore do not agree with the general expectation that the low salinity, high turbidity, and water stratification conditions that characterize these areas negatively affect bull kelp abundance (Schoch & Chenelot, 2004; Schroeder et al., 2020; Springer et al., 2010). Complex dynamic interactions between biotic and abiotic factors are likely determining these patterns (García-Reyes et al., 2022), where a negative influence on sea urchin abundance and/or performance (e.g., lower grazing or reproductive success) through predation or changes in salinity, temperature, or substrate characteristics could, directly and indirectly, benefit bull kelp.

The oversimplified sea urchin-kelp food web also does not lend to a full understanding of bull kelp resistance, where key species interactions including sea urchin herbivory could still remain in persistent patches. It is widely accepted that greater biodiversity in an ecosystem leads to greater ecological stability (Tilman & Downing, 1994). However, despite several studies documenting the loss of bull kelp, along with the proliferation of sea urchins, there is a paucity of information on how bull-kelp-associated community assemblages have changed in northern California, as most of what we know about the decline of bull kelp forests in the Pacific NW coast has been studied through remote sensing (e.g., Cavanaugh et al., 2023; García-Reyes et al., 2022; Hamilton et al., 2023; Pfister et al., 2018; Schroeder et al., 2019), which provides no information on the benthic community component. Further, very few studies have focused on how land–sea connections influence kelp forests. The few that have described these linkages have looked at the impacts of high turbidity and low salinity on kelp abundance in estuaries, as well as poor water quality impacts from urbanized areas (Foster & Schiel, 2010; Schoch & Chenelot, 2004), or have documented kelp subsidies to coastal food webs at the land–ocean interface (Foley & Koch, 2010; Polis & Hurd, 1996; Rechsteiner et al., 2018). But, to date, there is no evidence as to which land–sea connections might impact sea urchin abundance or behavior in a way that influences kelp forest resistance.

Here, we assess the bull kelp community assembly of the northern California coastal region, as well as the relationship between species composition and environmental factors, including land–sea connections, to shed light on what factors are driving bull kelp resistance in persistent habitat patches after a massive decline and to evaluate how the associated community might have changed. We used a combination of subtidal surveys and satellite remote sensing data of bull kelp forest canopy cover

across nine sites with persistent patches along a gradient of bull kelp abundance to examine the key biotic and abiotic associations. We also developed an experiment under controlled conditions to assess the influence of salinity on bull kelp-herbivory rates by sea urchins. We tested the hypothesis that the resistance of bull kelp is determined by factors negatively affecting sea urchin abundance, specifically: (1) higher benthic diversity in the community assemblage could lead to greater ecological resistance, shown by high bull kelp persistence, cover, and abundance and low sea urchin abundance; (2) proximity to river mouths might benefit bull kelp populations and drive its persistence and abundance by lowering sea urchin populations or changing behavior in freshwater-influenced zones.

METHODS

Study sites and field surveys

To characterize kelp forest communities, we surveyed nine sites in northern California, USA, with a consistent historical presence of bull kelp forests and where bull kelp forests were present before the massive decline (CDFW, 2023; Cavanaugh et al., 2023). All sites formerly had abundant bull kelp forests and currently represent a kelp-persistence-and-abundance continuum from no kelp to remnant kelp patches (Figure 1). Each site was surveyed during three consecutive years (i.e., field seasons) in September/October of 2020, 2021, and 2022.

For each site and field season, two to three transects were conducted on SCUBA to characterize bull kelp and sea urchin abundance, the associated algal and invertebrate community, and the geomorphic characteristics of the benthic habitat. For each transect (2 m × 30 m), abundance of surface and subsurface canopy-forming fleshy macroalgae species was counted, including *N. luetkeana* (hereinafter bull kelp), *Stephanocystis osmundacea*, *Pterygophora californica*, *Macrocystis pyrifera*, *Egregia menziesii*, *Laminaria farlowii*, *Laminaria ephemera*, and *Laminaria sinclairii* (from now on *Laminaria* spp.), *Laminaria setchellii*, *Alaria marginata*, *Sargassum horneri*, *Sargassum muticum*, *Costaria costata*, *Desmarestia* spp., and *Dictyonium californicum*. For invertebrates, only a selection of indicator species was included based on the most abundant species in preliminary surveys and historical surveys by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO, www.piscoweb.org) and Reef Check California. PISCO is a consortium of universities that has conducted annual kelp forest monitoring in California and Oregon since 1999. Reef Check California is a citizen science nonprofit organization

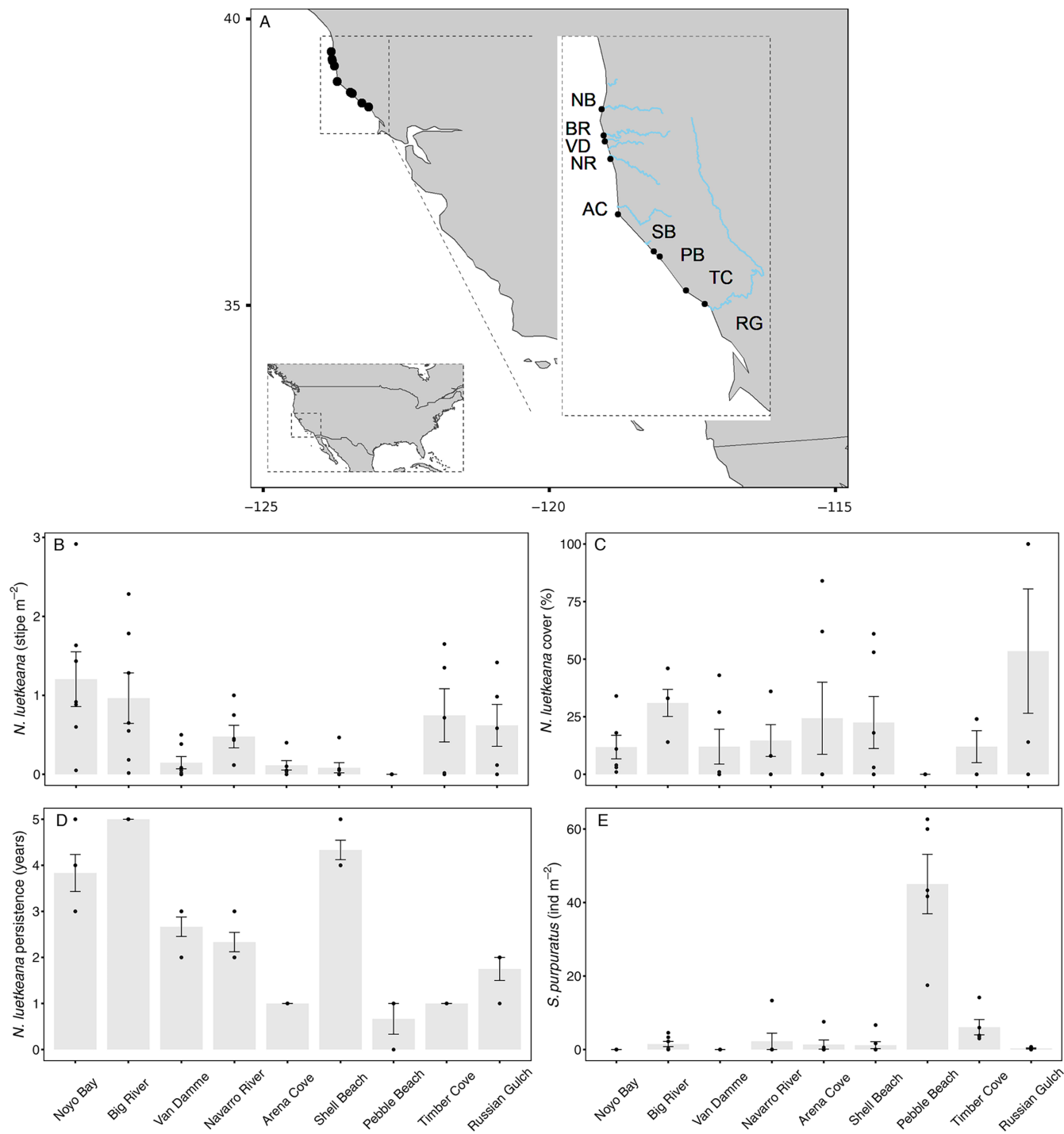


FIGURE 1 (A) Study sites in northern California, USA, with the historical presence of bull kelp (*Nereocystis luetkeana*) forests before the massive decline of 2014–2016. Sites had formerly abundant bull kelp forests and currently represent a kelp persistence continuum from no kelp to remnant kelp patches. The sites are represented by the first two letters of each site name (see labels along x-axes of panels D and E). (B) Bull kelp abundance, (C) bull kelp cover, (D) bull kelp persistence, and (E) purple urchin *Strongylocentrotus purpuratus* abundance. Bar plots represent the average values and SE of data collected on each site during the years 2020, 2021, and 2022. Dots show raw data.

(www.reefcheck.org) that has conducted kelp forest monitoring in California MPAs since 2006. Thus, invertebrates included the sea urchins *S. purpuratus* (herein-after purple urchin) and *Mesocentrotus franciscanus*, the

sea stars *Patiria miniata*, *P. helianthoides*, *Pisaster giganteus*, *Pisaster brevispinus*, and *Pisaster ochraceus*, the abalone *Haliotis rufescens*, and the sea cucumber *Parastichopus parvimensis*. For areas along a transect

with too many sea urchins to count (i.e., urchin barrens), urchins were subsampled by counting 20 urchins in a single 2 m × 1 m quadrat and then visually estimating that density for the remaining transect. Then, the total cover of each substrate type (sand or rock, including cobble, boulder, and reef) and calcareous algae was calculated as the percentage of the total number of meters of each category from the total. Geomorphologic relief was calculated by estimating the highest and lowest points in a 0.5-m² box of substrate every meter along the 30-m transect and was broken down into four different categories: (a) 0: 0 to 10 cm, (b) 1: >10 cm to 1 m, (c) 2: >1 m to 2 m, and (d) 3: >2 m. For statistical analyses, we calculated the mean relief across each transect.

Data sources for long-term kelp cover and freshwater input

We calculated bull kelp cover and persistence at each site and survey year (2020–2022) using a time series of high-resolution satellite data that spanned the northern California coastline from 2016 to 2022. Annual maps of bull kelp canopy extent were derived from surface reflectance data from the PlanetScope constellation, which contains over 130 operational CubeSats that collectively provide global multispectral imagery at 3 m resolution on a near-daily basis. We used a machine learning approach to create binary classifications from an average of five images per month from September and October of each year, which were then merged to represent annual bull kelp canopy coverage (see Cavanaugh et al., 2023 for more details). This method has been shown to accurately estimate kelp canopy presence when kelp canopy covers about 20% of the pixel or 1.8 m² and showed good agreement with the California Department of Fish and Wildlife (CDFW) data (see more details below) when the two datasets temporally overlapped (Cavanaugh et al., 2023). We characterized annual bull kelp cover within a 100-m radius of the transect, and we characterized persistence as the number of years in the last 5 years prior to the survey year that bull kelp was present within this radius. If the satellite data reported no kelp canopy within the 100-m radius, bull kelp was considered absent for that site and year.

Additionally, bull kelp was considered functionally absent for a given year if a site contained less than 5% of kelp canopy compared to the total area of potential bull kelp habitat. We calculated the area of potential habitat by combining our satellite time series with an aerial survey dataset created by CDFW. CDFW conducted annual occupied aircraft vehicle surveys of bull kelp canopy between late summer and winter along certain sections

of the California coastline from 1989 to 2016, with some years offering full coverage of the coastline of the state of California (CDFW, 2023). The surveys contain complete coverage of our study region at 2 m resolution for 9 years (1989, 1999, 2003–2005, 2008, and 2014–2016), with partial coverage for 4 years (2002, 2009, 2010, and 2013). Potential bull kelp habitat was defined as any location where kelp canopy was observed in either historical CDFW data or our PlanetScope dataset (i.e., the composite of these datasets). For example, 54 m² of kelp canopy were present at Timber Cove in 2017 (Figure 1), which accounted for ~0.6% of the total available habitat, so it was excluded as a persistent year.

To index freshwater input at each site, we used the mean annual flow rate for the nearest river for each year by averaging the mean monthly flow rates (from October to September of the next year), which encompasses the bull kelp gametophyte and sporophyte growing season. The *California Unimpaired Flows Database v2.1.1* (<https://rivers.codefornature.org/>; Zimmerman et al., 2022) provides estimates of mean monthly flow for all rivers along the northern California coast; these were used to calculate the annual flow rate. Distance from the kelp transect to the nearest river mouth was calculated using the Haversine method representing the shortest travel paths between two points. These analyses were made using the *geosphere* package in R software (Hijmans, 2022; R Core Team, 2023).

In situ salinity data at study sites were not available, but a 30-year record of high-frequency salinity data sampled at the Bodega Marine Laboratory (BML) from the University of California Davis located in Bodega Bay, USA (38°18'58.2" N, 123°04'10.2" W), located ~30 km south of the southernmost study site shows that salinities below 33.0 psu are regularly observed in nearshore waters in the northern California kelp habitat (Figure 2) influenced by streams and rivers together with atmospheric discharge. The salinity of the BML intake water is sampled every 5 min using the automated sensors of the SeaBird Electronic SBE16+ (see <https://boon.ucdavis.edu/obs/shoreline/sw-sensor-info>). Data are quality-controlled and aggregated into hourly median values to exclude any effect of erroneous outliers that may remain in the quality-controlled data. While in dry years, like 2021 and 2022, there is <1% chance of salinity dropping below 32.0 psu, there are brief events during which salinity may drop lower for several hours. In wet years like 2017 and 2019, salinity is below 30.0 and 31.0 psu, respectively, for 5% of the year (i.e., more than 400 h cumulatively) and events can drop salinity to 26.0 or 27.0 psu during brief events—introducing the possibility of both press and pulse stress in winter and spring months. The BML site is ~5 km away from the closest river mouth (i.e., Salmon Creek) and the distance from most of our kelp transects to the nearest

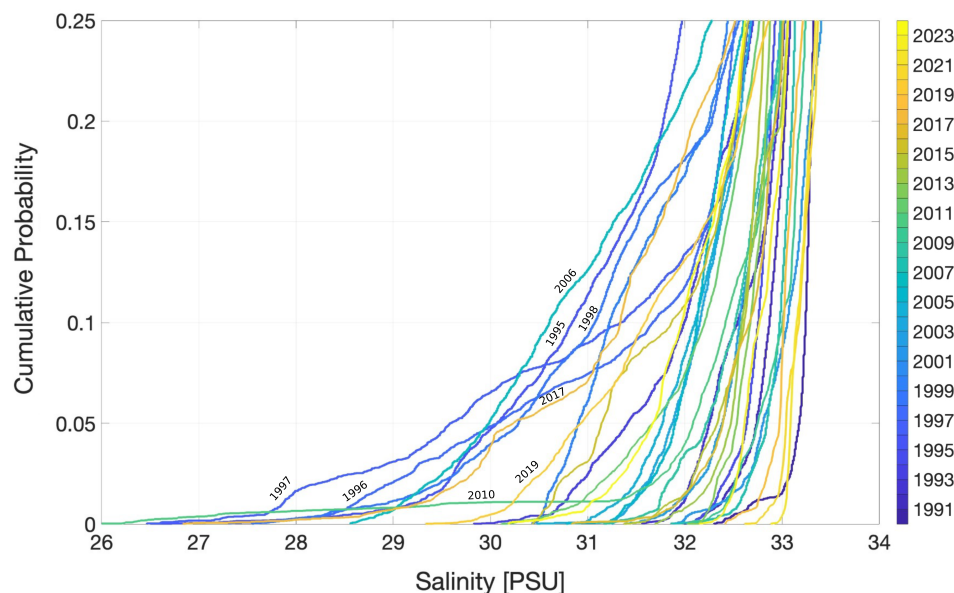


FIGURE 2 Cumulative distribution for salinity measured at the Bodega Marine Laboratory for water years 1991–2023. By convention, a “water year” in California starts in October of the previous calendar year and ends in September of the nominal calendar year. Probability values are calculated from median hourly data (raw data are sampled every 5 min). The labels show years with values below 30 psu.

river mouth is shorter (range 31 m to 6.9 km) suggesting that salinity values will most likely fluctuate to values even lower than at the BML site.

Experiment testing sea urchin herbivory across a salinity gradient

To investigate the influence of freshwater on purple urchin grazing rates on bull kelp, we ran a series of feeding assay experiments at different salinities in static (no-flow) conditions in a temperature-controlled laboratory (12°C) at Sonoma State University (Rohnert Park, California, USA). The experiment included four salinity treatments ($n = 10$ replicate aquaria per treatment: 20, 25, 30, and 35 psu, with a single no-urchin control for each salinity treatment $n = 4$). These salinity values were chosen based on the few available pieces of information about the salinity range directly measured in locations with the presence of *N. luetkeana*, where 20 psu is the bookend of minimum values reported (Chenelot, 2003; Lind & Konar, 2017). For each salinity treatment, except the 35 psu treatment, we diluted seawater with DI water until the appropriate salinity was reached. Sand-filtered seawater was collected at BML at 33 psu, so we used Instant Ocean Sea Salt (Instant Ocean, Blacksburg, Virginia, USA) to raise salinities to 35 psu. Salinity levels were measured with a Yellow Springs Instruments Data Sonde connected to a salinity probe (Yellow Springs, Ohio, USA).

For the feeding assay, we collected 60 adult sea urchins (~5 cm in diameter) from Arena Cove, California, USA (Figure 1A). Prior to the assay, sea urchins were acclimated in two 20-L tanks (30 sea urchins per tank, 12°C and 33 psu) with flowing seawater for 3 days and without food. Then, salinity batches were prepared, and sea urchins were placed individually into the aquaria (1.1 L, $N = 40$) previously filled with the corresponding salinity treatment for 48 h. All aquaria had a lid with no air space and tubing connected to air flow to supply sea urchins with adequate dissolved oxygen levels. The day before the assay, we collected four fresh bull kelp stipes from Doran Beach, California, USA (38°18'52.4" N, 123°2'20.8" W), and transported them to the laboratory where they were kept in a 4°C refrigerator overnight. For the assay, the bull kelp stipes were cut into 5 g fresh mass (FM) rings with two rings offered to each sea urchin.

The feeding assays ran for 72 h. We inspected sea urchins at 0, 24, 48, and 72 h after initiation of the experiment, and assessed health indicators (presence of grazing activity, upright spines, and waving pedicellariae) to ensure that each sea urchin remained healthy. At the completion of the assays, we gathered all remaining kelp and sea urchins and measured their biomass. Biomass was measured after the samples sat in paper towels at room temperature for 1 h to rid any excess water. Bull kelp consumption was calculated by subtracting the final kelp FM from the initial FM and normalizing by sea urchin FM. To account for kelp senescence during the

trial, we adjusted the initial FM kelp with the control data (initial amount – amount due to senescence in the absence of grazing) and then calculated the total amount of bull kelp consumed.

Data analysis

The relationships between kelp abundance, kelp cover, and kelp persistence (variables obtained using different sampling methods, subtidal assessment vs. remote sensing) were analyzed using linear regressions.

We used multiple multivariate approaches to characterize community composition and kelp resistance across our sites in northern California and to explore relationships between community patterns based on abundance data of each species with kelp abundance, cover, and persistence, and abiotic factors (freshwater influence and substrate characteristics). First, we used nonmetric multidimensional scaling (nMDS) with Bray–Curtis dissimilarities to assess species communities among sites. Next, we used a permutational multivariate ANOVA (PERMANOVA) to assess the variation in the community composition among sites and years, and also among nMDS groups to confirm these results. We used 9999 permutations and a Bray–Curtis similarity matrix. Significant terms and interactions were evaluated with pseudo-*t* statistic pairwise comparisons. Differences in multivariate dispersion were tested by PERMDISP analysis on the same matrix. A one-way similarity percentage (SIMPER) analysis based on the results from the nMDS and PERMANOVA was used to identify which species primarily accounted for the observed differences among identified communities and identified the most dominant species as those species with relative abundance >5% within each group. Then, we used a distance-based redundancy analysis (dbRDA) with Bray–Curtis dissimilarity to assess the direct linear relationship between the species assemblages and the different environmental variables measured (i.e., kelp cover, kelp persistence, percentage of sand, mean relief, distance to freshwater sources and flow). Significant species vectors were overlaid on the RDA ordination to examine relationships between species and environmental variables. Species vectors represent raw Pearson correlation calculated for each species with the original RDA axes. The significance of the model was tested using ANOVA-like permutation tests with 9999 permutations. Prior to all these analyses, species abundance data followed a log + 1 transformation. All other data were square root transformed, except for percentage metrics that were arcsine transformed. Species that only appeared once in one transect were not considered in

the analysis. These analyses were made using the *vegan* package in R software (Oksanen et al., 2022; R Core Team, 2023).

To further explore freshwater influence as a mediator of transitions from kelp forest to sea urchin barren, we analyzed the relationship between kelp and sea urchin abundance, along with the relationship between sea urchin abundance and freshwater input indexed by mean annual flow rates and distance to the nearest freshwater source. We used generalized linear mixed-effects models (GLMMs) for all three analyses to determine the relationships. We included site and year as random factors. Given the distribution of count data with many zeroes, we considered two error distributions for each model: poisson and negative binomial, and tested each model with and without zero inflation. All models were run using the *glmmTMB* package in R software (Brooks et al., 2017; R Core Team, 2023). We used model selection to select the best fitting model using the Akaike information criterion (AIC) tool in the *MASS* package in R software (R Core Team, 2023; Venables & Ripley, 2002). Once the top model was selected, we used a model reduction procedure by running models with all possible combinations of factors, selecting the lowest-scoring model with 2 AIC units of difference from the rest of the models. The significance of the independent variable (i.e., fixed factor) was evaluated by comparing the best model to the null model, performing a likelihood ratio χ^2 test, which tests whether reduction in the RSS is statistically significant or not. To test the effect of salinity treatment (20, 25, 30, 35 psu) on purple urchin bull kelp consumption rates, we used a generalized linear model with the Tweedie distribution in the *glmmTMB* package in R software (Brooks et al., 2017; R Core Team, 2023). Post hoc analysis was run by calculating estimated marginal means with the *emmeans* package in R software (Lenth, 2025; R Core Team, 2023). Normality and homoscedasticity in univariate statistical analysis were explored via visual estimation of trends of model residuals (errors associated with homogeneity of variance, independence, and normality).

RESULTS

Kelp abundance (measured via SCUBA transects) was not related to remotely sensed kelp persistence ($df = 1, 45, R^2 = 0.05, F = 3.53, p = 0.07$), but it was positively related to kelp cover ($df = 1, 45, R^2 = 0.1, F = 6.015, p = 0.02$), although this relation was not strong (see also Figure 1). The nMDS separated communities among sites, dividing them into three main groups (stress 0.18) (Figure 3). A bull kelp-dominated group including Noyo Bay, Van Damme, Arena Cove, and Big River, where *P.*

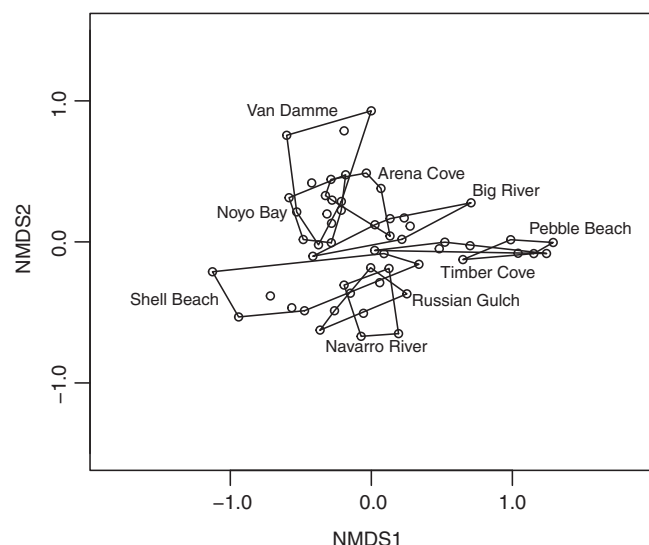


FIGURE 3 Nonmetric multidimensional scaling (nMDS) results of community structure in the study sites with kelp persistent patches. Data points represent transects from each site sampled from 2020 to 2022.

californica (20%) was the most dominant species, followed by *Desmerastia* spp. (17%), *S. purpuratus* (13%), *N. luetkeana* (12%), *Laminaria* spp. (11%), and *L. setchellii* (9%). A sea urchin-dominated group represented mainly by Pebble Beach but also Timber Cove, where *S. purpuratus* appears as the only dominant species with a relative abundance higher than 45% and total abundance of 45 ± 18 individuals m^{-2} (mean $\pm$ SD) and 6 ± 5 individuals m^{-2} for each site, respectively. A subsurface canopy-forming macroalgae group including Shell Beach, Russian Gulch, and Navarro River, where *L. setchellii* was the most dominant species (29%), followed by *S. purpuratus* (21%), *P. californica* (17%), *Laminaria* spp. (12%), and *A. marginata* (7%), respectively. The PERMANOVA showed differences in community composition among sites ($df = 8, 46, F = 8.6983, p < 0.001$) but not among years ($df = 2, 52, F = 0.9858, p = 0.435$), where PERMDISP showed no differences in dispersion ($df = 8, 46, F = 1.6005, p = 0.151$). Post hoc analysis showed that all sites showed significant differences except Pebble Beach and Timber Cove, Big River and Timber Cove, and Noyo Bay and Van Damme. This confirms the nMDS results, where Timber Cove and Big River community compositions are apparently in transition to that of Pebble Beach (a dominant sea urchin site). The second PERMANOVA further confirmed the differences among the three groups of sites shown by the nMDS ($df = 2, 52, F = 16.284, p < 0.001$).

The SIMPER analyses showed that the average dissimilarity in community composition among the three groups was high (57%–69%) (Appendix S1: Table S1). The

main species responsible for the dissimilarity (up to 50% average dissimilarity) among the group of sites dominated by bull kelp and sites dominated by sea urchins were *S. purpuratus*, *P. miniata*, *P. californica*, *M. franciscanus*, *N. luetkeana*, *H. rufescens*, and *Desmerestia* spp. The main species responsible for the dissimilarity among the group of sites representing a canopy-forming macroalgae habitat and sites dominated by sea urchins were *S. purpuratus*, *P. miniata*, *L. setchellii*, *P. californica*, *M. franciscanus*, *Laminaria* spp., and *N. luetkeana*. Finally, the main species responsible for the dissimilarity among the group of sites representing subsurface canopy-forming macroalgae habitat and the group of sites dominated by bull kelp were *L. setchellii*, *Desmerestia* spp., *H. rufescens*, *Laminaria* spp., *N. luetkeana*, *S. purpuratus*, *A. marginata*, *P. ochraceus*, *P. californica*, and *E. menziesii*. Overall, only three species, *N. luetkeana*, *P. californica*, and *S. purpuratus*, contributed to determining the main differences among all the three groups.

The dbRDA ($df = 6, 40, F = 2.9759, p < 0.001, R^2 = 0.37$) showed that variation in species communities across sites studied was mainly related to the influence of freshwater as well as the bottom substrate type (Figure 4). Canonical axis 1 separated the sites by bottom substrate type and persistence of kelp, while canonical axis 2 separated the sites based on the flow and distance to freshwater sources. Thus, the first axis represented a substrate-type gradient, from rocky shores that provide tridimensional structure and create a habitat for purple urchins and higher kelp coverage, to smooth sandy bottoms where kelp is more persistent and purple urchins are less abundant. The second axis separated sites based on the strength and proximity of freshwater sources, showing that bull kelp abundance was positively correlated with freshwater flow.

Our analysis of the relationship between kelp abundance and sea urchins determined that sea urchin abundance was a good predictor of bull kelp abundance. The model selection determined the best-fitting error distribution was a negative binomial, and the selected model included sea urchin abundance as a predictor with site as a random factor explaining some variation ($AIC = 439.19$, dispersion parameter = 0.46, site variance = 0.62, site SD = 0.79; Appendix S1: Table S2). Analysis of the sea urchin and bull kelp abundance relationship revealed a negative relationship (estimate = -0.0014 , SE = 0.0006, $p = 0.003$; Appendix S1: Table S2). Our analysis of the relationship between sea urchin abundance and runoff strength (mean annual flow rate; Figure 5B) determined that mean annual flow rate was a good predictor of sea urchin abundance. The model selection determined the best-fitting error distribution was a negative binomial, and the selected model had mean annual flow rate as an

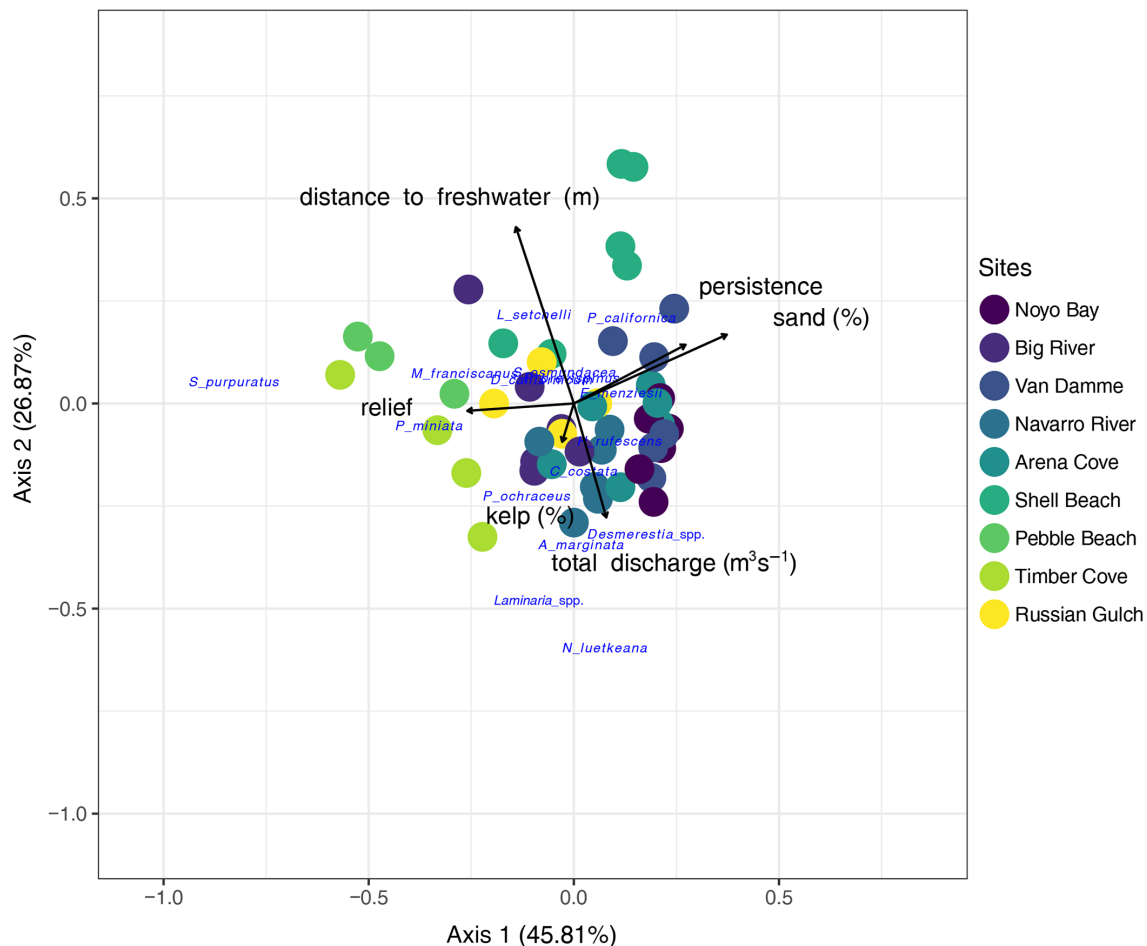


FIGURE 4 Distance-based redundancy analysis (dbRDA) triplot and relationships among species abundance, environmental variables, and sites. Environmental variables are shown as arrows. Colors represent the different sites.

explanatory variable with site as a random factor explaining some variation (AIC = 431.47, dispersion parameter 0.867, site variance = 20.44, site SD = 4.52; Appendix S1: Table S2). There was a significant negative relationship between mean annual flow rate and sea urchin abundance (estimate = -0.5216 , SE = 0.48, $p = 0.001$; Figure 5B; Appendix S1: Table S2). Lastly, our analysis between sea urchin abundance and runoff proximity (distance to nearest freshwater source; Figure 5C) determined that distance to freshwater was a good predictor of sea urchin abundance. The model selection determined the best-fitting error distribution was a negative binomial, and the selected model had distance to freshwater included as an explanatory variable with site as a random factor explaining some variation (AIC = 433.56, dispersion parameter 0.728, site variance = 10.28, site SD = 3.21; Appendix S1: Table S2). There was a significant positive relationship with distance to the nearest freshwater source (estimate = 0.0006, SE = 0.0004, $p = 0.003$; Figure 5C; Appendix S1: Table S2) on purple urchin abundance.

Finally, our sea urchin feeding experiment showed that purple urchin herbivory rates decreased with decreasing salinity (dispersion parameter = 0.06, estimate = 0.13, SE = 0.02, $p < 0.0001$; Figure 6). In particular, herbivory rates at 20 psu were significantly lower than at the rest of the treatments, and herbivory rates at 25 psu were also significantly lower than at 35 psu (Appendix S1: Table S3).

DISCUSSION

Following the massive regional bull kelp decline in northern California, remaining kelp patches exhibited variation in the community assemblage, with abundances of bull kelp *N. luetkeana* and purple urchin *S. purpuratus* dominating the primary community states. The precise mechanisms underlying the differences in the assemblages appear to be associated with the influence of freshwater and benthic habitat type on the effect of purple urchins on bull kelp abundance. Specifically, we found that bull kelp cover and abundance increased near

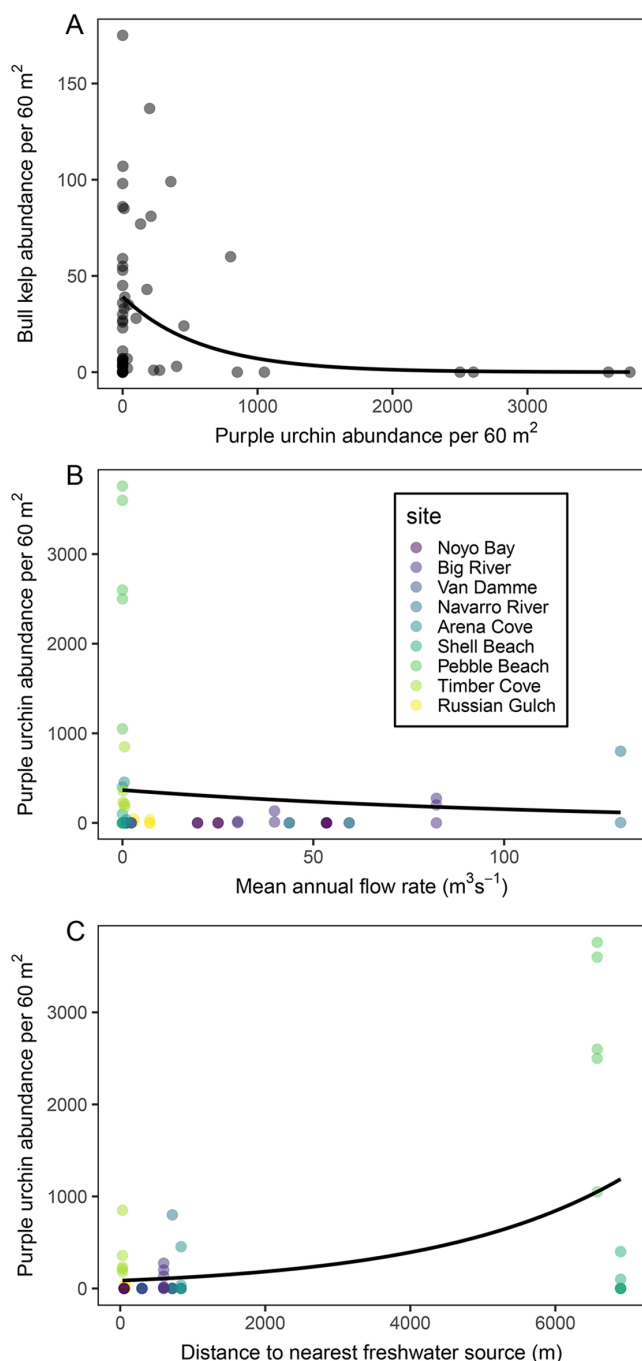


FIGURE 5 Results of generalized linear mixed-effects models (GLMMs) testing the relationship between (A) sea urchin and bull kelp abundance, (B) annual freshwater flow rate calculated from mean monthly estimates of flow rates and purple urchin abundance, and (C) distance to nearest freshwater sources and purple urchin abundance. Each point represents an individual transect ($N = 56$), and site is indicated for panels (B) and (C) since it was included in the final selected models. Modeled lines are derived from a negative binomial distribution.

freshwater sources, while the abundance of purple urchins decreased. We also found that higher bull kelp persistence and lower purple urchin abundance were

related to the presence of a sandy bottom interspersed with rocky bottom, likely indicating effects of sedimentation processes. Our experimental results shed light on potential mechanisms behind this pattern, as lower salinity reduced purple urchin herbivory on bull kelp. Overall, these findings suggest that bull kelp resistance in northern California could be driven by land–sea connections and the influence of freshwater.

Three main community states were found where before there were abundant bull kelp forests: sites still dominated by bull kelp, sites dominated by purple urchins, and sites represented by a subsurface canopy-forming macroalgae community. The main differences among these states were mainly related to levels of bull kelp and purple urchins. Thus, the number of dominant species decreased from bull-kelp-dominated sites with six species to sea urchin-dominated sites with only purple urchins appearing as the main species. In all states, the relative abundance of purple urchins in the community assemblage was high, ranging from 13% in bull-kelp-dominated sites to 21% and 45% in the subsurface canopy-forming macroalgae sites and sea urchin-dominated sites, respectively. Moreover, total sea urchin abundances in most sites (see Figure 1) were higher than those in historical registers (0–1.7 individuals m^{-2} before 2014) confirming an increasing trend toward sea urchin barrens previously described by Rogers-Bennett and Catton (2019). Purple urchins were among the most dominant species in all cases, and Pebble Beach (45 ± 18 individuals m^{-2}) already showed abundances close to what has been described for sea urchin barrens in the region (Filbee-Dexter & Scheibling, 2014; Rogers-Bennett & Catton, 2019). The presence of sea urchin barrens at sites where kelp forests thrived before has been described in many locations around the world (Filbee-Dexter & Scheibling, 2014; Ling et al., 2014); likewise, here, the abundance of bull kelp was much higher in previous decades (García-Reyes et al., 2022; McPherson et al., 2021; Rogers-Bennett & Catton, 2019).

The subsurface canopy-forming macroalgae community found at Shell Beach, Russian Gulch, and Navarro River sites could be a transitional state to a sea urchin barren after the loss of bull kelp. Although, it could be an alternate stable community where the low abundance of bull kelp benefits other macroalgal species through allowing more access to light and other resources. This could be the case for the kelp *L. setchellii*, in which higher abundance (20% more abundant in the subsurface canopy-forming macroalgae community) and higher resistance to warmer temperatures (Muth et al., 2019) could be compensating for the loss of bull kelp through purple urchin grazing (Connell & Ghedini, 2015; Thornber et al., 2008). Further, *L. setchellii* could be limiting recruitment and potential recovery of bull kelp

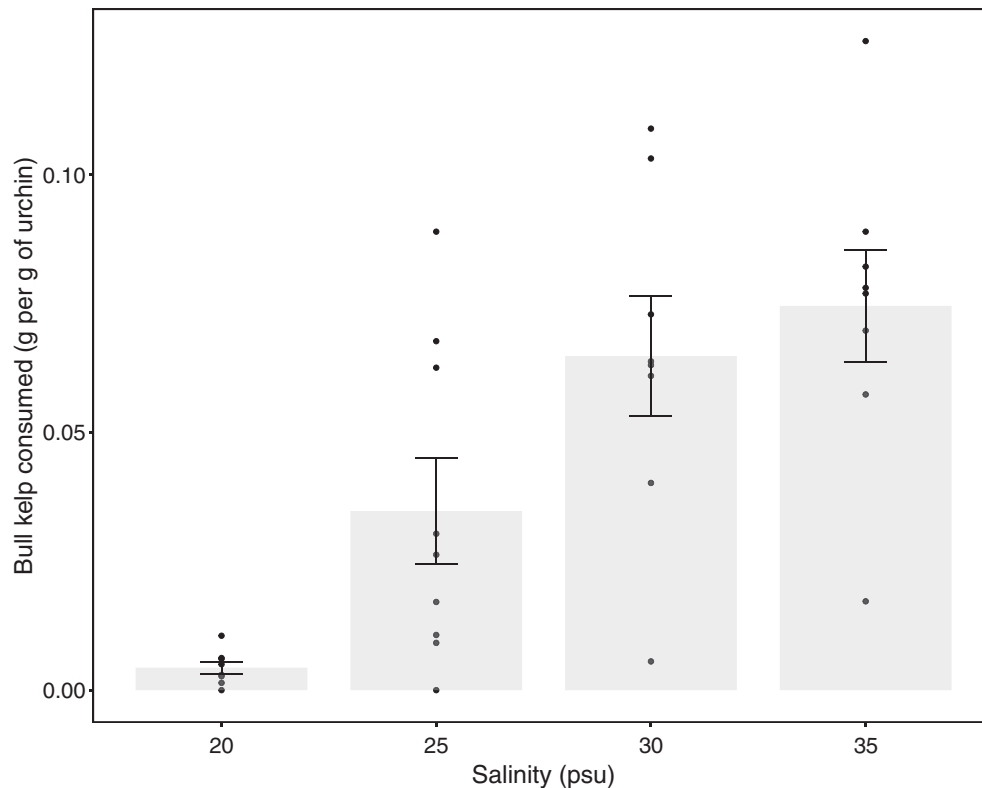


FIGURE 6 Bar plot showing the differences in purple urchin herbivory across four salinity treatments ($N = 10$ aquaria replicates per treatment; mean $\pm$ SE). The effect of salinity was significant ($p < 0.0001$) using a generalized linear model (GLM) with a tweedie distribution. Solid circles show raw data.

(Dobkowski et al., 2019). Continued observations in the near future are required to confirm these pathways, particularly the presence of a subsurface canopy-forming-macroalgae-dominated community with little to no bull kelp in it, as well as more information on sea urchin grazing on these species. While it appears that these three primary communities follow the decline in the bull kelp ecosystem coast-wide, the scarcity of past and long-term subtidal data on bull kelp communities in the NW Pacific coast precludes understanding of these changes, as no baseline can be determined. This contrasts with the many studies using remote sensing techniques to describe long-term changes in bull kelp canopy cover (Cavanaugh et al., 2023; García-Reyes et al., 2022; McPherson et al., 2021; Pfister et al., 2018; Schroeder et al., 2019), highlighting the need for combined monitoring strategies to understand natural ecosystem changes.

Our research shows an association between bull kelp persistence and freshwater influence in northern California. The effect could be directly related to reduced salinity that, as shown here, could reduce the grazing pressure of purple urchins on bull kelp, without affecting

the performance of the bull kelp (Farrugia Drakard et al., 2025; Lind & Konar, 2017). This warrants further research, as no studies have looked at the potential combined effects of salinity and herbivory in macroalgae, and only a few studies in other macrophytes have evaluated effects for hypersaline environments (Bell et al., 2019; Renault et al., 2016). While limited nearshore salinity data are available, some unpublished data from this region corroborate the long-term record from BML, which shows low-salinity events with salinities as low as 31 psu in most years and low-salinity events with salinities below 30 psu in some years (see Figure 2). While the oceanography of the BML site is complex because it is exposed to runoff from local sources (Estero Americano, Salmon Creek) and regional sources (Tomales Bay, Russian River, San Francisco Bay), recent generic models show how a low-salinity zone can be expected in the vicinity of the mouths of small rivers and creeks in California (Basdurak et al., 2020; Basdurak & Largier, 2022). Further, during large wave events, river outflow can be trapped nearshore and mixed to the bottom (Kastner et al., 2019; Speiser & Largier, 2024),

exposing nearshore sites to even lower salinities. An estimate of the spatial extent of this freshwater-influenced zone in the absence of wind can be obtained from model results published by Basdurak et al. (2020; see their Figure 10 for flow rates of 1, 10, and $30 \text{ m}^3 \text{ s}^{-1}$). For instance, the Navarro River flow in winter is typically between 10 and $100 \text{ m}^3 \text{ s}^{-1}$, rising to several $100 \text{ m}^3 \text{ s}^{-1}$ during high-flow events, and flows between 1 and $10 \text{ m}^3 \text{ s}^{-1}$ persist through the spring into early summer during wet years. In the context of northern California, their model shows that a salinity contour of ~ 29 psu can reach ~ 2000 m south of the mouth and ~ 3000 m north of the mouth for flows of $30 \text{ m}^3 \text{ s}^{-1}$, and about half of that distance for flows of $10 \text{ m}^3 \text{ s}^{-1}$. While freshwater influence may extend further, this contour is a good indicator of the extent of salinities low enough to impact sea urchin grazing based on our results—and closer to the mouth, one can expect lower salinities with likely greater impact on sea urchin grazing. While other rivers may have freshwater outflow an order of magnitude smaller than the Navarro River, even those rivers will often exceed $10 \text{ m}^3 \text{ s}^{-1}$ in winter, and one can expect salinities of 29 psu and lower within a zone extending ~ 1000 m from the mouth of the river in general. These rough estimates are consistent with our field results that show low sea urchin abundance for sites associated with flow over $\sim 10 \text{ m}^3 \text{ s}^{-1}$ and for sites within ~ 1000 m of a river mouth. In the presence of strong winds, the nearshore zone of freshwater influence may extend further due to onshore trapping and wind-driven alongshore stretching of the freshwater plume (Basdurak & Largier, 2022; Speiser & Largier, 2024); however, in this case, salinities may not be as low due to increased mixing and dilution.

There may be several other mechanisms for explaining the association of kelp persistence with proximity to river mouths, including runoff-related phenomena like turbidity (Speiser & Largier, 2024) and sedimentation (Griggs & Hein, 1980). Notably, higher bull kelp persistence, as well as lower purple urchin abundance, was correlated with the presence of smooth sandy bottom habitats interspersed with rocky patches. While extensive sandy habitats preclude kelp establishment (Schroeder et al., 2020), a mosaic of sand and rock habitat patches may benefit bull kelp persistence by reducing sea urchin abundance, including reduced sea urchin settlement and post-settlement survival (Boada et al., 2018) and/or increased risk of predation (Farina et al., 2018). Similarly, there is an apparent paradox in kelp doing well where waters are more turbid (i.e., near river mouths), as prior studies have found bull kelp absent or at very low abundances in turbid estuaries (Schoch & Chenelot, 2004). However, our sites only experience turbidity during brief river flow events (Speiser &

Largier, 2024), and clear water with high light and nutrients is present during most of the year, specifically during the early growing season in spring (Largier et al., 2006). Thirdly, prior reports of kelp loss during high-flow events (Davis et al., 2022) are likely related to high water velocities and physical damage rather than low salinities. It has been demonstrated that bull kelp is present at locations that reach salinities of 20 psu (Chenelot, 2003) and early life stages survive under mid-to-low salinity conditions (Farrugia Drakard et al., 2025; Lind & Konar, 2017), as do the larval stages of purple urchins (Roller & Stickle, 1985).

In this study, we evaluated the ecological resistance of bull kelp ecosystems by measuring patterns of persistence, cover, and abundance (Figure 1). All these variables show bull kelp ecosystem traits and seemed to relate positively, but the strength of that relation was low, as many factors can affect the remote sensing measurements, thus not being representative of all species traits (e.g., abundance or biomass) (McPherson & Kudela, 2022). While bull kelp abundance was measured in situ, persistence and kelp cover were measured through remote sensing techniques, and these can be far from perfect as understory bull kelp could have not been detected by satellite imagery (Schroeder et al., 2019). There could also be a lag effect from persistence to abundance driven by a reduction in spore formation and germination success (Springer et al., 2007). Therefore, more historical persistence of bull kelp does not necessarily imply more abundance in a particular year due to natural variability in the population, as has been shown before (Pfister et al., 2018), which highlights the importance of studying response variables on different scales and with different methods in studies of ecological resistance.

Identifying the factors that drive resistance of bull kelp is critical for informing management and recovery through conservation and restoration strategies. The remaining bull kelp habitat patches are sources of spores that are known to disperse locally (Burnett et al., 2024), and thus it is important to preserve a network of patches. Restoration could focus on sites with freshwater influence as well as habitat mosaics (sandy bottom interspersed with rocky bottom), and it could focus on sea urchin removal, in situ spore release, and/or sporophyte transplants (Eger et al., 2022). It is widely recognized, and has become apparent in this study, that the lack of oceanographic data prevents understanding of the full set of abiotic factors influencing bull kelp resistance (see Hamilton et al., 2023; Kennedy et al., 2024 for data gaps on the study region). Similarly, the lack of biological data precludes assessment of baseline patterns and constrains the determination of goals for conservation. Continued subtidal observations of bull kelp communities combined

with remote sensing techniques and spatially explicit oceanographic monitoring are crucial to inform conservation and restoration actions and build resilience for the future.

AUTHOR CONTRIBUTIONS

Aurora M. Ricart: Conceptualization; data curation; formal analysis; writing—original draft; funding acquisition. **Julieta B. Gómez, Rachael H. Karm, Abigail S. Dias, Maria G. Velázquez, and Taylor Nelson:** Investigation; data curation; writing—review and editing. **John L. Largier:** Formal analysis; data curation; writing—review and editing. **Katherine C. Cavanaugh and Kyle C. Cavanaugh:** Formal analysis; writing—review and editing. **Brent B. Hughes:** Conceptualization; data curation; formal analysis; writing—review and editing; project administration; funding acquisition.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Ricart et al., 2025) are available in the DIGITAL CSIC repository: <https://doi.org/10.20350/DIGITALCSIC/17472>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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