**TITLE:** Sea otter recovery buffers century-scale declines in California kelp forests

**AUTHORS:** Teri E. Nicholson,[a]* Loren McClenachan,[b] Kisei R. Tanaka,[a] and Kyle S. Van Houtan [a,c]*

**AFFILIATIONS:** [a] Monterey Bay Aquarium, 886 Cannery Row, Monterey, California 93940 USA; [b] Department of History and School of Environmental Studies, University of Victoria, Victoria, British Columbia, V8W 3P4, Canada; [c] Duke University, Nicholas School of the Environment, Durham, North Carolina 27708 USA.

* Send correspondence to: tnicholson@mbayaq.org

kyle.vanhoutan@gmail.com

**RUNNING HEAD:** historical California kelp forest

**KEY WORDS:** nature-based solutions, climate resiliency, keystone species, heat extremes, historical ecology

**No. ABSTRACT WORDS**: 195

**No. MAIN TEXT WORDS**: 3,778

**No. REFERENCES:** 82

**No. FIGURES:** 4

****** UNDERGOING JOURNAL PEER REVIEW ******

****** PLEASE DO NOT DISTRIBUTE *****

## ABSTRACT

The status of kelp forests and their vulnerability to climate change are of global significance. As the foundation for productive and extensive ecosystems, understanding the long-term trends in kelp is critical to coastal ecosystem management, climate resiliency, and restoration programs. In this study, we curate historical US government kelp inventories, develop methods to compare them with contemporary surveys, and use a machine learning framework to evaluate and rank the drivers of change for California kelp forests over the last century. Historical surveys documented *Macrocystis* and *Nereocystis* kelp forests covered approximately 120.4 km$^2$ in 1910-1912, which is only slightly above surveys in 2014-2016 (112.0 km$^2$). These statewide comparisons, however, mask dramatic regional changes with increases in Central California (+57.6%, +19.7 km$^2$) and losses along the Northern (-63.0%, -8.1 km$^2$), and Southern (-52.1%, -18.3 km$^2$) mainland coastlines. Random Forest models rank sea otter (*Enhydra lutris nereis*) population density as the primary driver of kelp changes, with benthic substrate, extreme heat, and high annual variation in primary productivity also significant. This century-scale perspective identifies dramatically different outcomes for California's kelp forests, providing a blueprint for nature-based solutions that enhance coastal resilience to climate change.

## INTRODUCTION

Kelp forest ecosystems, and the essential services they provide, are under threat worldwide [1, 2]. Located in every ocean basin, and spanning 25% of the planet's temperate and arctic coastlines, canopy-forming kelps are the foundational basis of unique marine ecosystems [3, 4]. These ecosystems supply critical services including refuge habitat for commercially important fisheries, nutrient recycling and carbon storage, protection from seabed erosion, and highly productive assemblages of biodiversity [5-7]. Though they are considered important for global carbon budgets [1, 8], kelp forests are not currently included in blue carbon initiatives [9]. Understanding the magnitude and drivers of kelp declines is therefore key to developing integrated conservation plans to promote the persistence of these ecosystems, their services, and coastal resilience regionally and globally.

Kelp forests are vulnerable to multiple threats across a range of temporal and spatial scales. In the last decade, marine heatwaves have become intense, persistent [10, 11], and  globally common, with particular severity in historically cool, largely temperate regions [12] that contain the major kelp ecoregions [13]. At the organismal scale, prolonged heat stress intensifies nutritional depletion, directly damages tissue, diminishes reproduction, accelerates senescence, and increases kelp mortality [2]. At the population scale, persistent extreme heat reduces kelp recruitment, and can ultimately convert kelp forest ecosystems to communities dominated by benthic turf algae [14, 15]. Over decadal time scales, regional threats like water quality and substrate loss have impacted kelp survival, especially where coastal development has increased sedimentation, turbidity, and harmful algal blooms [2, 16]. In extreme cases, sediment accumulation may smother the native benthos, prevent kelp resettlement, and permanently transform bedrock to soft-sediment [17, 18]. Finally, trophic disruptions, such as overhunting of a keystone predator, the southern sea otter (*Enhydra lutris nereis*), have occurred over century-long time scales, corresponding with losses of kelp forests [19]. These impacts often act synergistically, so as environmental conditions deteriorate, diminishing canopy litter can create sea urchin swarms on the remnant kelp stands [20], especially where disease or overharvesting of invertebrate predators [21, 22] exacerbates an already-poor ecosystem state.

This combination of important services and significant threats prioritizes a need to develop informed benchmarks for kelp forest restoration. Historical ecology has been particularly effective at interpreting data sources from the past to identify important sources and scale of human impacts to nature. As a result, early nautical charts, expedition narratives, consumption records, ethnographic accounts, and museum collections—for example—can be used to demonstrate broad trends and have uncovered massive megafauna declines and ecosystem transformations during the last century [23-28]. Despite the inherent differences in contemporary and historical survey methods, thoughtful analyses may provide comparisons necessary for setting conservation or management goals. To date most kelp forest assessments rely on *in situ* or remote sensing datasets from the last 50 years [1, 2], which may downgrade important ecological relationships and underestimate restoration potential, particularly given the long time scale of decline and potential interactions among drivers of change. Extending the period of record for kelp forest ecosystems may therefore be vital to better understand sources and impacts of the full suite of anthropogenic stressors, predict future trends, inform conservation efforts, and design effective restoration [29].

The California coast presents a unique opportunity to develop an historically informed assessment of kelp forests. The state's marine geography extends nearly 10° of latitude, encompasses more than 1,600 km of linear coastline, and hosts two major canopy-forming kelps (*Macrocystis pyrifera*, *Nereocystis luetkeana*) that occur along a gradient of human impacts. Surrounding these kelp forests is a cascade of climatic influences [30], characterized in large part by the productive upwelling of the California Current system. Onshore lies a mosaic of intensely modified regions (urbanization, agriculture) and well-managed terrestrial and marine protected areas. In central California, the southern sea otter population is gradually recovering from a persistent ecological extinction and resuming its keystone function [22, 31]. Within this complex setting of environmental factors, comparison of historical and contemporary canopy cover surveys may yield novel insights into kelp forest dynamics through time.

Here, we generate spatially explicit historical reference points of California kelp forest cover and assess the dominant drivers of change over the last century. We digitize, georeference, and quantify historical kelp surveys, compare them to modern aerial survey data, assess carbon storage, and generate a 100-year record across several spatial scales. Importantly, this timescale captures the major human drivers of change in this system, including recent warming, coastal development, and the decline and initial recovery of sea otters following protection in 1911. To accompany these kelp data, we curate a suite of environmental driver datasets and use Random Forest (RF) modeling to rank their influence on changes in canopy cover. This provides a more informed account of the long-term status of California kelp forest ecosystems and identifies natural strategies for climate resilience and ecosystem restoration.

## METHODS

### *Kelp Cover Time Series*

To assess century-scale changes in kelp forests throughout California, we analyzed an historical data source from early 20th century U.S. government ship-based surveys of its Pacific coast commercial resources, led by three scientists, George B. Rigg, Frank M. McFarland and Wesley C. Crandall [32]. Their data have been foundational to understanding kelp forest dynamics in Washington state [33, 34] and provide a similar opportunity for examining change throughout California. While invaluable as a source of long-term information, several factors suggest these historical surveys may represent a conservative baseline. As an inventory of commercially harvestable kelp, scientists only mapped large beds measuring > 2.5 ha. Additionally, the government scientists who performed the surveys observed that kelp coverage was “unusually low” [32]. Though historical assessments of the distribution of California kelp forests are regrettably few—a main impetus for this present study—the surveyors’ anecdotal observation is in agreement with historical assessments from Washington state that describe 1911 as a 50-year (1880-1930) kelp canopy minimum [33]. Nonetheless, considering the highly dynamic nature of kelp cover in space and time [35] and the additional need for historical reference points to assess long-term ecological change [27, 29], here we develop a cautious methodology to compare historical and contemporary kelp survey data.

The historical dataset is contained in 26 map sections of the California coastline, representing ship-based surveys from 1911-1912 with additional beds reported from 1910. To extract individual kelp beds, we georeferenced each map to fixed reference points from the California state shapefile [36], confirming alignment by matching survey depths with modern bathymetry data. Within each survey map, we then digitized canopy cover by tracing each designated kelp bed. This resulted in 186 polygons described as *Macrocystis*, *Nereocystis* or mixed kelp species along the California mainland with an additional 56 patches in the Channel Islands. For each harvestable bed, historical surveyors attributed 6 discrete kelp densities – from “very thin” to “very-heavy” – they derived empirically in meticulous detail [32]. We explored using these quantitative densities [32] as a correction factor (see Supplemental Material) to discount the area of the smoothed historical kelp bed polygons (Figure 1A), but developed a stepwise routine to facilitate comparing historical and contemporary kelp data (see below).

We obtained contemporary kelp canopy estimates from CDFW aerial surveys (https://bit.ly/3bI1D4l) [37] for 2014-2016, encompassing a similar 3-year period. These surveys captured high-resolution multispectral imagery that were later downsampled to 2m resolution and generated into shapefiles of kelp polygons. This procedure has become an established method for coastal monitoring and ground-truthing coarser (30m) LANDSAT imagery [34, 35], especially when kelp cover is sparse [38-40] or fringes rugose coastlines [41]. Monitoring was standardized to occur during the fall season of peak kelp abundance and when tidal currents, fog and glare are at their minima [37]. To build a contemporary dataset comparable with the three-year historical survey, we used ArcGIS tools [36] to overlay the 2014, 2015, and 2016 shapefiles (Figure 1B), then created a novel layer by outlining the union of kelp polygons. The resulting outlined shapefile (Figure 1C) mimicked the resolution and form of the historical “harvestable” kelp bed output by further smoothing pixelated vector data that originated as high-resolution raster imagery, and by excluding all polygons < 2.5 ha. Next, we used the “intersect” function to calculate regional mean polygon overlap values between the unioned and outlined contemporary kelp shapefiles (Figure 1D), to be used as correction factors for estimating kelp canopy area from the historical maps. To create a comparably scaled statewide historical benchmark, we discounted the area of each harvestable kelp bed from the 1910-1912 surveys by applying the correction factors for northern, central, and southern California. These regional boundaries (marked at Pigeon Point and Point Conception) are widely recognized in marine ecology and specifically relevant here due to kelp composition; northern California is dominated by *Nereocystis*, southern is exclusively *Macrocystis*, and the central region is a mixture of the two.

To compare the historical vector and contemporary raster datasets, we overlayed both georeferenced surveys with a 500 m linear coastal transect, extending from shoreline to the 30 m isobath. This linearized binning of the California coastline, from the Mexico (0 km) to Oregon border (1,620 km), is our geospatial framework for all datasets and analyses. We then characterized century-scale changes in kelp forests along California’s mainland coast by calculating the difference between recent (2014-2016) and historical (1910-1912) canopy area within each 500 m unit. To contextualize and visualize local trends, we then fit a uniform-span locally weighted regression (“LOESS”, $\alpha = 0.075$) to these data [42]. For the historical kelp surveys, we calculated the standing biomass of kelp carbon from bed areas, derived densities [32] and species-specific wet kelp to dry carbon biomass ratios [43, 44]. For recent surveys, we used a similar procedure but applied area-weighted averages for bed density and wet-to-dry biomass conversions derived for each region using the historical surveys. For all surveys, we express kelp carbon storage in $CO_2$ equivalents and calculate its social cost—the estimated costs of economic damages from $CO_2$ emissions or benefits from $CO_2$ removal [45]. While international carbon frameworks typically conduct $CO_2$ accounting in terms of C sequestration, these relationships for kelps are currently unresolved at scale. Until such empirically verified sequestration rates exist, here we report kelp $CO_2$ equivalents in terms of standing biomass—a metric which is of value.

### *Driver Datasets and Analytical Models*

Next, we identified and curated spatially resolved environmental features that represent likely drivers of regional kelp ecosystem changes over the last century. To assess the potential effects of long-term oceanographic warming events (e.g., ENSO, marine heatwaves), we examined two gridded, monthly 1° × 1° SST products (HadlSSTv1.1, COBESSTv2) and one 0.25° × 0.25° product (NOAA OISST) [46-48]. Similar to previous work [13], we defined extreme heat as exceeding the 95th percentile of SST observed during the first 50 years of record (1870-1919) for each calendar month within each coastal grid cell, averaged from the HadlSSTv1.1 and COBESSTv2 data series. With these historical benchmarks, we quantified extreme heat over the contemporary period (1983-2016) with the finer scale NOAA OISST product. For the same contemporary period, we calculated the months with mean NOAA OISST values ≥ 20 °C, representing a maximum physiological tolerance for *Macrocystis* recruitment [49, 50]. In addition to climate, we characterized contemporary coastal benthic habitat by proportion of hard substrate, using data derived from the California Seafloor and Coastal Mapping program [51]. To incorporate trophic dynamics, we calculated 2014-2016 mean sea otter population density from annual USGS range-wide spring surveys throughout central California [52]. We also integrated an approximate measure of human-related stressors by obtaining 30 arc-second gridded (~1 $km^2$) coastal (within 2.5 km of shore) population data [50]. To explore effects of net primary productivity (NPP) variability on changes in kelp canopy, we acquired available (2003-2016) monthly estimates from the Vertically Generalized Production Model (VGPM; https://bit.ly/3kQBgO8). From these data, we estimated both annual and monthly mean measures of variability along the California coastline at a spatial resolution of 0.083° × 0.083°. To standardize all datasets and match with kelp cover, we assigned all variables to the closest 500 m coastal segment, applying a uniform-span locally weighted regression ("LOESS", $\alpha$ = 0.075) to factors where data are nonstationary (sea otters, humans) or derived from coarser scale models (SST, NPP).

Finally, we modeled the relationships between environmental features and kelp cover changes using RF [53]. RF is a type of machine learning algorithm that generates random subsets of model inputs to predict the response variable, through bootstrapping a set of training data (sampled with replacement) and growing a "forest" of diverse and uncorrelated "trees" [54, 55]. Here the RF framework is appealing as it capably describes non-linear and non-parametric relationships, provides robust model predictions with an unbiased assessment of the generalized error, and offers unique insight into variable interactions (partial dependency visualizations). More generally, machine learning is becoming critical in conservation science to manage large, sensor-based data streams into efficient analytical workflows and system learning [56]. Previously, we applied RF elsewhere [24, 57-59] in a similar manner to understand long-term changes in marine ecosystems.

Within our RF model, we used raw (or nontransformed) data series for the output variable (kelp differences) and resolved, static input variables (hard substrate), but transformed or smoothed (LOESS, $\alpha$ = 0.075) input factors where data are nonstationary (sea otter and human population densities) or derived from coarser scale models (SST heat extremes, and NPP variances). The model excludes coastal transect bins where kelp was not detected during any surveys, so that a zero result singularly refers to a lack of change in kelp forested areas, not the absence of this ecosystem. To ensure sampling independence, we tested for spatial autocorrelation among model residuals (Moran's $I$ = -0.01) [60]. We then improved model performance by eliminating highly correlated variables [61], and tuning model parameters ('mtry' and 'ntree') using a simple grid search routine. We also assessed model robustness by randomly generating 100 iterations of training and validation datasets, the summarized results to characterize model performance and rank variable importance [54]. Finally, to examine interactive effects between factors influencing kelp changes, we created partial dependency plots, pairing key environmental drivers from the final model output. All analyses were conducted in version 4.0.3 of the R statistical environment [62].

## RESULTS

California's overall kelp canopy area declined slightly (-6.9%, -8.4 $km^2$) between historical (1910-1912) and contemporary (2014-2016) time periods, but differences among regional trends were dramatic along the mainland (Table 1). Gains in central California (+57.6%, +19.7 $km^2$) nearly compensated for losses in the northern (-63.0%, -8.1 $km^2$) and southern (-52.1%, -18.3 $km^2$) regions. By comparison, kelp in the offshore Channel Islands declined slightly (-4.5%, -1.7 $km^2$) in part from significant increases at San

Miguel (32%) and San Nicolas (68%) Islands, which balanced losses from all other islands. Figure 2 plots century kelp area differences along a continual mainland transect from south to north California. The 3 most extreme kelp declines occur at both margins of the southern California Bight (e.g., from Santa Barbara to San Diego) and near Cape Mendocino in the north where there was a near total loss (Figure 2). By contrast, kelp canopy increased nearly everywhere throughout the central coast.

The estimated historical standing biomass of carbon in California kelp amounted to 556.5 kt $CO_2$, with 444.6 kt $CO_2$ on the mainland, and 111.9 kt $CO_2$ in the Channel Islands during the 1910-1912 survey composite (Table 1). Though kelp canopy declined over the last century, we estimate carbon biomass may have increased by 5.3% to 586.0 kt $CO_2$ in the 2014-2016 survey. This is the result of regional differences in species composition, their associated implications for the density of kelp beds, and the consequent carbon composition of kelp tissues (see Supplementary Material). We estimate increases of 57.6% in the total standing biomass of kelp in the central California (252.7 to 398.3 kt $CO_2$), steep declines in the northern (-63.2 kt $CO_2$, -63.0%) and southern (-47.8 kt $CO_2$, -52.1%) regions, and a modest decline in the Channel Islands (-5.1 kt $CO_2$, -4.5%). These reginal trends represent a dramatic spatial realignment of California kelp. In 1910-1912, 45.4% of California's kelp carbon biomass was in central California, which jumped to 68.0% in 2014-2016. Changes in the estimated social cost of carbon kelp follow biomass proportionally, with a slight increase from $US 103.0M in 1910-1912 to $US 108.4M in 2014-2016 (Table 1), with the same regional realignment.

Sources of influence on kelp canopy cover (sea otters, substrate, climate, NPP variability, and humans) varied along the transect revealing areas of higher and lower potential resilience and impact (Figure 3). Kelp canopy gains throughout central California indicate a confluence of optimal conditions, where sea otters are recovering (Figure 3E), extreme heat and annual NPP variability are low (Figure 3A-B, F-G, hard substrate is abundant (Figure 3C), and human populations (and coastal development) are minimal overall (Figure 3D). In southern California, where kelp declines were greatest, the opposite conditions are true. Perhaps due to greater seasonal variability of NPP (Figure 3F), Northern California experienced major kelp forest declines despite several positive features – abundant hard substrates, low human population densities, and a lack of absolute extreme heat (SST ≥ 20 °C). However, no California region is free from extreme marine heat (Figure 3A, F), and sea otters are functionally absent outside the state's central coastline (Figure 3E).

The measured (Figure 4A) and modeled (Figure 4B) influences to California kelp forest changes show that kelp increased with the population density of sea otters (and their ecosystem functions), declined with the prevalence of extreme heat and NPP variability, declined where hard substrates were scarce, and was ambiguously influenced by human population density. Even though relative and absolute measures of climate change might affect kelp physiology differently, these two climate factors were highly correlated (Figure 3AB). Following best practices [61], we removed the less resolved absolute heat stress series from the model, improving model performance. The resulting RF model explained > 70% of the data variability. Trophic dynamics (i.e., sea otter presence or absence), hard benthic substrate, extreme marine heat represented by a fixed historical benchmark from before and during the earliest kelp survey data, and NPP variability explain most of the observed changes in California kelp (Figure 3C). Benefits to kelp occurred where sea otters are now relatively abundant, with model predictions indicating kelp stabilization or gains at population levels > 0.05 sea otters $ha^{-1}$. While extreme heat was a dominant model factor explaining kelp changes (Figure 4C), its effect declined where kelp losses were highest (Figure 4A-B).

Apart from individual variable effects, understanding variable interactions to model outputs can provide greater practical insights. Figure 4D examines interactions among model features using two-way partial dependency plots (PDPs). This shows the primary effect of sea otters on kelp changes, enhancing gains across a gradient of hard substrate and buffering losses from extreme heat, NPP variability, and human population density (Figure 4D). Sea otters exerted the greatest influence on kelp ecosystem resilience (e.g., blue shaded area in Figure 3D) corresponding to regional kelp canopy expansion between 1910 and 2016. In their absence, kelp declined from every other stressor (loss of hard substrate, ocean warming, NPP variability, and humans.

## DISCUSSION

Assessing ecological trends over relevant temporal and spatial scales is essential to identify the full magnitude and key drivers of change, but reliable information rarely exists over this time span. Here, we extend a previously reported 35-year baseline [1] by nearly seventy years along the full extent of California's coastline, which spans nearly 10° of latitude and represents a broad range of coastal ecosystem states, from highly impacted, densely populated industrial outfalls to more remote, nearly intact marine protected areas with recovering sea urchin predators. By examining environmental factors related to century-scale, spatially resolved kelp canopy changes along California's mainland coastline, we identify four important findings. First, although overall statewide canopy decline was low, regional changes were dramatic with central California kelp forest gains nearly offsetting losses along northern and southern mainland coastlines (Table 1, Figure 2). Second, the presence of sea otters outweighed all other environmental factors, representing a strong driver of kelp forest gains by increasing canopy resilience to impacts from more detrimental factors (Figures 2-4). Third, in the absence of sea otters, extreme heat and high annual variation in NPP productivity corresponded most with declines (Figures 3-4). Fourth, we translate our kelp area metrics to carbon accounting and social costs to assess the importance of kelp ecosystems and their climate resiliency in global conservation and policy frameworks.

Our identification of substantial regional declines in kelp canopy over the last century suggests staggering alterations of California's coastline, capturing not only recent losses in northern California [22] but mid-century decreases along the southern transect [17, 63]. However, this may reflect a fraction of true losses incurred during the last two centuries when considering effects of nineteenth-century, grassland erosion from cattle grazing and crop cultivation along southern California coastal watersheds [26]. By the early 1900s, rapid, unmanaged agricultural development yielded an estimated 10-fold increase in sediment deposition from the Los Angeles and Orange county alluvial plain, smothering historically abundant marine granite substrate and a complex benthos formed by millennia of shelled invertebrates and gravel, which may have provided suitable substrate to support extensive offshore kelp forests [26]. After 1900, port excavations, inadequate wastewater management, and shallow sewage outfalls degraded nearshore kelp beds off the southern California coastline [17, 18, 64, 65] during dramatic, mid-twentieth century human population growth [66]. Where kelp forests remained, anchoring to softer sediments increased their vulnerability to catastrophic removal from more severe and frequent seasonal storms in a warming ocean [67]. Such patterns are like effects seen in other nearshore ecosystems, like coral reefs, where impacts from early agricultural development and land use resulted in sedimentation and loss prior to the onset of acute global climate change [23, 25]. Our findings here suggest that managing terrestrial land use is an important component of maintaining and restoring the health of marine and coastal ecosystems, alongside managing contemporary impacts from warming oceans. Future research that reconstructs benthic substrate dynamics over a similar 100-year time may provide greater insights into long-term drivers and resiliency planning for kelp ecosystems.

Perhaps most notably, we found that kelp canopy declines along northern and southern mainland regions of the state were offset by gains within the central coast, corresponding with the presence of sea otters. Absent from our model, we found similar trends among the Channel Islands with kelp canopy gains along islands where sea otters are observed or recovering (San Miguel and San Nicolas Islands) balancing dramatic losses among all others, where sea otters are absent (Santa Rosa, Santa Cruz, Anacapa, Santa Barbara, Santa Catalina, and San Clemente). Sea otter recovery is currently limited to central California and San Nicolas Island, where protections and active reintroductions have been most effective [58, 68, 69]. Although sea otters are recognized as integral to healthy kelp forests throughout the North Pacific [70-72], their role in California, where trophic cascades and species assemblages are complex [30, 73, 74], is more difficult to measure. Our results suggest that otters are critical to maintaining kelp forest health throughout their range, buffering long-term kelp loss where their population densities are highest in central California (Figures 2-4). Sea otter populations may contribute to increased climate resilience by providing for a multitude of kelp ecosystem services, perhaps including carbon storage, but recent research from a spatially constrained section of the central California coast [74] suggests otters may be limited in recovering kelp ecosystems from a barren state where conditions are already degraded by coastal development. The role of otters in increasing natural climate resiliency underscores the potential for trophic rewilding—the reintroduction of herbivores and carnivores to systems where they have been lost—to support climate change resistance and resiliency. Research from terrestrial ecosystems suggest that carbon cycling may benefit from such trophic rewilding [75]. Higher elephant densities in central African rainforests, for example, led to shifts toward larger trees with higher wood density, enhancing carbon storage [76]. Across ecosystems, this role of animals in carbon storage has been underappreciated [77]. Given that marine megafauna populations across the globe approach 90% [78], the co-benefits of restoring marine animal populations to enhance biodiversity and natural climate resiliency must be given serious consideration.

Our results demonstrate the damaging effects of warming temperatures on kelp [14, 15, 22, 79, 80], especially within ecosystems already subjected to trophic downgrading. The large spatial scale of our analysis also allows insight into pockets of resilience and vulnerability. For example, our finding that the effect of extreme marine heat declined when kelp losses were highest is consistent with previous research, suggesting local adaptation and heat tolerance in southern California [81]. Single species *Macrocystis* stands are dominant in this region, and this species occurs on 4 continents and in 4 ocean sub-basins (real-time crowdsourced data at https://bit.ly/3QNEgoI), likely indicating significant genetic and phenotypic plasticity [82, 83]. Northern California, by contrast, saw more moderate extreme heat and human populations, yet had similar extreme declines in kelp cover by comparison to southern California. Unlike southern California, northern California is more dominated by *Nereocystis* stands. *N. luetkeana* has a limited distribution in the North Pacific and an annual life cycle, perhaps conferring less phenotypic diversity and greater susceptibility to extreme heat [84].

Collectively, our results provide valuable information about the importance of restoring trophic relationships and minimizing stressors from coastal development to increase kelp forest resilience within a warming and more variable climate. Although kelp enhancements have been successful at the small scale [8], California lacks coordinated, broad scale activities, and these are also rare globally. Large-scale kelp forest restoration programs might benefit from recognition and support from international blue carbon initiatives. Blue carbon initiatives currently focus on mangroves, sea grass meadows, and salt marsh ecosystems [85]. The omission of kelp forests may underestimate the carbon storage potential from coastal ecosystems [5, 9] while also reducing programmatic resources and strategic capacity for nearshore ecosystem restoration. The addition of macroalgae into carbon crediting initiatives may provide funding for restoration and gardening initiatives that offer potential solutions to rebuilding marine resources and their economic, cultural, and life-supporting value in a world where climate change continues to alter and threaten coastal communities. As an example, our historical estimate of 2.04 tg $CO_2$ equivalents stored in California kelp has an estimated monetized value of $ 377.2M, as determined by the most recent "social cost of $CO_2$" (mean projection, 2020 USD) [45]. This historical monetized value of $CO_2$ equivalents in California kelp is $ 324.2M greater than the value ($ 53.0M) estimated from the 0.29 tg $CO_2$ in the 2014-2016 survey average.

Although interpreting historical data is imperfect and not without limitations, long-term ecological records are essential for understanding ecosystem dynamics, climate resiliency, and effective restoration [29]. Because kelp is highly variable across seasons and individual years [35], we focused on comparing kelp maximums (or spatial unions) observed across two multi-year time periods, separated by a century. To resolve differences between ship-based and aerial survey methods, we created less granular, blocky patches from aerial surveys, mimicking the historical data, then calculated regional canopy area discount rates based on contemporary values. While the corrected historical kelp area may underestimate historical canopy cover, it provides a conservative record to compare with contemporary data. Given the meticulous and extensive nature of the historical inventories [32], and the global significance of kelp ecosystems, these historical data presented an important opportunity.

Our century-long evaluation of trends in California highlights a dramatic regional decline, resulting from anthropogenic effects of climate warming, coastal development, and trophic disruptions. This magnitude of California kelp deforestation is greater than other reported assessments [1, 8] perhaps from a finer geographic scale and longer baseline reference, which may still underrepresent true losses when considering human impacts before 1900. Our study also indicates that among stressors, a warming climate has a profound single influence, but this factor may be enhanced by the sedimentation and smothering of nearshore benthic substrates during rapid coastal development. Where coastal development is managed (or mitigated), recovery of sea otters and their trophic relationships may increase kelp forest resiliency to climate change, especially when warming temperatures intensify sea urchin recruitment and herbivory. Restoration of California's coastline resources requires the rapid implementation of innovative, collaborative, and sustainable ocean gardening strategies to address climate change and prevent further decline in kelp forest ecosystems.

**DATA AVAILABILITY:** All datasets and code used here are available at the third-party repositories GitHub (https://bit.ly/3pvUkQI) and Open Science Framework (https://osf.io/gsjex/).

*REVIEWER NOTE: these repositories are currently private and will become public when the manuscript is accepted for publication.*

**AUTHOR CONTRIBUTIONS:** All authors designed the study and wrote the manuscript. TN and LM curated the data, TN wrote the code, and TN and KV analyzed the data and generated the figures.

**FUNDING:** This research was supported by generous donor contributions to the Monterey Bay Aquarium.

**ACKNOWLEDGEMENTS:** E. Mapstone, W. Rex, T. Wang, C. Ross aided in the georeferencing and curation of historical data. J. Fujii improved earlier versions of this manuscript. C. Pfister and K. Miranda provided data and advice on kelp carbon storage. C. Colgan advised on carbon pricing schemes.

**COMPETING INTERESTS:** The authors declare no competing interests.

## TABLE and FIGURE CAPTIONS

**Table 1. Statewide and regional changes in California kelp over the last century.** At the state level, the total area (-6.9%), carbon biomass (+5.3%), and social costs (+5.3%) of harvestable kelp beds (see Methods) were not considerably different from 1910-1912 to 2014-2016 surveys. These trends, however, obscure stark regional differences that encompass a dramatic shift of California kelp over this period. In central California, kelp increased 57.6%, growing 19.7 $km^2$ and adding an estimated 145.6 kt $CO_2$. In all other regions kelp declined. Most notably, northern California saw 63% declines in kelp amounting to an estimated 8.1 $km^2$ and 63.2 kt $CO_2$ lost. The overall decline in kelp canopy area with a simultaneously estimated increase in kelp carbon biomass over time highlights regional differences in species composition and associated bed density and carbon content. The estimated social cost of kelp carbon follows the biomass trends, and in both periods exceeds $US 100M.

**Figure 1. Regional discount rates for comparing historical and contemporary kelp canopy surveys.** Regional mainland examples of (A) historical maps and noted harvestable beds, (B) composite of contemporary (2014-16) CDFW aerial surveys, (C) their reframing at comparable scale (or as harvestable beds), and (D) proportional canopy cover distributions derived from the intersections of (B) and (C) throughout California. The 1911-12 kelp survey represents an effort by the US Department of Agriculture to assess potash resources from California's summer to fall seaweed canopy. Similarly, during the mid-summer to fall seasonal peak, CDFW periodically conducted annual statewide aerial surveys of kelp canopy from 1989 through 2016.

**Figure 2. Century-scale, mainland kelp canopy losses throughout northern and southern regions of California slightly surpassed increases along the central coastline**. Mainland kelp canopy resources depicted by (A) total area (ha), and (B) changes within nearshore habitat (≤ 30m depth) during 1911-12 and 2014-2016 (composite) from (C) the Mexico to Oregon state border (0 to 1620 km). Canopy area gains along central California nearly offset losses within northern and southern coastal regions (see Table 1). To better visualize broad regional trends, we fit a locally weighted regression (LOESS, span 0.075) to these kelp features. Kelp canopy changes between contemporary and historical surveys are indicated by circles, with gains in blue and losses in red. All measurements reflect peak seasonal abundance in kelp from mid-summer through fall. Southern-central and central-northern region dividing landmarks are Point Conception and Pigeon Point, respectively, with San Francisco Bay, Monterey Bay, Santa Barbara Channel, Los Angeles Basin, and San Diego Bay noted as geographic features.

**Figure 3. Potential coastal sources of influence to statewide kelp canopy area**. (A) Sea surface temperature (SST) heat extremes and (B) kelp climate maximum events (≥ 20° C) occurred most frequently throughout the southern or low latitude portion of (H) California. We estimated occurrence of coastal heat extremes by calculating mean-monthly frequency of events (1983-2016) within the 95th percentile of historical SSTs recorded from 1870 to 1919. (C) Hard seafloor substrate (≤ 30-meter depth) is more abundant throughout northern and central coastal regions, nearly the reverse distribution of (D) human population density. (E) Sea otter population densities are greatest within the central portion of the state's coastline, where recovery is occurring. (F) Monthly and (G, J) annual net primary productivity (NPP) variability distributions are nearly mirror opposites, corresponding with greater seasonality in northern California and longer cycles of extreme climate conditions in the southern coastline. Raw data are indicated by circles and smoothed using a uniform-span, locally weighted regression (LOESS, $\alpha$ = 0.075). During analysis, we used transformed data to characterize both nonstationary factors (i.e., sea otter, humans) and environmental data derived from coarser scale models (i.e., SST, NPP).

**Figure 4. Large-scale SST anomalies and net primary productivity variability corresponded most with overall kelp canopy declines, but sea otter density mitigated statewide losses**. (A) Pair-wise

comparisons, and (B) modeled individual conditional expectations (ICE) from the Random Forest (RF) model outputs for the highest ranked variables. Predominantly soft seafloor substrate, moderately high temperature heat extreme frequency and NPP variabilities, and densely populated coastlines related most strongly with canopy kelp losses. By contrast, sea otters corresponded with minimal to low declines, or even kelp gains at higher population densities (> 0.05 ha $^{-1}$). We assigned (C) variable importance rankings from comparative increases in model MSE when each factor was removed. Overall, this six factor RF model explains 71% of variability related to century-scale kelp canopy area changes. (D) Two-way partial dependency plots describe the predicted interactions between impact of selected factors on kelp canopy changes. Here losses increase with *y^*, symbolized with warm colors. Among all environmental factors, only sea otters consistently correspond with predicted gains in kelp canopy area.

## REFERENCES

1. Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, et al. Global patterns of kelp forest change over the past half-century. Proceedings of the National Academy of Sciences. 2016;113(48):13785-90.
2. Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF. Status and trends for the world's kelp forests. World seas: an environmental evaluation: Elsevier; 2019. p. 57-78.
3. Dayton PK. Ecology of kelp communities. Annual review of ecology and systematics. 1985;16(1):215-45.
4. Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, et al. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental conservation. 2002:436-59.
5. Filbee-Dexter K, Wernberg T. Substantial blue carbon in overlooked Australian kelp forests. Scientific Reports. 2020;10(1):1-6.
6. Smale DA, Burrows MT, Moore P, O'Connor N, Hawkins SJ. Threats and knowledge gaps for ecosystem services provided by kelp forests: a northeast A tlantic perspective. Ecology and evolution. 2013;3(11):4016-38.
7. Vásquez JA, Zuñiga S, Tala F, Piaget N, Rodríguez DC, Vega JA. Economic valuation of kelp forests in northern Chile: values of goods and services of the ecosystem. Journal of Applied Phycology. 2014;26(2):1081-8.
8. Eger AM, Marzinelli EM, Christie H, Fagerli CW, Fujita D, Gonzalez AP, et al. Global kelp forest restoration: past lessons, present status, and future directions. Biological Reviews. 2022.
9. Macreadie PI, Anton A, Raven JA, Beaumont N, Connolly RM, Friess DA, et al. The future of Blue Carbon science. Nature communications. 2019;10(1):1-13.
10. Frölicher TL, Laufkötter C. Emerging risks from marine heat waves. Nature communications. 2018;9(1):650.
11. Oliver EC, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, et al. Longer and more frequent marine heatwaves over the past century. Nature Communications. 2018;9(1):1-12.
12. Arafeh-Dalmau N, Schoeman DS, Montaño-Moctezuma G, Micheli F, Rogers-Bennett L, Olguin-Jacobson C, et al. Marine heat waves threaten kelp forests. Science. 2020;367(6478):635-.
13. Tanaka KR, Van Houtan KS. The recent normalization of historical marine heat extremes. PloS Climate. 2022;1(2):e0000007.
14. Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, et al. Climate-driven regime shift of a temperate marine ecosystem. Science. 2016;353(6295):169-72.
15. Filbee-Dexter K, Wernberg T, Grace S, Thormar J, Fredriksen S, Narvaez C, et al. Marine heatwaves and the collapse of marginal North Atlantic kelp forests. Scientific reports. 2020;10(1):1-11.
16. Friedlander AM, Ballesteros E, Bell TW, Caselle JE, Campagna C, Goodell W, et al. Kelp forests at the end of the earth: 45 years later. Plos one. 2020;15(3):e0229259.
17. Foster MS, Schiel DR. Loss of predators and the collapse of southern California kelp forests (?): alternatives, explanations and generalizations. Journal of Experimental Marine Biology and Ecology. 2010;393(1-2):59-70.
18. Kvitek RG, Leisten TM, Iampietro PJ, Bretz CK. Santa Monica Bay mapping project (SMBMP)—final report and GIS user's guide. California State University Monterey Bay, Seaside, CA.: Seafloor Mapping Lab, 2003.
19. Estes JA, Palmisano JF. Sea otters: their role in structuring nearshore communities. Science. 1974;185(4156):1058-60.
20. Harrold C, Pearse JS. The ecological role of echinoderms in kelp forests. Echinoderm studies. 1987;2:137-233.
21. Ling S, Johnson C, Frusher S, Ridgway K. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences. 2009;106(52):22341-5.
22. Rogers-Bennett L, Catton C. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Scientific reports. 2019;9(1):1-9.
23. Cramer KL, Jackson JBC, Donovan MK, Greenstein BJ, Korpanty CA, Cook GM, et al. Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. Science Advances. 2020;6(17):eaax9395.

24. Gagné TO, Hyrenbach KD, Hagemann ME, Van Houtan KS. Trophic signatures of seabirds suggest shifts in oceanic ecosystems. Science Advances. 2018;4(2):eaao3946.

25. McClenachan L, O'Connor G, Neal BP, Pandolfi JM, Jackson JB. Ghost reefs: Nautical charts document large spatial scale of coral reef loss over 240 years. Science Advances. 2017;3(9):e1603155.

26. Tomašových A, Kidwell SM. Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. Proceedings of the Royal Society B: Biological Sciences. 2017;284(1856):20170328.

27. Zu Ermgassen PS, Spalding MD, Blake B, Coen LD, Dumbauld B, Geiger S, et al. Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. Proceedings of the Royal Society B: Biological Sciences. 2012;279(1742):3393-400.

28. Miller EA, McClenachan L, Uni Y, Phocas G, Hagemann ME, Van Houtan KS. The historical development of complex global trafficking networks for marine wildlife. Science Advances. 2019;5(3):eaav5948.

29. Alagona PS, Sandlos J, Wiersma YF. Past imperfect: using historical ecology and baseline data for conservation and restoration projects in North America. Environmental Philosophy. 2012;9(1):49-70.

30. Tanaka KR, Van Houtan KS, Mailander E, Dias BS, Galginaitis C, O'Sullivan J, et al. North Pacific warming shifts the juvenile range of a marine apex predator. Scientific reports. 2021;11(1):3373.

31. Hatfield BB, Yee JL, Kenner MC, Tomoleoni JA. California sea otter (Enhydra lutris nereis) census results, spring 2019. US Geological Survey, 2019 2327-638X.

32. Cameron F, Crandall W, Rigg G, Frye T. Potash from Kelp. US Department of Agriculture Report, no 100. 1915;(April).

33. Berry HD, Mumford TF, Christiaen B, Dowty P, Calloway M, Ferrier L, et al. Long-term changes in kelp forests in an inner basin of the Salish Sea. PLOS ONE. 2021;16(2):e0229703.

34. Pfister CA, Berry HD, Mumford T. The dynamics of Kelp Forests in the Northeast Pacific Ocean and the relationship with environmental drivers. Journal of Ecology. 2018;106(4):1520-33.

35. Cavanaugh KC, Siegel DA, Kinlan BP, Reed DC. Scaling giant kelp field measurements to regional scales using satellite observations. Marine Ecology Progress Series. 2010;403:13-27.

36. ESRI. ArcGIS Version 10.8.1. Redlands, CA: Environmental Systems Research Institute, Inc.; 2020.

37. CDFW. Science Spotlight: Kelp Surveys. 2017.

38. Hamilton SL, Bell TW, Watson JR, Grorud-Colvert KA, Menge BA. Remote sensing: generation of long-term kelp bed data sets for evaluation of impacts of climatic variation. Ecology. 2020;101(7):e03031.

39. Finger DJ, McPherson ML, Houskeeper HF, Kudela RM. Mapping bull kelp canopy in northern California using Landsat to enable long-term monitoring. Remote Sensing of Environment. 2021;254:112243.

40. McPherson ML. Mapping Kelp Forests Using Existing and Emerging Remote Sensing Techniques: University of California, Santa Cruz; 2021.

41. Nijland W, Reshitnyk L, Rubidge E. Satellite remote sensing of canopy-forming kelp on a complex coastline: A novel procedure using the Landsat image archive. Remote Sensing of Environment. 2019;220:41-50.

42. Cleveland WS, Devlin SJ, Grosse E. Regression by local fitting: methods, properties, and computational algorithms. Journal of econometrics. 1988;37(1):87-114.

43. Miranda KK, Weigel BL, McCoy SJ, Pfister CA. Differential impacts of alternate primary producers on carbon cycling. Ecology. 2021;102(9):e03455.

44. Rassweiler A, Reed DC, Harrer SL, Nelson JC. Improved estimates of net primary production, growth, and standing crop of Macrocystis pyrifera in Southern California. Ecology. 2008;99(9):2132-.

45. Rennert K, Errickson F, Prest BC, Rennels L, Newell RG, Pizer W, et al. Comprehensive Evidence Implies a Higher Social Cost of CO2. Nature. 2022.

46. Banzon V, Smith TM, Chin TM, Liu C, Hankins W. A long-term record of blended satellite and in situ sea-surface temperature for climate monitoring, modeling and environmental studies. Earth Syst Sci Data. 2016;8(1):165-76.

47. Hirahara S, Ishii M, Fukuda Y. Centennial-scale sea surface temperature analysis and its uncertainty. Journal of Climate. 2014;27(1):57-75.

48. Rayner N, Parker DE, Horton E, Folland CK, Alexander LV, Rowell D, et al. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research: Atmospheres. 2003;108(D14).

49. Deysher LE, Dean TA. In situ recruitment of sporophytes of the giant kelp, Macrocystis pyrifera (L.) CA Agardh: effects of physical factors. Journal of experimental marine biology and ecology. 1986;103(1-3):41-63.

50. Graham MH, Vasquez JA, Buschmann AH. Global ecology of the giant kelp Macrocystis: from ecotypes to ecosystems. Oceanography and Marine Biology. 2007;45:39.

51. Johnson SY, Cochrane GR, Golden NE, Dartnell P, Hartwell SR, Cochran SA, et al. The California seafloor and coastal mapping program–providing science and geospatial data for California's state waters. Ocean & coastal management. 2017;140:88-104.

52. USGS. California sea otter population annual survey data. 2014-2016.

53. Liaw A, Wiener M. Classification and regression by randomForest. R news. 2002;2(3):18-22.

54. Breiman L. Random forests. Machine learning. 2001;45(1):5-32.

55. Hastie T, Tibshirani R, Friedman J. Overview of supervised learning. The elements of statistical learning: Springer; 2009. p. 9-41.

56. Tuia D, Kellenberger B, Beery S, Costelloe BR, Zuffi S, Risse B, et al. Perspectives in machine learning for wildlife conservation. Nature Communications. 2022;13(1):792. doi: 10.1038/s41467-022-27980-y.

57. Becker SL, Brainard RE, Van Houtan KS. Densities and drivers of sea turtle populations across Pacific coral reef ecosystems. PloS one. 2019;14(4):e0214972.

58. Becker SL, Nicholson TE, Mayer KA, Murray MJ, Van Houtan KS. Environmental factors may drive the post-release movements of surrogate-reared sea otters. Frontiers in Marine Science. 2020;7.

59. Gagné TO, Hyrenbach KD, Hagemann ME, Bass OL, Pimm SL, MacDonald M, et al. Seabird Trophic Position Across Three Ocean Regions Tracks Ecosystem Differences. Frontiers in Marine Science. 2018;5.

60. Paradis E, Schliep K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics. 2019;35(3):526-8.

61. Wei T, Simko V. R package “corrplot”: Visualization of a Correlation Matrix (Version 0.84). 2017.

62. R_Core_Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria2020.

63. North WJ. Evaluation, management, and cultivation of Macrocystis kelp forests. California Inst. of Tech., Pasadena, CA (USA). WM Keck Lab. of Engineering …, 1978.

64. Bascom W. The effects of waste disposal on kelp communities: US Department of Commerce; 1984.

65. Schott JW, Fish CDo, Game. Dago Bank and Its "Horseshoe Kelp" Bed: State of California, Resources Agency, California Department of Fish and Game; 1976.

66. Schiff KC, Allen MJ, Zeng EY, Bay SM. Southern California. Marine Pollution Bulletin. 2000;41(1-6):76-93.

67. Bedford D. Giant kelp. In: Leet W, Dewees C, Klingbeil R, Larson E, editors. California's living marine resources: a status report. Sacramento, CA: University Of California, Division of Agriculture and Natural Resources …; 2001. p. 277-81.

68. Boustany AM, Hernandez DA, Miller EA, Fujii JA, Nicholson TE, Tomoleoni JA, et al. Examining the potential conflict between sea otter recovery and Dungeness crab fisheries in California. Biological Conservation. 2021;253:108830.

69. Mayer KA, Tinker MT, Nicholson TE, Murray MJ, Johnson AB, Staedler MM, et al. Surrogate rearing a keystone species to enhance population and ecosystem restoration. Oryx. 2021;55(4):535-45. Epub 2019/09/20.

70. Watson J, Estes JA. Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. Ecological Monographs. 2011;81(2):215-39.

71. Estes JA, Duggins DO. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs. 1995;65(1):75-100.

72. Rasher DB, Steneck RS, Halfar J, Kroeker KJ, Ries JB, Tinker MT, et al. Keystone predators govern the pathway and pace of climate impacts in a subarctic marine ecosystem. Science. 2020;369(6509):1351-4.

73. Moxley JH, Nicholson TE, Van Houtan KS, Jorgensen SJ. Non-trophic impacts from white sharks complicate population recovery for sea otters. Ecology and Evolution. 2019;9(11):6378-88.

74. Smith JG, Tomoleoni J, Staedler M, Lyon S, Fujii J, Tinker MT. Behavioral responses across a mosaic of ecosystem states restructure a sea otter–urchin trophic cascade. Proceedings of the National Academy of Sciences. 2021;118(11):e2012493118.

75. Smith P, Arneth A, Barnes DKA, Ichii K, Marquet PA, Popp A, et al. How do we best synergize climate mitigation actions to co-benefit biodiversity? Global Change Biology. 2022;28(8):2555-77.

76. Berzaghi F, Longo M, Ciais P, Blake S, Bretagnolle F, Vieira S, et al. Carbon stocks in central African forests enhanced by elephant disturbance. Nature Geoscience. 2019;12(9):725-9.

77. Schmitz OJ, Wilmers CC, Leroux SJ, Doughty CE, Atwood TB, Galetti M, et al. Animals and the zoogeochemistry of the carbon cycle. Science. 2018;362(6419):eaar3213.

78. Lotze HK, Worm B. Historical baselines for large marine animals. Trends in ecology & evolution. 2009;24(5):254-62.

79. Butler CL, Lucieer VL, Wotherspoon SJ, Johnson CR. Multi-decadal decline in cover of giant kelp Macrocystis pyrifera at the southern limit of its Australian range. Marine Ecology Progress Series. 2020;653:1-18.

80. Raybaud V, Beaugrand G, Goberville E, Delebecq G, Destombe C, Valero M, et al. Decline in kelp in west Europe and climate. PloS one. 2013;8(6):e66044.

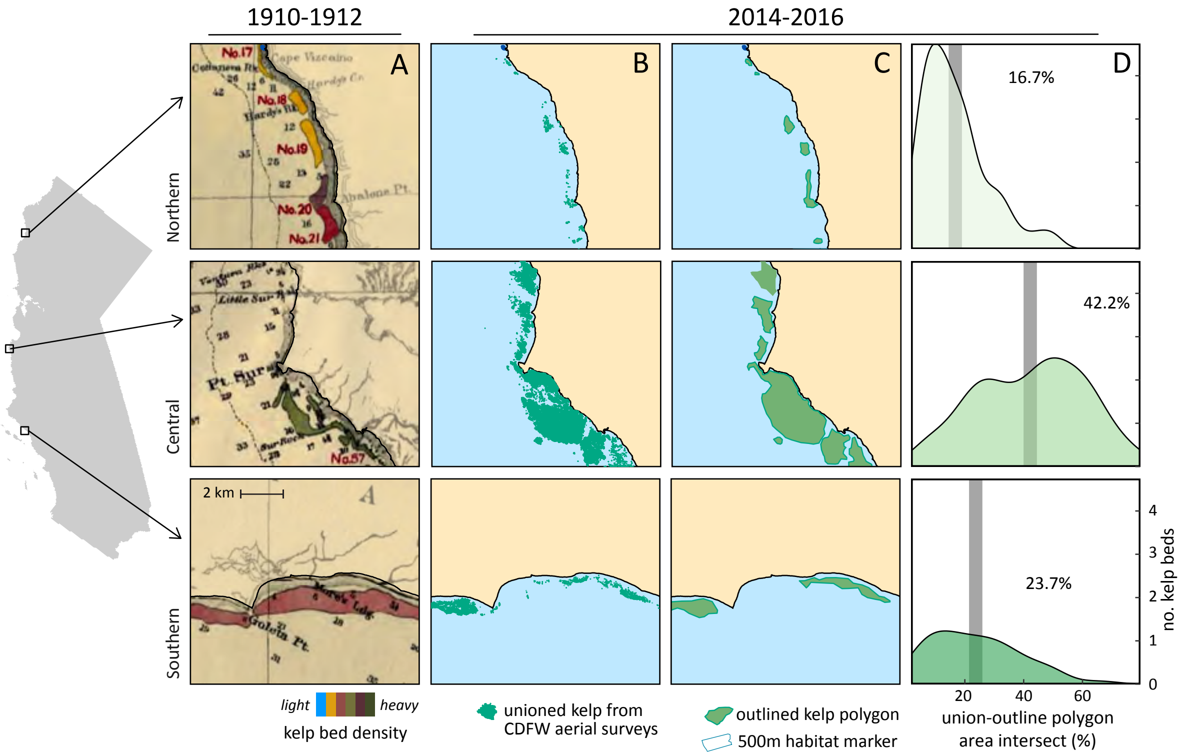
81. Hollarsmith JA, Buschmann AH, Camus C, Grosholz ED. Varying reproductive success under ocean warming and acidification across giant kelp (Macrocystis pyrifera) populations. Journal of Experimental Marine Biology and Ecology. 2020;522:151247.

82. Wernberg T, Coleman MA, Bennett S, Thomsen MS, Tuya F, Kelaher BP. Genetic diversity and kelp forest vulnerability to climatic stress. Scientific Reports. 2018;8(1):1-8.

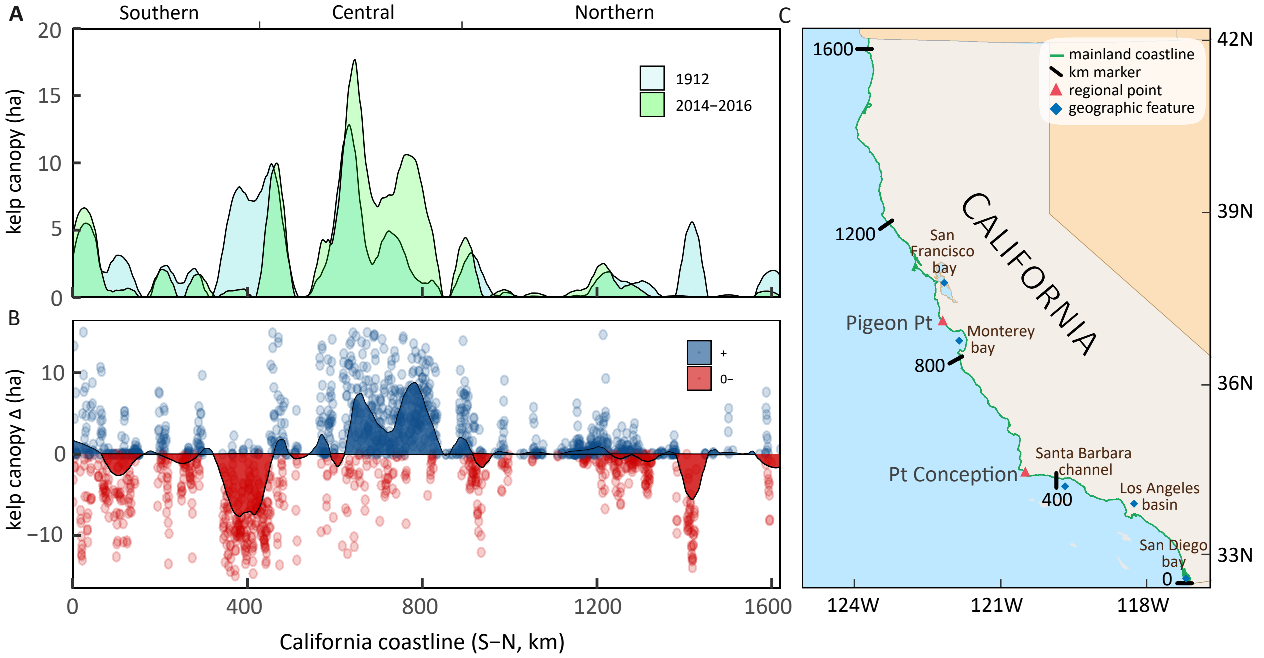
83. Edwards MS. Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. Oecologia. 2004;138(3):436-47.

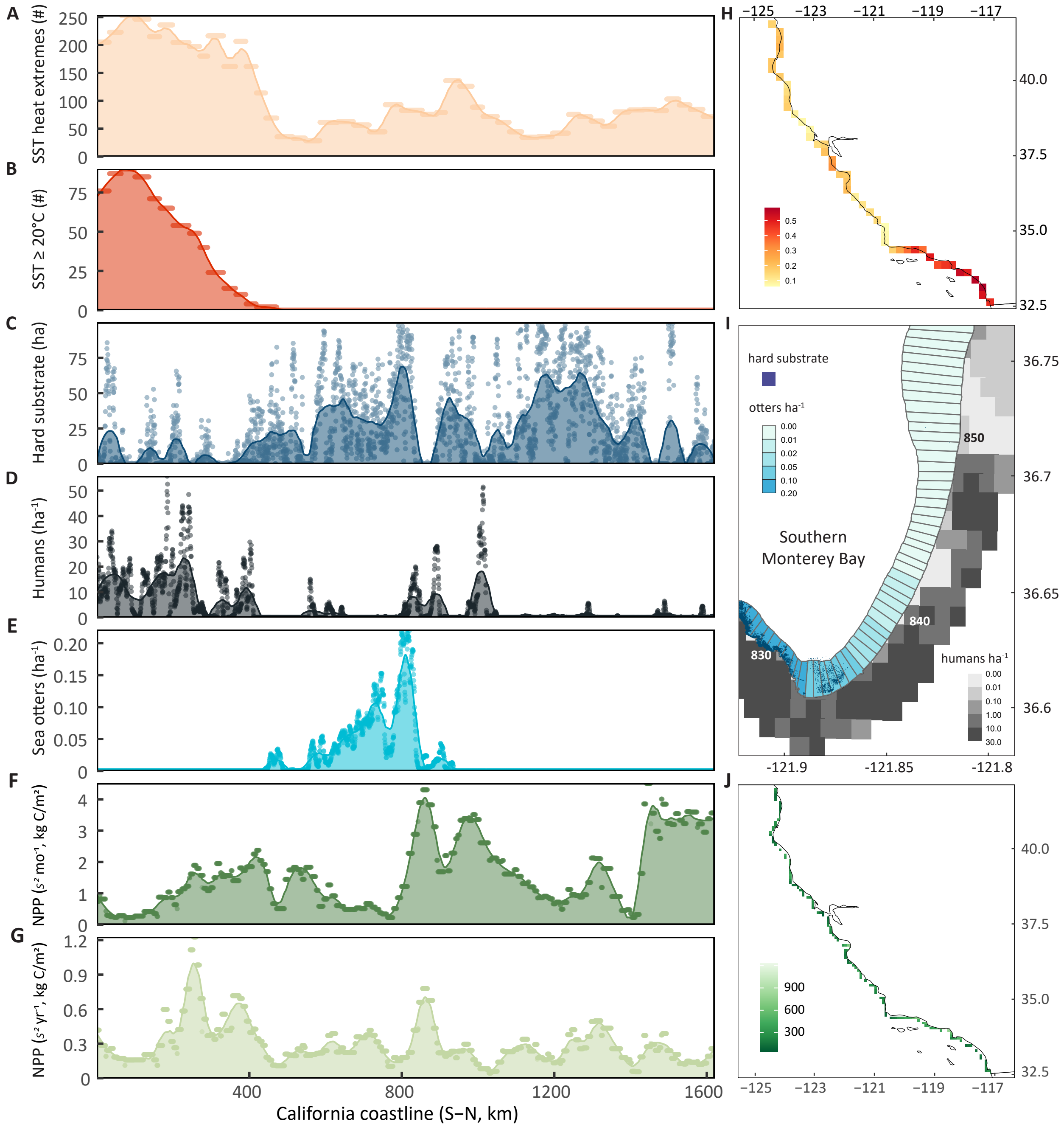
84. Wernberg T, Thomsen MS, Tuya F, Kendrick GA, Staehr PA, Toohey BD. Decreasing resilience of kelp beds along a latitudinal temperature gradient: potential implications for a warmer future. Ecology letters. 2010;13(6):685-94.

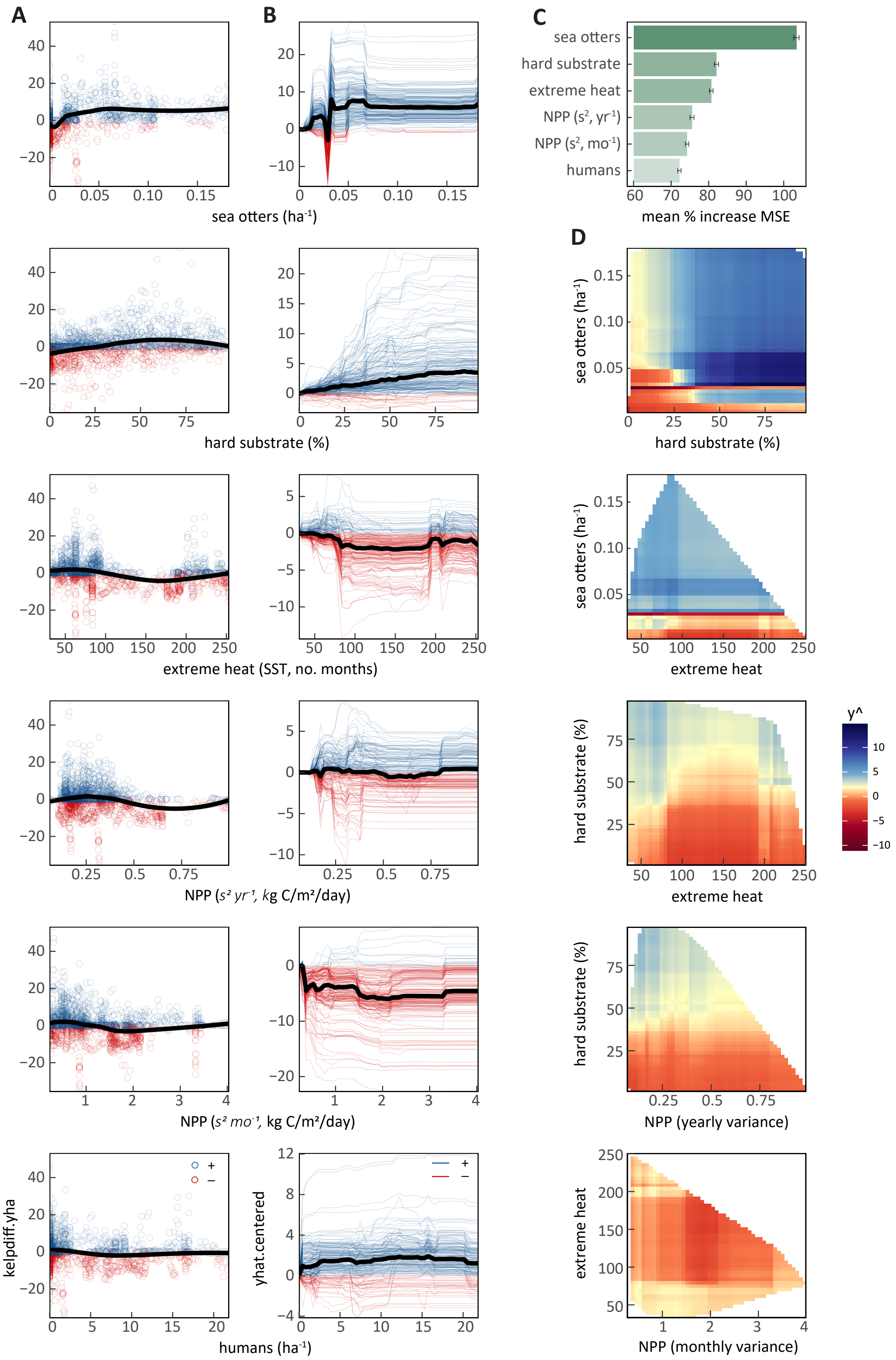
85. Nelleman C, Corcoran E, Duarte CM, Valdes L, DeYoung C, Fonseca L, et al. Blue carbon: The role of healthy oceans in binding carbon: UNEP/FAO/UNESCO/IUCN/CSIC; 2008.



1910-1912
2014-2016
Northern
Central
Southern
A
B
C
D
No.17
Cape Vizcaino
No.18
Hardy's Rk.
No.19
No.20
No.21
Abalone Pt.
Little Sur
Pt. Sur
Sur Rock
No.57
2 km
Goleta Pt.
16.7%
42.2%
23.7%
4
3
2
1
0
no. kelp beds
20
40
60
union-outline polygon area intersect (%)
light
heavy
kelp bed density
unioned kelp from CDFW aerial surveys
outlined kelp polygon
500m habitat marker


A
Southern
Central
Northern
kelp canopy (ha)
20
15
10
5
0
1912
2014–2016
B
kelp canopy Δ (ha)
10
0
−10
+
0−
0
400
800
1200
1600
California coastline (S–N, km)
C
mainland coastline
km marker
regional point
geographic feature
CALIFORNIA
1600
1200
San Francisco bay
Pigeon Pt
Monterey bay
800
Santa Barbara channel
Pt Conception
400
Los Angeles basin
San Diego bay
0
42N
39N
36N
33N
124W
121W
118W

A
SST heat extremes (#)
250
200
150
100
50
0
B
SST ≥ 20°C (#)
75
50
25
0
C
Hard substrate (ha)
75
50
25
0
D
Humans (ha⁻¹)
50
40
30
20
10
0
E
Sea otters (ha⁻¹)
0.20
0.15
0.10
0.05
0
F
NPP (s² mo⁻¹, kg C/m²)
4
3
2
1
0
G
NPP (s² yr⁻¹, kg C/m²)
1.2
0.9
0.6
0.3
0
400
800
1200
1600
California coastline (S–N, km)
H
−125
−123
−121
−119
−117
40.0
37.5
35.0
32.5
0.5
0.4
0.3
0.2
0.1
I
hard substrate
otters ha⁻¹
0.00
0.01
0.02
0.05
0.10
0.20
850
Southern Monterey Bay
840
830
humans ha⁻¹
0.00
0.01
0.10
1.00
10.0
30.0
36.75
36.7
36.65
36.6
-121.9
-121.85
-121.8
J
40.0
37.5
35.0
32.5
900
600
300
−125
−123
−121
−119
−117


A
B
C
D
sea otters (ha⁻¹)
hard substrate (%)
extreme heat (SST, no. months)
NPP (s² yr⁻¹, kg C/m²/day)
NPP (s² mo⁻¹, kg C/m²/day)
humans (ha⁻¹)
kelpdiff.yha
yhat.centered
+
−
sea otters
hard substrate
extreme heat
NPP (s², yr⁻¹)
NPP (s², mo⁻¹)
humans
mean % increase MSE
60
70
80
90
100
extreme heat
NPP (yearly variance)
NPP (monthly variance)
y^
10
5
0
−5
−10