Regional Environmental Change (2024) 24:104
https://doi.org/10.1007/s10113-024-02260-1

ORIGINAL ARTICLE

Setting deeper baselines: kelp forest dynamics in California over multiple centuries

Jennifer C. Selgrath[1,6] · James T. Carlton[2] · John Pearse[3] · Timothy Thomas[4] · Fiorenza Micheli[1,5]

Received: 26 October 2023 / Accepted: 25 May 2024 / Published online: 6 July 2024

Abstract
Kelp forests have deteriorated globally due to anthropogenic stressors. There is an urgent need to extend baselines, to understand the processes that underlie the persistence and recovery of kelp forests, and to distinguish the normal range of ecosystem variability from more extreme changes. Using a mixed-method, historical ecology approach, we integrate archival data, oral histories, and contemporary ecological data to examine the dynamics of kelp forests over a multi-decadal to multi-century time-period in central California. We focus on sea otters, sunflower seastars, sea urchins, kelp cover, kelp species dynamics, and climate. From 1826 to 2020, kelp was highly variable. There were seven periods of low kelp cover and two periods of exceptionally low kelp cover (1897–1899; 2014–2016) following El Niño-Southern Oscillations (ENSOs). Exceptionally low kelp cover did not occur when two predators—seastars and sea otters—were both present. In all cases, kelp recovered following times of extremely low cover, with a lag, which was extended by the duration of warm water anomalies (ENSO Recovery Lag). Kelp remained low for approximately 2 years following 80% of ENSOs. The greatest kelp decline (12-fold) was in Santa Cruz (northern Monterey Bay). Herbivore populations (sea urchins) were highly variable over the past century and exhibited short- and long-term changes in abundance. Sunflower seastars were present in low, stable abundances prior to seastar wasting disease (1938–2013, mean density = $0.02/m^2$) when they declined by 97.5%. Insights from this reconstruction indicate that kelp recovery following extended warm water anomalies exhibits a lag and occurs over multiple years.

Keywords Ecological baseline · Historical ecology · *Pycnopodia* · Sea otter · Sea urchin · Trophic cascade

Introduction

Global habitat loss threatens the persistence and functioning of terrestrial, freshwater, and marine ecosystems (e.g., biodiversity loss, species range shifts, altered productivity) (Lotze

Communicated by Wolfgang Cramer

John Pearse has passed away during the publication process of this paper.

✉ Jennifer C. Selgrath
jennifer.selgrath@noaa.gov

James T. Carlton
jcarlton@williams.edu

Timothy Thomas
timsardine@yahoo.com

Fiorenza Micheli
micheli@stanford.edu

1 Hopkins Marine Station, Oceans Department, Stanford University, Pacific Grove, CA 93950, USA

2 Coastal & Ocean Studies Program, Williams College-Mystic Seaport, Mystic, CT 06355, USA

3 University of California, Santa Cruz, Santa Cruz, CA 95064, USA

4 J. B. Phillips Historical Fisheries Project, Monterey, CA 93940, USA

5 Stanford Center for Ocean Solutions, Stanford University, Pacific Grove, CA 93950, USA

6 Present Address: NOAA Channel Islands National Marine Sanctuary | CPC, University of California Santa Barbara, Ocean Science Education Building 514, MC 6155, Santa Barbara, CA 93106-6155, USA

et al. 2006). Kelp forests, which are marine biodiversity and productivity hotspots, are particularly vulnerable habitats along many of the world's temperate rocky coasts (Schiel and Foster 2015). Kelp forests provide shelter and food (living and detrital kelp) for a great many species, and alter biophysical properties of coastlines (Steneck et al. 2002). While kelp beds and/or canopy cover may be ephemeral and quickly eliminated, they are often capable of rapid recovery (Krumhansl et al. 2016). However, the persistence of these habitats is influenced by a variety of interacting stressors including nutrient enrichment, increasing CO_2, high wave exposure, and temperature (Strain et al. 2014).

Long-term perspectives are important for illuminating ecological change, outlining possible future scenarios, and informing conservation measures. Importantly, long-term estimates of environmental change benefit from using a diversity of sources. Diverse knowledge systems have been important for understanding many aspects of historical environmental change that have not been well documented by western science (Thurstan et al. 2015) including population declines (Lee et al. 2018), extinctions (Carlton 2023), fisheries dynamics (Selgrath et al. 2018), the extent—and loss—of critical habitats (McClenachan et al. 2017; Costa et al. 2020), the provision of ecosystem services (Tomscha and Gergel 2014), and setting baselines for restoration (Thurstan et al. 2015). Documenting deeper, more accurate baselines is vital because inaccurate baselines can lead to misguided management (Pauly et al. 1998). Yet due to the absence of historical research, new baselines are frequently set long after humans altered ecosystems by having removed habitats, or altered the densities, demographics, size structures, or interactions of species (McClenachan et al. 2015).

Integrating diverse types of data, and diverse perspectives, have the potential to deepen knowledge of ecosystems, particularly when the use of such datasets follows best practices and addresses the limitations of sources (Carlton 1994; Neis et al. 1999; Selgrath and Gergel 2019). Approaches for analyzing and integrating informative sources such as Indigenous and Local Knowledge (ILK), navigational charts, journals, newspaper articles, and photographs are well established in fields such as history and anthropology (McClenachan et al. 2015). Such data sources can be synthesized and converted into relative abundances (Lotze et al. 2006) through triangulation (i.e., cross-referencing among data sources) (Jick 1979), and derived from strong inference (Platt 1964). The value of employing and combining both qualitative and quantitative data to inform historical ecology has been well-addressed (for example, Ferretti et al. 2015; Santana-Cordero and Szabo 2019). Formal evaluations of such methods have found them to be reliable and replicable, particularly when biases or limitations are identified and accounted for (Al-Abdulrazzak et al. 2012; Selgrath et al. 2016; Mason et al. 2019).

Maps and charts represent one type of historical data source which can contain information about the past distribution of critical habitats and species. Historical map data represent presence-only data (Costa et al. 2020) and can be influenced by a variety of factors including scale and the cartographer's interpretation of survey field notes. One example is the documentation of the spatial extent of the canopy of kelp forests. From an ecological perspective, kelp canopy cover (as depicted in both historical and contemporary maps) can be a variable proxy for kelp density (e.g., for the abundance of all laminarian kelps). Kelp cover is a widely recognized method to estimate and track kelp abundance in contemporary analysis (e.g., satellite maps) (Foster and Schiel 1988; Bell et al. 2020; Arafeh-Dalmau et al. 2021), and is considered to be an Essential Ocean Variable by The Global Ocean Observing System (Satterthwaite et al. 2021).

Widespread evidence indicates that high levels of grazing pressure from herbivores can catalyze the loss of primary producers, such as kelp (Miller et al. 2022). Recent analyses, however, report evidence for a complex interaction of stressors (Strain et al. 2014). Kelp forests have long been considered to be dominated by top-down control by herbivores (e.g., the top-down sea otter-urchin-kelp trophic cascade (first described in Estes and Palmisano 1974)). However, regional differences in the strength of single-species interactions, sea surface temperature, and upwelling can influence the importance of these dynamics (Foster and Schiel 2010; Hauri et al. 2013; Wing et al. 2022; Shelton et al. 2018). In the eastern Pacific Ocean, for example, regional differences lead to a latitudinal gradient in species diversity (Steneck et al. 2002). Contemporary kelp ecosystems may also be impacted by water quality (Shears et al. 2008), and climate-related factors such as sea surface temperature (SST), El Niño-Southern Oscillation (ENSO) events, and marine heat waves (MHWs) (Wernberg et al. 2016). Despite considerable research, the relative importance of top-down control, herbivory, and physical drivers remains contested.

Following the widespread and widely concerning declines of kelp forests along the Pacific coast of North America (Rogers-Bennett and Catton 2019; Arafeh-Dalmau et al. 2023), we sought insights into kelp decline by filling in the existing approximately 200-year gap between Indigenous and archeological records (Jones et al. 2011), and contemporary ecological surveys. The documented decline of kelp in Monterey Bay, CA, was surprising in part because the iconic ecological paradigm of the trophic cascade between predatory sea otters, their herbivorous urchin prey, and the urchins' kelp resources predicts that sea otters in central California would buffer kelp forests from heavy grazing by herbivores (McLean 1962; Estes and Palmisano 1974; Nicholson et al. 2024). We re-examine kelp forest dynamics in the context of this paradigm through analysis of a novel multi-decadal to multi-century data set (Figure S1, Table S1). We focus on species with known or hypothesized interactions, and expand on the sea otter-urchin-kelp cascade to include predatory sunflower seastars (*Pycnopodia helianthoides*). We ask four questions: (1) how has the abundance of four strongly-interacting kelp forest species changed over time; (2) how has kelp abundance been impacted by multiple stressors; (3) how has the relative abundance of canopy-forming kelp species changed over time; and (4) how do trends translate into broad periods of social-ecological change?

Methods

Study area

Our research focused on kelp forest ecosystems in central California, USA (here, Año Nuevo (37°07′35.4″N, 122°19′35.4″W) in the north to Big Sur (36°06′16.2″N, 121°37′19.8″W) in the south (Fig. 1). This temperate, upwelling-driven ecosystem is characterized by high biodiversity. The social-ecological history of central California has been documented for over 200 years by historical and contemporary sources due to the region's history of Tribal nations, exploration, European colonization, maritime trade, and Western science (Ogden 1941; Osio et al. 1996; Micheli et al. 2020; Vileisis 2020). We divided central California

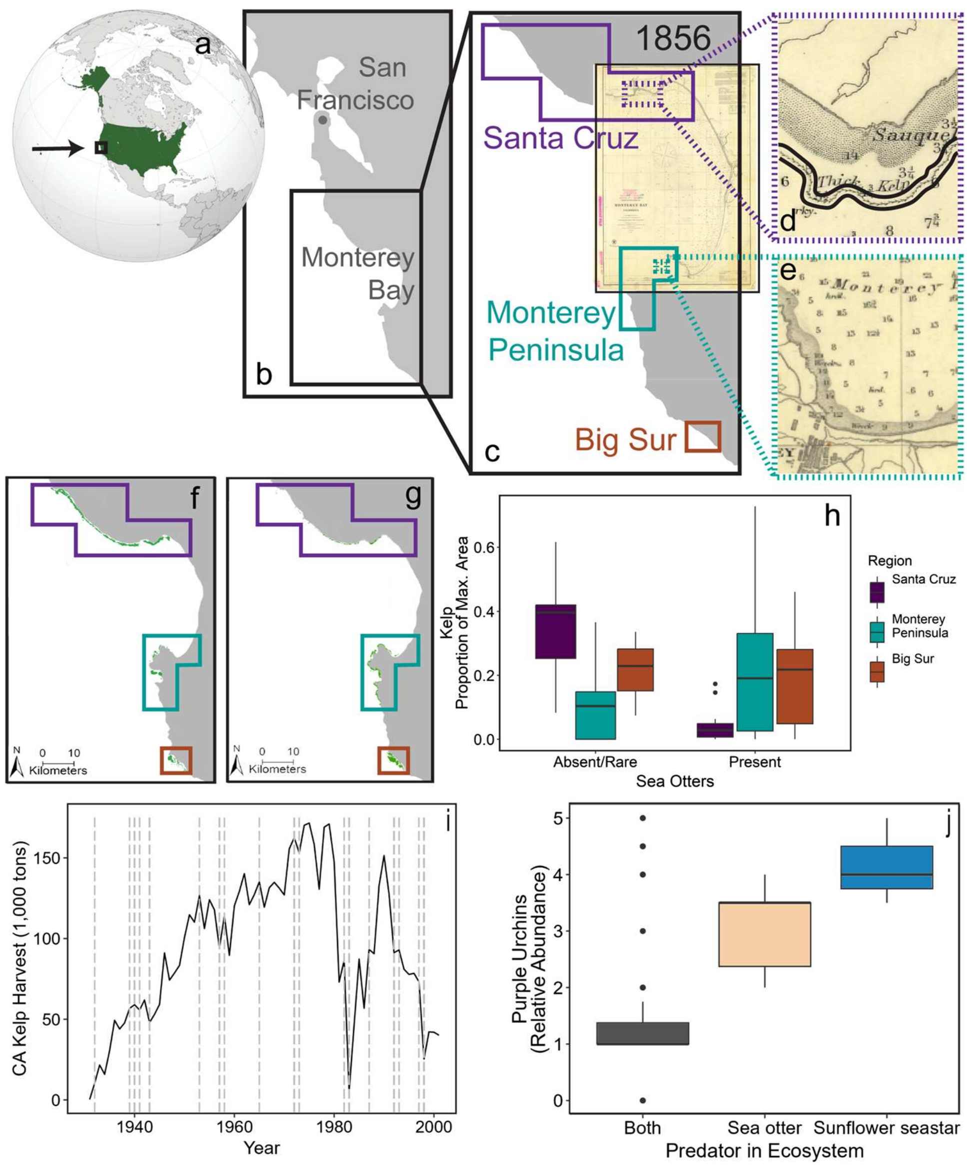

Fig. 1 Study area, examples of historic charts documenting kelp beds, and kelp abundance in central California. (**a**) Location of study area in central California on a world map (Wikipedia). (**b**) Central California. (**c**) Chart of Monterey Bay (1856) showing the three study regions: Santa Cruz (purple), Monterey Peninsula (blue), and Big Sur (orange). Dotted lines represent close ups. Chart sources in Table SI6. (**d**) Kelp in Santa Cruz (1856). Black lines indicate kelp documented by charts. (**e**) Absence of kelp in Monterey Bay (1856). (**f**) All locations where kelp was recorded on historical maps and charts (1856–1934). (**g**) All locations where kelp was observed by CDFW aerial surveys (1989–2016). (**h**) Box plots of changes in the spatial extent of canopy-forming kelp during periods when sea otters were extirpated or exceedingly rare (Absent/Rare) or re-established (Present). (**i**) Historic kelp harvest in California (1931–2001). Dashed lines indicate years with ENSO events that were classified as medium + or greater (historical) or MEI v2.0 values ≥ 1.5 (contemporary). (j) Relative abundance of purple sea urchins in relationship to the combination of predators that were present (1934–2020)

into three regions, north to south: Santa Cruz, Monterey Peninsula, and Big Sur.

Data sources

To identify historical baselines and longitudinal dynamics of kelp forest ecosystems, we assembled a multi-decadal to multi-century dataset which integrated historical and contemporary information focused on central California largely from the early-1800s onward (Figs. S1–S4; Table S1). We evaluate trends in the relative abundance of sea otters (*Enhydra lutris nereis*; hereafter "otters"), predatory sunflower seastars (*Pycnopodia helianthoides*), herbivorous purple urchins (*Strongylocentrotus purpuratus*, hereafter "urchins"), and two species of canopy forming kelp (giant kelp *Macrocystis pyrifera* and bull kelp *Nereocystis luetkeana*; hereafter "kelp"). We did not include red urchins (*Mesocentrotus franciscanus*) in formal analyses over historical time periods because there was insufficient information about their abundances over a multi-decadal period. Instead, we qualitatively discuss changes in their abundances.

Qualitative and quantitative data sources include narrative accounts (1602 onward), archival maps (1852–1934), 48 oral histories (1939–2020), ENSO reconstructions (1820–2020), kelp harvest records (1931–1999), and ecological surveys (1985–2020) (Figs. 2, S1–S4; Tables S1–S8). We use archeological records and Indigenous knowledge as reference where available, but focus on integrating sources onward from the exploration and colonization of California by Europeans.

Archival documents

Diverse historical accounts provide early narrative descriptions of the social-ecological system of central California (Fig. S3). We searched collections that focused on west coast history for accounts of early explorers, traders, and religions figures who were active in central California (Table S2). Next, we searched early natural history and scientific books, field notes, newspaper articles, historical art, and reports that provided accounts of natural history and environmental conditions. Since historical documents are not indexed for

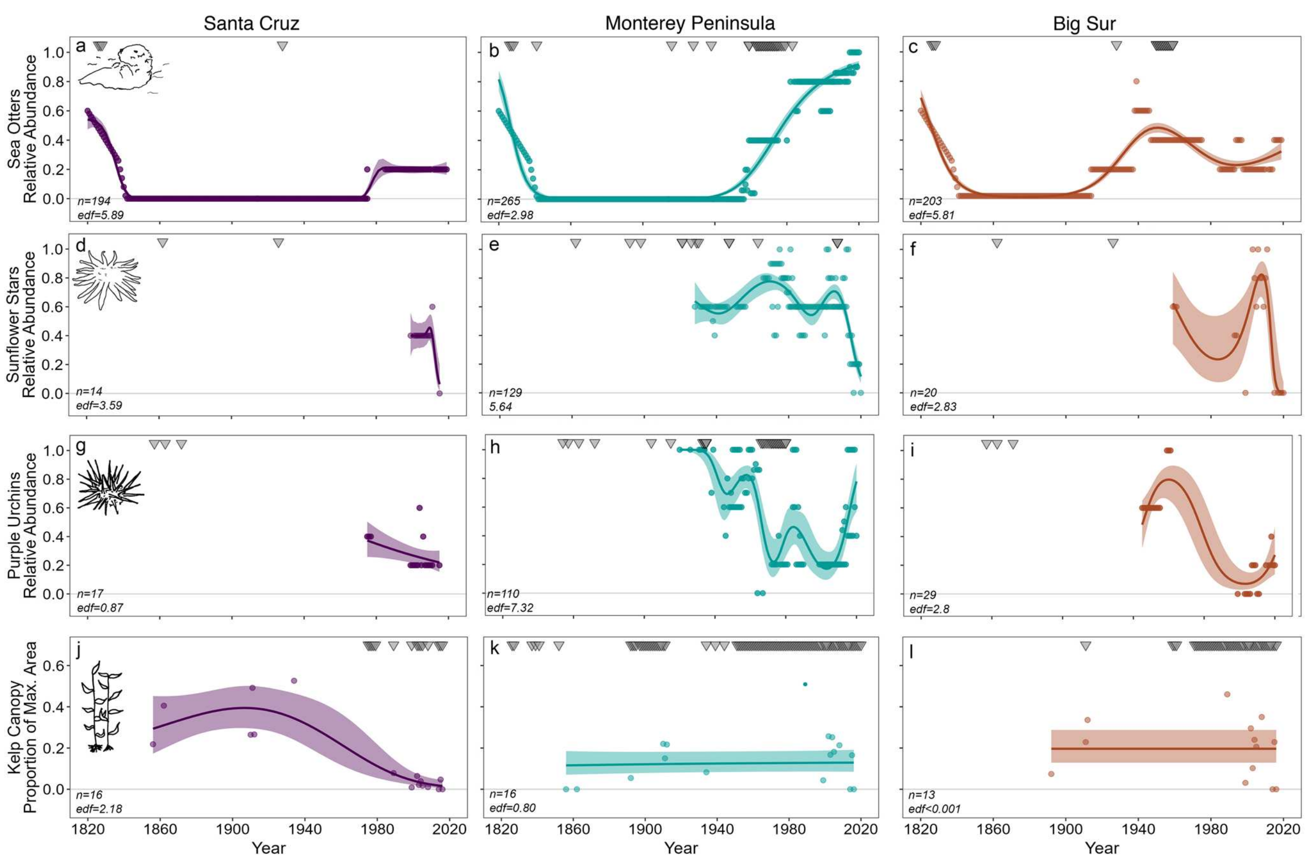

Fig. 2 Changes in the abundance of coastal marine life in central California by region. Points are grand mean values of the relative abundance of southern sea otters, sunflower seastars, and purple urchins, or the proportional spatial extent of kelp. Lines are predictions from generalized additive models. Ribbons are 95% confidence intervals of predicted lines. Grey triangles indicate years with qualitative, presence only observations. Presence only observations were included in trend interpretation, but not models

ecological terms, historical sources were identified using the expert knowledge of librarians at Stanford University's Hopkins Marine Station (Pacific Grove, CA) and authors (JP, JTC, TT), and were supplemented with searches for historical literature referencing the three regions and four focal species (Fig. S1. Sources and data are listed in Tables S1–S7). We reviewed identified documents to assess if they contained descriptions of natural history.

We considered four types of abundance values: (1) presence only; (2) relative abundance; (3) quantitative abundance; and for kelp, (4) percent cover (methods described in the Kelp Map sections below) (Table S7). First, when qualitative descriptions of species' existence could not be translated to relative abundances, we considered these records to represent presence-only data. We used presence-only data to triangulate against other data sources and used the information in qualitative assessments of change. Second, we developed a standardized rubric for translating qualitative descriptions of abundance to relative abundance values (scale 0–5) (Table S3 and R Code on Github). Third, for quantitative abundance records (e.g., ecological transects, published data), we assigned densities to relative abundances (range 0–5) based on the mean and standard error values for all records of that species (Table S4). When data were only available in graphs, we estimated the density values from the figures. We considered relative abundances derived from both qualitative and quantitative sources to be consistent within species, but not comparable across species.

El Niño-Southern Oscillations and marine heat waves

To assess long-term ENSO and MHW patterns, we used historical ENSO time series (1770–1983) and continued the historical series with contemporary MEI (multivariate ENSO index) estimates (1984–2020) and MHW records (Table S7) (Quinn et al. 1987; Gergis and Fowler 2009; NOAA 2020). We considered that a year was influenced by an ENSO when the year had a MEI 2.0 value ≥ 1.5, or when the ENSO was classified as Medium + or greater by historical analyses (Quinn et al. 1987; Gergis and Fowler 2009; NOAA 2020).

Sea surface temperature records

To assess changes in SST, we used daily sea surface temperature measured at Hopkins Marine Station since 1919 (Breaker and Miller 2023).

Kelp maps

Kelp maps: archival sources We used a total of seven archival maps (five nautical charts and two kelp surveys), which we considered to represent presence-only data (Costa et al. 2020). Nautical charts which documented kelp were surveyed from 1856 to 1934 (Fig. 1; Table S6). The US Department of Agriculture conducted two surveys of kelp (1911, 1912), which included maps with species-level resolution (Table S6). For all archival maps, we documented the map name, number, scale, year of the last survey, survey date (where available), and first year of publishing (Table S6). For charts published in multiple years, we only considered the first edition.

To extract kelp data from archival maps, we first photographed paper maps and downloaded maps that had been previously scanned by libraries and NOAA. Second, we georectified digital maps using satellite images and control points from stable features (e.g., rock outcrops) to reduce root-mean-square error (ArcGIS 10.7.1) (Costa et al. 2020). Third, we demarcated kelp areas using on-screen digitization. We traced the edges of the kelp symbology to create polygons depicting the area of kelp beds (Fig. 1d; Fig. S2). Where species information was available, we assigned kelp bed polygons to one of three groups: giant kelp (*Macrocystis*); bull kelp (*Nereocystis*); or mixed beds (similar amounts of *Macrocystis* and *Nereocystis*).

Kelp maps: contemporary sources The contemporary spatial extent of canopy forming kelp was documented by the California Department of Fish and Game (now California Department of Fish and Wildlife, CDFW) during a series of aerial kelp surveys (1989–2016), available as shapefiles (Table S6; Movie S1). When both canopy and subsurface canopy data were available in later years (2008–2016), we restricted maps to canopy to improve data consistency through time (R. F. Miller, CDFW, pers. comm., 2020). We attempted to find earlier aerial photos taken by CDFW (e.g., 1972–1977), but the agency no longer maintained these records (R. F. Miller, CDFW, pers. comm., 2020). We documented methods and survey months when such data were available in shapefile metadata (Table S5).

Kelp maps: estimates of error To assess the locational accuracy of the archival maps, we set a reliability criterion that considered the local depth in which kelp was located. We used a depth threshold of 40 m to account for known depth ranges, kelp movement with currents and tides, residual processing errors, and cartographic variability (e.g., line thickness) (Costa et al. 2020). We overlaid the polygons on a 10-m resolution bathymetry map of California. We classified map reliability based on the percentage of kelp that was mapped in shallow (< 40 m) vs deep (> 40 m) areas (four classes: very high (> 99% of kelp mapped in shallow areas), high (> 80%), medium (> 60% mapped in shallow areas), and low (> 40% mapped in shallow areas)).

Kelp maps: estimates of kelp cover To account for the fact that different extents were mapped across years, we restricted our analysis of kelp canopy cover to areas where kelp canopy was documented by archival maps for a minimum of 3 years (Fig. 1).

We calculated kelp area as the total area where kelp-forming canopy was documented in 1 year (t) in the spatial extent covered by the mapped area (m) in each region (r):

(i) Kelp area$_{tmr}$ = Total area of canopy forming kelp in time (t) in mapped area (m) in each region (r).

To standardize estimates of kelp area, we next identified the maximum area of kelp canopy that was ever mapped in any year ($t_1 - t_i$) using any method for each region (r):

(ii) Maximum area $t_1 - t_{i\ r}$ = Maximum area of kelp mapped across all years ($t_1 - t_i$) in each region (r).

Finally, for each map, we calculated proportion of maximum area in time (t) as the kelp area in time (t) divided by the maximum area of kelp canopy that was ever mapped in a region (r):

(iii) Proportion of maximum area$_t$ = Kelp area$_{tmr}$ / Maximum area $t_1 - t_i$.

We used the proportion of maximum area as the standardized measure of kelp cover in all quantitative analyses. Additionally, we calculated a second standardized kelp cover metric as the maximum extent where kelp occurred in any year (maximum extent) within the mapped area (m). This yielded similar trends, and we thus proceeded with the method described above.

Oral histories

To document changes in coastal marine species and conditions of the coastal ecosystem, we conducted semi-structured oral history interviews ($n = 48$ respondents). We used snowball sampling to select respondents who had first-hand experience with the marine biota and ocean conditions of the central Californian coast. Initial respondents were identified through personal networks of the authors (JP, JC, JTC, TT, and FM) who had worked in central California for decades. We included individuals who fell into two categories of ocean-knowledge: people who had worked in the region for (a) a long-term period (e.g., scientists, historians based in the region) or (b) a finite period (e.g., former ocean-focused graduate students). We obtained informed consent from all participants. Although several respondents had not lived in central California for many years, the ocean in the region made a strong impression on their memories. Most respondents (54%) resided along the central California coast for less than 10 years (duration: range = 3–54 years; median = 8 years), placing their memories within discrete date ranges.

We conducted interviews both in person and virtually through Zoom (stanford.zoom.us). We also received written survey responses from six individuals. Interview and survey data (hereafter “oral history data”) were transcribed and respondents were provided the opportunity to make corrections. Final data were thematically coded using grounded theory. We used NVivo and documented the presence, abundance, and location of species, including observations of changes over time (Table S8). Oral history data also included distribution information regarding both species of canopy forming kelp, *Macrocystis* and *Nereocystis*. Species density estimates from oral histories were typically qualitative (e.g., “a lot”; “hardly any”). Following the methods for historical data (see above), we standardized responses by assigning specific descriptions to different abundance levels (range 0–5) (Table S3). For kelp records, we weighted observations from three kelp experts higher than other respondents, which allowed us to capture their specific experiences with ENSO dynamics that were not mentioned by other respondents. Abundance levels were relative to each species. All interviews were reviewed for accuracy by JP and JCS.

Contemporary ecological data

We compiled contemporary ecological data (sea otters, purple urchins, sunflower seastars, kelp cover, kelp species) from several sources: USGS otter surveys (1985–2019), unpublished field data (2002, F.M.), published field data (various), PISCO database (1999–2020), ReefCheck database (2006–2019), CDFW kelp harvest data (1916–2001), and CDFW aerial kelp surveys (2003–2016) (sample sizes in Table S1, references in Table S6, Table S7). To facilitate data comparison, we converted density data (e.g., purple urchins per m^2) to relative abundance values (range 0–5). For kelp maps, we used equal intervals to set relative abundances. For contemporary datasets, we set relative abundances based on the mean and standard deviation of survey values for each species considered (Table S4). We then integrated data from archival sources, oral histories, and contemporary ecological surveys.

Kelp harvest data

To provide a complementary source of relative kelp abundance, we obtained CDFW records of kelp harvest for the state (1931–2001) (Table S7). Although long-term trends in these data may be influenced by harvest effort rather than state-wide kelp abundance, we used these data to look for short-term changes in harvest following ENSO events, which we infer were influenced by ENSO conditions.

Analyses

Q1. How has the abundance of four strongly interacting kelp forest species changed over time?

First, we assessed broad-scale trends for each organism using generalized additive models (GAMs). We standardized estimates of sea otter density by converting estimates to the number of otters per km^2 of habitat based on a 30-m depth range (Laidre et al. 2001). Second, we integrated these quantitative models with qualitative data and used strong inference (Platt 1964) and triangulation (Jick 1979; Rhemtulla and Mladenoff 2007) to assess periods of change across the entire time period. Since GAM analyses were restricted to years with relative abundance data and/or contemporary ecological data, this integration enabled us to obtain holistic trend information for the four focal organisms. GAMs allow for non-linear relationships between the response variable and explanatory variables (Zuur et al. 2010). We analyzed trends separately for each region (Santa Cruz, Monterey Peninsula, Big Sur) due to significant interactions among Regions (region interaction p-value < 0.05 for all models) and built GAMs with a quasibinomial distribution. We removed one outlier based on visual inspection of the data. For all species, we compared models with and without correlation structures (Zuur et al. 2010). We found that models without correlation structures performed equal or better to models with correlation structures, and did not include correlation structures in our final GAM models.

Q2. How has kelp abundance been impacted by multiple stressors?

Q2. Method 1: Maximizing mapped years (1856–2016) To assess change in kelp cover over a 160-year period, we used mapped kelp canopy data to model how kelp cover has changed over time (1856–2016). We used a reduced set of variables due to the relatively shorter time series of several datasets, and the fact that historical map years were not the same as ENSO years. Thus, we examined how kelp cover corresponded to year, sea otter presence, and region. With these variables, we used generalized least square models (GLS) which allow for unequal data spacing through time and uses variance co-variates to model different variances among factors (Zuur et al. 2010). We modeled temporal autocorrelation using the auto-regressive moving average autocorrelation structure (corARMA) and heterogeneity of variances to account for the gradual return of sea otters. We first modeled the variance structure and then built a backward stepping model. We identified the best fit model using AICc values. We conducted all analyses in R 4.2.2 (R Core Team 2022) using packages tidyverse, dplyr, nlme, modelr, MuMIn, mgcv, tidymv, and mgcViz.

Q2. Method 2: Maximizing variables (1934–2020) Since more datasets were available during the twentieth century, we modeled how the relative abundance of kelp (1934–2020) corresponded to changes in the relative abundance of sea otters, sunflower seastars, urchins, as well as ENSOs, MHW, and mean annual SST. We focused on the Monterey Peninsula region which had the longest and most complete data. We combined sunflower seastar and sea otter data into a factor representing the ecologically significant predators present in the system. Measures of urchin and sunflower seastar abundance had small gaps. We thus interpolated the values for up to 6 years for sunflower seastars and up to 3 years for urchins. We used a longer period for sunflower seastars due to their long-term population stability, prior to the wasting disease (see "Results" section below). We considered the presence of ENSOs and MHW (1), and propose a new indicator—ENSO Recovery Lag (2):

(1) *ENSO Presence* in a year (Binary)

$$\text{ENSO/MHW Absent}: ENSOPresence = 0$$
$$\text{ENSO/MHW Present}: ENSOPresence = 1$$

(2) *ENSO Recovery Lag* (*ERL*): a measure of the lag effect that multi-year or clustered ENSO and/or MHW events have on ecosystem recovery. Here we define multi-year events as multiple back-to-back or clustered years of ENSOs and/or MWH. We define clustered events as ENSO or MHW with short return-periods.

(a) First year (y) of a <u>new</u> ENSO/MHW event resets the ERL value

$$\text{If } ENSOPresence = 1 \text{ and } ERL_{y-1} \geq 1,$$
$$ERL_1 = 0$$

(b) Consecutive years of ENSO and/or MHW

$$\text{If } ENSOPresence = 1 \text{ and } ERL_{y-1} \leq 0,$$
$$ERLy = ERL_{y-1} - 1$$

(c) Years (y) with no ENSO/MHW

$$ERL_y = ERL_y - 1 + 1$$

Take, for example, a 2-year, back-to-back ENSO which started after a decade with no ENSOs so that ERL$_y > 0$. In the first year of the ENSO, ERL$_1 = 0$. In the second year of the ENSO, ERL$_2 = -1$. Each year after the ENSO ended would increase the value by one: ERL$_3 = 0$, ERL$_4 = 1$, etc.

With these variables, we used GLS models (described above) and modeled temporal autocorrelation using corARMA and heterogeneity of variances based on the kelp data source.

Q2. Method 3: Mixed methods (1850–2020) Finally, we qualitatively integrated the results from the quantitative models above with other data sources of kelp abundance (e.g., oral histories, narrative accounts) using triangulation and strong inference.

Q3. How has the relative abundance of canopy-forming kelp species changed over time?

We evaluated shifts in the abundance and spatial distribution of the two canopy forming kelp species. We focused our analysis of changes in kelp species in the Monterey Peninsula region because this region had the longest record documenting species-specific information. For species assessments, we quantified trends in two sub-regions: Monterey Bay (Monterey, Pacific Grove) and Outer Monterey Peninsula (Carmel, Asilomar) due to the different oceanographic conditions between the sites (Ricketts et al. 1985).

Q4. How do trends translate into broad periods of social-ecological change?

Finally, we synthesized the social-ecological trends that we observed to see how the timing of changes in central California aligned with cultural periods that for regions of North America and Europe have characterized stages of cultural and market development (see Lotze et al. 2006). We integrated information from all data sources considering trends in human society, environmental conditions, and the abundance of key species.

Results

Q1. How has the abundance of four strongly interacting kelp forest species changed over time?

Sea otters

Overall, sea otters declined following extensive hunting, returned to the Monterey Peninsula (1955–1965), and to Santa Cruz in the late-1970s. For thousands of years during the Hunter-Gatherer cultural period, sea otters were hunted by Ohlone and Esselen Tribal Nations (Fig. S4). The low level of urchins in middens suggests that during this period, kelp forests in central California were stable (Fig. S4). Due to the maritime fur trade (1785–1911), otters were effectively extirpated in all of California, except Big Sur by the 1820s (Table S5). Over 100 years later (1938), California otters were rediscovered in Big Sur and began expanding their range (Table S5). Otters returned to the Santa Cruz region in the late 1970s, and populations have subsequently stopped expanding northward (Fig. 2a; GAM population smoother for year: $R^2 = 0.98$, p-value < 0.001). Densities of contemporary otter populations (1985–2019) in the study regions ranged from 0.33 ($\pm$0.02 SEM) otters per km^2 in Santa Cruz (1985) to 18.46 ($\pm$0.86 SEM) otters per km^2 in the Monterey Peninsula (2017) (Fig. 2).

In the Monterey Peninsula, sea otters appeared on the outer coast in 1955, developed resident populations in 1959, and moved into Monterey Bay in 1965 (Fig. 2b). Otter densities increased from the late 1950s to the mid-1970s (Fig. 2b; GAM smoother for year: $R^2 = 0.92$, p-value < 0.001; Table S3), and densities remained relatively high from the mid-1980s–2013. During this period, otters in Monterey were at nearly three times their estimated carrying capacity for rocky habitat (estimated carrying capacity = 3.84 otters/km^2 (Laidre et al. 2001); mean density (1985–2013) = 10.8 ($\pm$0.02 SEM) otters/km^2). Monterey otter populations increased from 2014 to 2019 (Fig. 2b).

Sea otter abundances in Big Sur increased in the late 1930s and early 1940s (Fig. 2c; GAM population smoother for year: $R^2 = 0.87$, p-value < 0.001), declined over the next four decades, and then stabilized (Fig. 2c). Since 2013, otter populations in Big Sur have increased slightly.

Sunflower seastars

We found that sunflower seastars were discontinuously distributed, but common (1938–2013; Fig. 2d–f; mean density pre-Seastar Wasting Disease (SSWD) = 0.02 ($\pm$0.001 SEM) sunflower seastars/m^2), and declined 97.5% following SSWD. Sunflower seastars were first documented in California in 1862 and mentioned in Monterey in 1892 (Table S5). SSWD was first reported in Monterey in late 2013 when sunflower seastars declined dramatically (mean density post-SSWD = 0.0005/m^2 ($\pm$0.0001 SEM)). This decline in sunflower seastars was apparent in all regions: Santa Cruz (GAM population smoother for year: $R^2 = 0.73$, p-value = 0.05); Monterey (GAM population smoother for year: $R^2 = 0.50$, p-value < 0.001); and Big Sur (GAM population smoother for year: $R^2 = 0.71$, p-value = 0.01).

Urchins

Our analyses indicate that purple urchin abundances exhibited large population swings, but were frequently high during the period when otters were absent or rare and sunflower seastars were present (1920–1965). Urchins were primarily low between the return of otters and the outbreak of SSWD (Fig. 2g–i). Sea urchin species of central California were first formally described by western science in 1857 (purple sea urchin) and 1863 (red sea urchin), decades after the collapse of otter populations. Purple urchins in Santa Cruz declined through time following the return of otters (Fig. 1g) (GAM population smoother for year: $R^2 = 0.25$, p-value $= 0.05$), although the urchin data in Santa Cruz covers a relatively short period (1975–2015).

In the 1920s, purple urchins were widely abundant in Monterey (Fig. 2h). This decade was followed by a decline from the mid-1930s through 1946, suggesting limited recruitment (Table S5). Purple urchin densities spiked the following year (1947), likely because of a recruitment pulse in previous years. In Monterey, purple urchins remained abundant until otters returned in the mid-1960s (GAM population smoother for year: $R^2 = 0.62$, p-value < 0.001). Purple urchins in Big Sur followed similar patterns to those in the Monterey Peninsula (GAM population smoother for year: $R^2 = 0.76$, p-value < 0.001).

Following the re-establishment of sea otters in central California, purple urchins were stable at low abundances for multiple decades (Fig. 1g–i). Following the re-establishment of otters in Monterey, for example, purple urchins declined over a 20-year period (1965–1985). For the next 20 years (1985–2007), urchins remained at low abundances (e.g., 0.001/m^2). During this time, purple urchins sporadically exhibited recruitment pulses, but these did not lead to persistent population increases (Table S5). Sea otter predation, however, has not guaranteed that purple urchins remain rare. Otters in Monterey in 2020 were at their highest abundance in at least 180 years (Fig. 2b). Yet, oral history respondents reported high recruitment and survival of juvenile purple urchins in the Monterey region as early as 2008–2010 (Fig. 2g–i). By 2020, purple urchins had spiked to pre-otter abundances.

Red urchins were documented less frequently than purple urchins, possibly due to the mean abundance of red urchins being 16-fold lower than purple urchins through time (mean purple urchin density: 2.6 ($\pm$7.9) urchins per m^2; mean red urchin density: 0.16 ($\pm$0.59) urchins per m^2) (Fig. S5). Narrative records support that red urchins were less common than purple urchins during many periods (Table S5). Like purple urchins, red urchins sporadically exhibited short recruitment pulses that did not persist through time. Additionally, this species was regulated by physical disturbance such as storms (Cowen et al. 1982), predators (Pearse and Hines 1987), and disease (Pearse and Hines 1979).

Kelp

Our reconstruction of kelp canopy cover from maps (1856–2016; Fig. 2j–l; Fig. 1; Table S6) documented wide fluctuations in kelp cover through time in all regions and no significant increases in kelp cover following the return of sea otters (Table S3). Striking differences emerged, however, in kelp trends among regions.

Santa Cruz Kelp cover declined 12-fold between the mid-1800s/early-1900s (mean proportional cover $= 0.36$ ($\pm$0.13 SEM)) and recent times (1989–2016) (mean proportional cover $= 0.03$ ($\pm$0.03 SEM)) (GAM population smoother for year: $R^2 = 0.85$, p-value $= 0.001$; Fig. 2j).

Monterey Monterey kelp cover was highly variable within and across decades (Fig. 1k; GAM population smoother for year: $R^2 = 0.002$, p-value $= 0.22$). When central California otter populations were first extirpated (1826–1840), traders and navy commanders reported "immense" and "impenetrable" kelp beds (Fig. S3, Table S5). Following that period, in the 1850s and 1860s, kelp cover was low, but variable. By the 1890s, kelp cover was relatively high (Fig. 1k) and this trend appears to persist through the early 1950s when and oral history respondent reported "banks of kelp parallel to shore." During this period of kelp was relatively abundant, purple urchins in Monterey formed "great beds" and sunflower sea-stars were "discontinuously distributed in the entire region [and] fairly common" (Table S5). In 1959 and the early 1960s, kelp cover was very low. Oral history respondents reported "almost no kelp" in Monterey in 1959 and 1962. These observations mirror published, anecdotal comments that in Monterey (1959–1962), "large algae are heavily grazed upon, and the general appearance of these rocks is barren" (Table SI7) (McLean 1962). However, from the late 1960s onward, multiple data sources (oral histories, aerial surveys) reported abundant kelp for most years. Two exceptions occurred in 1997 and 2014–2016, coinciding with extreme warming events (ENSO and/or marine heat waves, discussed below).

Big Sur The spatial extent of kelp showed high inter-annual variability through time, but no overall trends (mean proportional cover $= 0.21$ ($\pm$0.13 SEM)) and recent times (1989–2016) (mean proportional cover $= 0.19$ ($\pm$0.15 SEM)) (Fig. 2l; GAM population smoother for year: $R^2 = < 0.01$, p-value $= 0.67$).

Q2. How has kelp abundance been impacted by multiple stressors?

Q2. Method 1: Maximizing mapped years (1856–2016)

Over the 160-year period, we found that the abundance of kelp exhibited two diverging trends. First, the relative abundance of kelp in the Santa Cruz Region exhibited a significant, 12-fold decline ($p < 0.001$) between the period when sea otters were absent (kelp maps: 1856–1934) and the period when sea otters returned (kelp maps: 1989–2016)

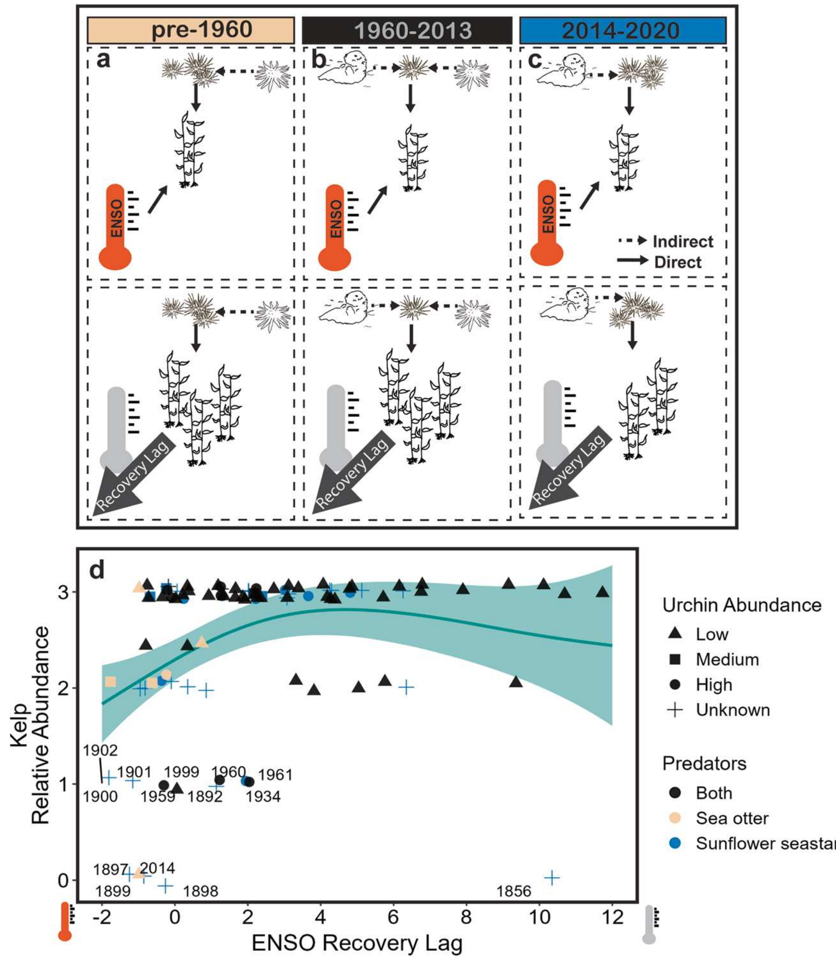

Fig. 3 Schematic diagrams and graph of relationships between kelp abundance and multiple stressors. (a–c) Schematics of indirect and direct effects influencing the abundance of kelp across three time periods. Indirect and direct stressors include predator abundance, herbivore abundance, and the ENSO Recovery Lag (ERL). ERL is a measure of the recovery time for kelp, given the duration of ENSOs. The ERL measure includes years with marine heat waves or ENSO events that were classified as medium + or greater (historical) or MEI v2.0 values ≥ 1.5 (contemporary). (**a**) Period pre-1960, which includes the 1957–1958 ENSO and earlier ENSOs. (**b**) Period beginning in 1960 when sea otters returned to Monterey until 2013 when seastar wasting disease started. (**c**) The period from 2014 to 2020 began when a multi-year marine heatwave and ENSO moved into central California. (**d**) Graph of relative abundance of kelp from 1826–2020 in relation to the types of predators, the relative abundance of sea urchins, and the ENSO Recovery Lag (ERL). Line indicates mean estimated values using Loess smoothers (lambda = 2)

(Fig. 1h; Fig. 2; Table S9). In contrast, the Monterey and Big Sur Regions showed small, but significant ($p = 0.02$) increases in kelp cover between the period when sea otters were present and the period when sea otters returned (Fig. 1h; Fig. 2; Table S9).

Q2. Method 2: Maximizing variables (1934–2020)

Across the 86-year period (1934–2020), GLS models of relative kelp abundance (1934–2020) indicate that kelp abundance declined slightly through time (year: $p < 0.001$; Table S10), but was significantly higher with a greater lag distance from ENSOs (ERL: $p < 0.001$; Table S10), and when there was a greater abundance of sunflower seastars ($p > 0.001$). Sea urchins had a negative influence on the abundance of kelp ($p = 0.02$ l; Table S10). SST was correlated with several of the variables; thus, we did not include it in the models.

From 1934 to 2020, sea urchin abundance was negatively correlated with the abundance of predators (sunflower seastars: Pearson product-moment correlation (PPMC) = −0.36, $p = 0.001$; sea otters: PPMC = −0.51, $p < 0.001$; Fig. 1j). The abundance of both predators was also correlated (PPMC: −0.38, $p < 0.001$).

Q2. Method 3: Mixed methods (1826–2020)

Considering all data sources across the 194-year period, we found that kelp abundances and purple urchin densities exhibited high variability over multiple decades or centuries (Fig. 2). We identified two periods with extremely low kelp abundances (kelp relative abundance < 0.25) (1897–1899, 2014–2016; Fig. 3d). Both periods occurred following ENSOs and when only one predator was present in the system (Fig. 2, Fig. 3d). A separate period of extremely low kelp occurred in 1856, but was not near an ENSO event. Periods of low kelp abundance (kelp relative abundance = 1) occurred following seven ENSO and MHW events (1892, 1900–1902, 1934, 1959–1961, 1999) (Fig. 3d). These periods of low kelp abundance following ENSOs occurred during years when two predators were present, or when only sunflower seastars were present in the ecosystem (Fig. 3d). Multiple-year warm water anomalies were always followed by periods of low kelp (Fig. 3d). The length of the warm water anomaly influenced the recovery period of kelp, and there was a lag in the time it took for kelp to recover (ENSO Lag Recovery (ERL)). The length of ERL was influenced by the number of consecutive years with warm water anomalies. In 80% of cases,

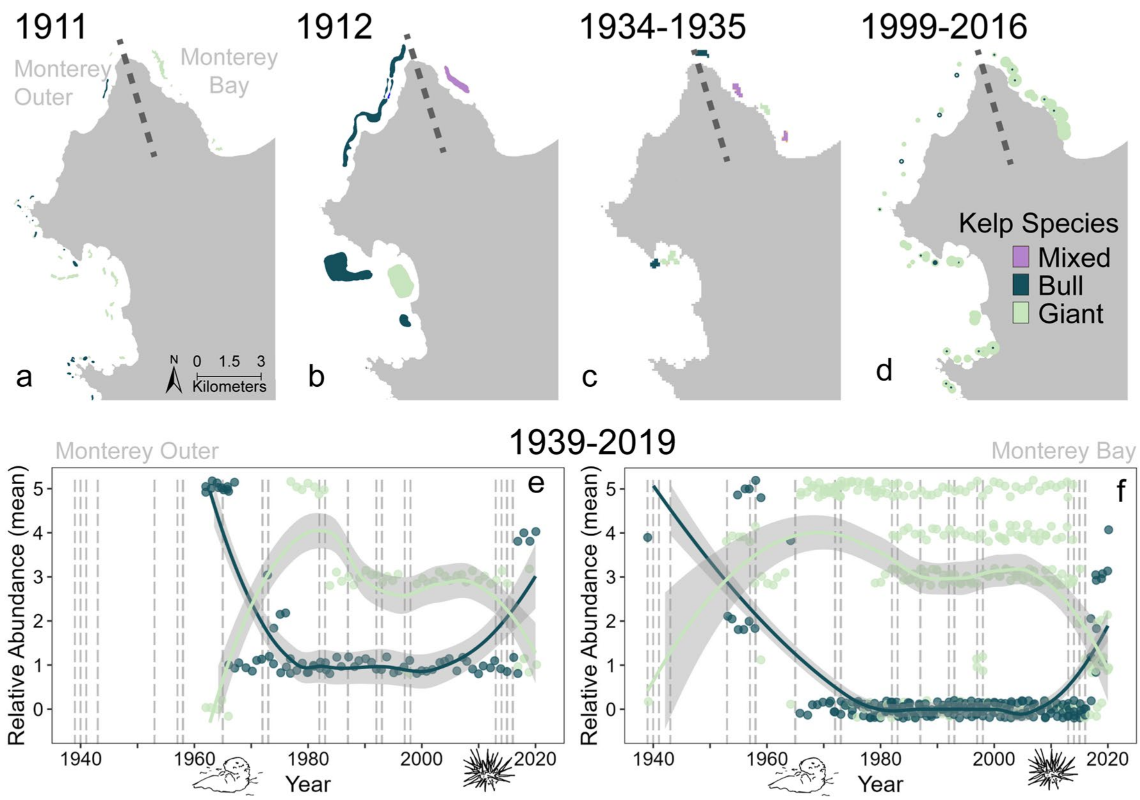

Fig. 4 The spatial distribution and relative abundance of canopy-forming kelp species in the Monterey Peninsula, CA (1911–2019). Canopy-forming kelp beds include bull kelp (*Nereocystis*), giant kelp (*Macrocystis*), and mixed beds both of species. Dashed lines indicate years with strong or greater ENSO events. (**a**–**d**) The spatial extent of kelp species 1911–2016. Dashed lines indicate the location of the boundary between Monterey Bay and the outer area of the Monterey Peninsula. (**e**–**f**) Trends in the relative abundance of bull kelp (*Nereocystis*) and giant kelp (*Macrocystis*) in the Outer Monterey Peninsula (1959–1919) and Monterey Bay (1939–2019). Lines indicate mean estimated values using Loess smoothers (lambda = 2) and grey ribbons indicate confidence intervals. Panels with multi- year periods indicate projects that surveyed kelp over multiple years

kelp recovered 2 years after the ENSO or MHW (Fig. 1i). Following several other ENSOs, kelp abundance remained moderate or high (kelp relative abundance ≥ 2). Urchin abundances during kelp declines were often unknown; however, low periods of kelp (kelp relative abundance = 1) occurred when the abundance of urchins was both low and high (Fig. 3d).

As part of the mixed-methods analysis, we also considered changes in kelp abundance as documented by kelp harvest data. For 80% of the ENSO events ranked strong or greater (1932–2001)—including the 1957–1959 ENSO—kelp harvest declined during the second year of multi-year ENSOs (i.e., $ERL \leq -1$) (Fig. 1d). Kelp harvests then returned to pre-ENSO levels within 1 or 2 years (Fig. 1i).

Q3. How has the relative abundance of canopy-forming kelp species changed over time?

We focused on the Monterey Peninsula to assess changes in the spatial distribution of giant kelp (*Macrocystis pyrifera*) and bull kelp (*Nereocystis luetkeana*). From 1970s onward, giant kelp consistently dominated the relatively protected coastline inside of Monterey Bay (Fig. 4). Following recent kelp deforestation (2015–2016) (Fig. 2; Fig. 3), mixed kelp forests and others dominated by bull kelp unexpectedly appeared inside Monterey Bay (2017–2020) (Fig. 4; Figs. S5–S6). Some oral history respondents stated that this change in dominant kelp species was unprecedented. For example, one respondent recalled that between 1972 and the 2016 deforestation by purple urchins, he had "never seen extensive bull kelp inside [southern] Monterey Bay." However, bull kelp was in fact relatively abundant inside of Monterey Bay from at least the early 1900s through the 1960s (Fig. 4). By the 1970s, single species stands of giant kelp replaced bull kelp and mixed stands. The decline in bull kelp in the 1960s and 1970s followed the re-establishment of sea otters and the declines in purple urchins.

Q4. How do trends translate into broad periods of social-ecological change?

The periods of coastal change (Fig. S2) mapped onto four of the Cultural Periods outlined by Lotze et al. (2006). Since the previously described Cultural Periods end in 2000, we expanded the periods to include the additional years covered by this study (2000–2020) by (1) extending the Global Market period to 2013 and (2) adding Release and Reorganizing (2014–2020). We named this new Cultural Period from the literature on abrupt social ecological change (i.e., *Panarchy*) (Holling 2004; Allen et al. 2014)—to describe the ongoing transformation of the coastal environment catalyzed by the consecutive MHW and ENSOs in the Eastern Pacific (2014–2016).

Discussion

By integrating diverse datasets from historical and contemporary sources, this study provides insight into multiple centuries of kelp forest dynamics. There was extremely high variability in the abundance of kelp across two centuries. Kelp abundance in Santa Cruz exhibited a 12-fold decline, while the other regions increased slightly over time. From 1826 to 2020, there were five periods with low kelp following warm water anomalies (ENSOs and MHW). Two periods had extremely low abundances of kelp following multiple years of warm water anomalies (1897-1899, 2014). Both periods with extremely low kelp occurred when only a single predator was present. None occurred when two predators were present, suggesting that two predators may be necessary to keep kelp from dropping to extremely low abundances following multi-year warm water anomalies. We documented a lag in kelp recovery time (ENSO Lag Recovery (ERL)), which was influenced by the length of the warm water anomalies. Such co-occurring dynamics highlight the critical need to track complex interacting stressors and showcase the historical ability of kelp canopy to recover following declines.

The novel finding that extensive kelp beds existed in Central California for over 100 years without sea otters poses a new question: *What stressor or combination of stressors in the late 1950s led to kelp declines?* Through multiple lines of evidence, we infer that the high urchin-low kelp pattern observed in 1959–1961 was catalyzed ENSO events, but that this stressor was overlooked because ENSO events were not widely recognized at that time. Supporting this finding is evidence that kelp canopy in San Diego, CA, in 1961 covered 0.89% of the extent that had been covered in 1955 (Tegner and Dayton 1991). Kelp declines to low or extremely low abundances were observed eight times (1826–2020). Excluding one observation (1856), all periods with low or extremely low kelp followed ENSO and MHW events.

Extremely low kelp in 1856, which did not follow an ENSO, occurred when Monterey was characterized by a rapidly growing human population, accompanying deforestation, and extensive ranching for missions and the hide-tanning industry (Burcham 1961). To our knowledge, historical sedimentation patterns in central California have not been documented. However, historical livestock grazing peaked in California around 1850. This practice catalyzed a strong sedimentation pulse, altered the composition of the coastal seafloor in southern California (Tomašových and Kidwell 2017), and is hypothesized to have impacted kelp across California (Nicholson et al. 2024). Intensification occurred in livestock grazing in the Monterey region around 1850 (Burcham 1961). We hypothesize this dynamic temporarily changed the rocky seafloor (required by kelp) to soft sediment, leading to the low kelp cover documented during the 1850s.

When considering the impact of ENSOs, it is critical to understand the recovery trajectories of kelp (California Ocean Protection Council 2021). We found that kelp recovery occurred after a time-lag (ENSO Recovery Lag). The abundance of kelp following ENSOs can be further influenced by interactions between invertebrate grazing and predators (Rogers-Bennett and Catton 2019). Despite the fact that sea otters in 2017–2019 consumed greater numbers of urchins than in previous decades (Smith et al. 2021), our results demonstrate that otters did not fully regulate regional urchin populations in 2017–2020. Regulation of urchins by otters would have been anticipated under the sea otter-urchin-kelp trophic cascade hypothesis.

Growing evidence suggests that urchin predation by sunflower seastars may have played an underappreciated role in maintaining kelp forests through time, and we found that the abundance of sunflower seastars was positively correlated with the abundance of kelp. As predators, sunflower seastars influence urchins through non-consumptive and consumptive mechanisms. Sunflower seastar predation can cue urchin sheltering behavior, thereby reducing rates of grazing (Byrnes et al. 2006). A long-term study (Monterey Peninsula, 1872–1981) inferred baseline predation of urchins by sunflower seastars based on remnant urchin tests—sunflower seastars ingest their prey whole (Pearse and Hines 1987). Pearse and Hines (1987) estimated that a low density of sunflower seastars (0.016 per m^2) was needed to suppress urchin outbreaks. Prior to SSWD, we found that sunflower seastar densities in Monterey were above this threshold (mean = 0.02 per m^2). Sunflower seastars consume 0.68 purple urchins day^{-1}, on average, and do not select well-fed over starved urchins (Galloway et al. 2023). This agnostic seastar behavior contrasts that of sea otters who typically prefer consuming fed urchins (Smith et al. 2021). Furthermore, sunflower seastars directly impact 4–7-cm urchins through predation (Burt et al. 2018). In central California, the 4–7-cm size class of purple urchins is estimated to be at 4–5 years old and older (Ebert 2010), given sufficient food. Thus, we hypothesize that the functional extirpation of sunflower seastars by 2014 is a possible mechanism underlying the recent increase in urchin abundance. However, there remains a need for better documentation of the role of sunflower stars in regulating urchin populations and urchin behavior.

The variable presence of bull kelp suggests that this opportunistic annual species (Dayton et al. 1984) may persist when urchin abundances are high. We found that the abundance of bull kelp in Monterey Bay declined following the return of sea otters, when herbivorous urchin declined. In contrast, bull kelp was present in higher densities and mixed species forests during periods when urchin populations were high (pre-1970s and post-2016). Before the recent marine heat wave and ENSO (2014–2016), bull kelp in northern California had extensive cover regardless of urchin densities (Rogers-Bennett 2013). This sustained co-existence provides further evidence of the capacity of bull kelp to maintain populations in the presence of urchins. In contrast, giant kelp, a perennial species that is adapted to compete effectively for light and nutrients (Dayton et al. 1984), appears dominant during low urchin abundances. This functional redundancy of canopy-forming kelp species has the potential to confer greater resilience on kelp forests in central California than in regions with only one commonly dominant species.

Simple and compelling models of ecosystem dynamics, such as a three-step otter-urchin-kelp system, may be a useful tool for conveying complex ecological concepts such as indirect effects. Such models have strong explanatory and predictive power in some contexts (Ripple et al. 2016); however, they may also create flawed expectations of a “silver bullet” solution to complex problems. Our findings suggest that simple trophic cascade models are not accurate for systems, such as central California, where single-species interactions are more diffuse due to diversity within functional groups (Eisaguirre et al. 2020; Malakhoff & Miller 2021; Steneck et al. 2002). Systems impacted by multiple stressors can benefit from ecosystem-based management, but guidance and research on ecosystem-based management of kelp forests remain surprisingly limited (Hamilton et al. 2022). Historical data sources can provide new insights for ecosystem-based management, although there are limitations to the accuracy and availability of historical data which need to be accounted for through methods such as triangulation.

Extending a deeper baseline provides a window into the long-term dynamics of kelp forest ecosystems. Our study demonstrates that following multi-year warm water anomalies, the presence of two predators indirectly prevented kelp from falling to extremely low abundances. Following all ENSO events where kelp declined, the recovery of kelp occurred after a lag, and that lag was extended by multi-year warm-water anomalies. We found that kelp has a strong capacity to recover, but that capacity was reduced by stressors (e.g., urchin outbreaks, predator loss, consecutive warm years). This suggests that management should reduce the risk of extremely low kelp abundances by protecting multiple predators, and by re-establishing predators where they have been lost. It also suggests a greater need for interventions following multi-year warm water anomalies when the ENSO Recovery Lag is greater. Thus, establishing historical baselines, predator restoration, monitoring, and developing techniques for effective and scalable restoration will be crucial for supporting kelp forests. A combination of all these actions is urgently needed to reverse the ongoing loss and degradation of one of the most productive and diverse marine ecosystems on this planet.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10113-024-02260-1.

Acknowledgements We thank Charles Baxter, Nancy Burnett, Vicki Pearse, James Watanabe, Robin Elahi, Megan Mach, Rodrigo Beas, Sue Kidwell, Jeanette Kihs, Amanda Whitmire, Don Kohrs, and Rebecca Miller and respondents of the oral history surveys. We thank Marc Shargal, Vern Fisher, and Patrick Webster for use of their photographs. We dedicate this paper to the memory of our co-author, John Pearse, and his immense contributions to science and education in California, and to the late Charles (Chuck) Baxter, an icon of marine ecology, natural history, and conservation of the Monterey Bay area. Support was provided by private gifts to Pacific Grove Museum of Natural History and to Hopkins Marine Station. FM acknowledges the support of the US NSF (2108566).

Data availability Archival and unpublished datasets analyzed during this study are available in the Dryad data repository Selgrath, Jennifer et al. (2024). Historical Kelp Forests in California Over Multiple Centuries [Dataset]. Dryad. https://doi.org/10.5061/dryad.xpnvx0khq and in Tables S5–S7. Oral histories are available at https://exhibits.stanford.edu/data/browse/monterey-bay-historical-ecology-and-biodiversity. The ecological survey and aerial kelp survey data that support the findings of this study are publicly available.

Code availability R code available from https://github.com/jselgrath/Historical KelpForests and Jennifer Selgrath. (2024). jselgrath/HistoricalKelpForests: historical_kelp_forests (v1.0). Zenodo. https://doi.org/10.5281/zenodo.12561615

References

Al-Abdulrazzak D, Naidoo R, Palomares M-LL, Pauly D (2012) Gaining perspective on what we’ve lost: the reliability of encoded anecdotes in historical ecology. PLoS ONE 7:e43386. https://doi.org/10.1371/journal.pone.0043386

Allen CR, Angeler DG, Garmestani AS, Gunderson LH, Holling CS (2014) Panarchy: theory and application. Ecosystems 17(4):578–589. https://doi.org/10.1007/s10021-013-9744-2

Arafeh-Dalmau N, Olguín-Jacobson C, Bell TW, Micheli F, Cavanaugh KC (2023) Shortfalls in the protection of persistent bull kelp forests in the USA. Biol Conserv 283:110133. https://doi.org/10.1016/j.biocon.2023.110133

Arafeh-Dalmau N, Cavanaugh KC, Possingham HP, Munguia-Vega A, Montaño-Moctezuma et al (2021) Southward decrease in the protection of persistent giant kelp forests in the northeast Pacific. Commun Earth Environ 2(1). https://doi.org/10.1038/s43247-021-00177-9

Bell TW, Allen JG, Cavanaugh KC, Siegel DA (2020) Three decades of variability in California’s giant kelp forests from the Landsat satellites. Remote Sens Environ 238:110811. https://doi.org/10.1016/j.rse.2018.06.039

Breaker LC, Miller LP (2023) One hundred years of daily sea-surface temperature from the Hopkins marine station in Pacific Grove, California: a review of the history, acquisition, and significance of the record. In: Hawkins SJ, Todd PA, Russell BD, Lemasson AJ, Allcock AL, Byrne M, Firth LB, Lucas CH, Marzinelli EM, Mumby PJ, Sharples J, Smith IP, Swearer SE (Eds) Oceanogr Mar Biol Annu Rev 61:376. CRC Press. https://doi.org/10.1201/9781003363873-2

Burcham LT (1961) Cattle and range forage in California: 1770–1880. Agri Hist 35(3):140–149. https://www.jstor.org/stable/3740625

Burt JM, Tim Tinker M, Okamoto DK, Demes KW, Holmes K et al (2018) Sudden collapse of a mesopredator reveals its complementary role in mediating rocky reef regime shifts. Proc R Soc B Biol Sci 285:10–12. https://doi.org/10.1098/rspb.2018.0553

Byrnes JEK, Stachowicz JJ, Hultgren KM, Randall Hughes A, Olyarnik SV et al (2006) Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. Ecol Lett 9:61–71. https://doi.org/10.1111/j.1461-0248.2005.00842.x

California Ocean Protection Council (2021) Interim action plan for protecting and restoring California's Kelp Forests. https://www.opc.ca.gov/webmaster/ftp/pdf/agenda_items/20210216/Item7_KelpActionPlan_ExhibitA_FINAL.pdf

Carlton JT (1994) Apostrophe to the ocean. Conserv Biol 12:1165–1167. https://doi.org/10.1007/BF02926408

Carlton JT (2023) Marine invertebrate neoextinctions: an update and call for inventories of globally missing species. Diversity 15(6):782–12. https://doi.org/10.3390/d15060782

Costa M, Le Baron N, Tenhunen K, Nephin J, Willis P et al (2020) Historical distribution of kelp forests on the coast of British Columbia: 1858–1956. Appl Geogr 120:102230. https://doi.org/10.1016/j.apgeog.2020.102230

Cowen RK, Agegian CR, Foster MS (1982) The maintenance of community structure in a central California giant kelp forest. J Exp Mar Bio Ecol 64:189–201. https://doi.org/10.1016/0022-0981(82)90152-6

Dayton PK, Currie V, Gerrodette T, Keller BD, Rosenthal R et al (1984) Patch dynamics and stability of some California kelp communities. Ecol Monogr 54:253–289. https://doi.org/10.2307/1942498

Ebert TA (2010) Demographic patterns of the purple sea urchin Strongylocentrotus purpuratus along a latitudinal gradient, 1985–1987. Mar Ecol Prog Ser 406:105–120. https://doi.org/10.3354/meps08547

Eisaguirre JH, Eisaguirre JM, Davis K, Carlson PM, Gaines SD, Caselle JE (2020) Trophic redundancy and predator size class structure drive differences in kelp forest ecosystem dynamics. Ecology 3. https://doi.org/10.1002/ecy.2993

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060. https://doi.org/10.1126/science.185.4156.1058

Foster MS, Schiel DR (1988) Kelp communities and sea otters: keystone species or just another brick in the wall? The Community Ecology of Sea Otters, pp 92–115. https://doi.org/10.1007/978-3-642-72845-7_5

Foster MS, Schiel DR (2010) Loss of predators and the collapse of southern California kelp forests (?): alternatives, explanations and generalizations. J Exp Mar Bio Ecol 393:59–70. https://doi.org/10.1016/j.jembe.2010.07.002

Ferretti F, Crowder LB, Micheli F (2015) Using disparate datasets to reconstruct historical baselines of animal populations. In: Kittinger JN, Mcclenachan L, Gedan KB, Blight LK (eds.), Marine historical ecology in conservation: applying the past to manage for the future (issue December, pp 63–85). University of California Press. https://doi.org/10.1525/california/9780520276949.003.0004

Galloway A, Graven S, Kobelt J, Heady WN, Okamoto DK et al (2023) Sunflower sea star predation on urchins can facilitate kelp forest recovery. Proc R Soc B. https://doi.org/10.1098/rspb.2022.1897

Gergis JL, Fowler AM (2009) A history of ENSO events since A.D. 1525: implications for future climate change. Clim Change 92:343–387. https://doi.org/10.1007/s10584-008-9476-z

Hamilton SL, Gleason MG, Godoy N, Eddy N, Grorud-Colvert K (2022) Ecosystem-based management for kelp forest ecosystems. Mar Policy 136:104919. https://doi.org/10.1016/j.marpol.2021.104919

Hauri C, Gruber N, Vogt M, Doney SC, Feely RA et al (2013) Spatiotemporal variability and long-term trends of ocean acidification in the California Current System. Biogeosciences 10:193–216. https://doi.org/10.5194/bg-10-193-2013

Holling CS (2004) From complex regions to complex worlds. Ecol Soc 9(1):11. https://www.ecologyandsociety.org/vol9/iss1/art11/ https://doi.org/10.5751/ES-00612-090111

Jick TD (1979) Mixing qualitative and quantitative methods: triangulation in action. Adm Sci Q 24:602–611. https://doi.org/10.2307/2392366

Jones TL, Culleton BJ, Larson S, Mellinger S, Porcasi JF (2011) Toward a prehistory of the Southern Sea Otter (Enhydra lutris nereis). In: TJB and Rick TC (ed) Human impacts on seals, sea lions, and sea otters: integrating archaeology and ecology in the northeast pacific (pp 243–271). University of California Press. https://doi.org/10.1525/california/9780520267268.003.0011

Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ et al (2016) Global patterns of kelp forest change over the past half-century. Proc Natl Acad Sci 113:13785–13790. https://doi.org/10.1073/pnas.1606102113

Laidre KL, Jameson RJ, Demaster DP (2001) An estimation of carrying capacity for sea otters along the California coast. Mar Mammal Sci 17:294–309. https://doi.org/10.1111/j.1748-7692.2001.tb01272.x

Lee LC, Thorley J, Watson J, Reid M, Salomon AK (2018) Diverse knowledge systems reveal social – ecological dynamics that inform species conservation status. Conservation Letter, 1–11. https://doi.org/10.1111/conl.12613

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG et al (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809. https://doi.org/10.1126/science.1128035

Malakhoff KD, Miller RJ (2021) After 15 years, no evidence for trophic cascades in marine protected areas. Proc R Soc B Biol Sci 288:20203061. https://doi.org/10.1098/rspb.2020.3061

Mason JG, Alfaro-Shigueto J, Mangel JC, Brodie S, Bograd J et al (2019) Convergence of fishers' knowledge with a species distribution model in a Peruvian shark fishery. Conserv Sci Pract 1:1–10. https://doi.org/10.1111/csp2.13

McClenachan LE, Cooper AB, McKenzie MG, Drew JA (2015) The importance of surprising results and best practices in historical ecology. Bioscience 65:932–939. https://doi.org/10.1093/biosci/biv100

McClenachan LE, O'Connor G, Neal BP, Pandolfi JM, Jackson JBC (2017) Ghost reefs: nautical charts document large spatial scale of coral reef loss over 240 years. Sci Adv 3:1–8. https://doi.org/10.1126/sciadv.1603155

McLean JH (1962) Sublittoral ecology of kelp beds of the open coast area near Carmel, California. Biol Bull 122:95–114. https://doi.org/10.2307/1539325

Micheli F, Carlton J, Pearse JS, Selgrath JC, Elahi R et al (2020) Field stations as sentinels of change. Front Ecol Environ 18:320–322. https://doi.org/10.1002/fee.2231

Miller KI, Blain CO, Shears NT (2022) Sea urchin removal as a tool for macroalgal restoration: a review on removing “the spiny enemies.” Front Mar Sci 9:1–18. https://doi.org/10.3389/fmars.2022.831001
Neis B, Schneider DC, Felt L, Haedrich RL, Fischer J et al (1999) Fisheries assessment: what can be learned from interviewing resource users? Can J Fish Aquat Sci 56:1949–1963. https://doi.org/10.1139/cjfas-56-10-1949
Nicholson TE, McClenachan L, Tanaka KR, Van Houtan KS (2024) Sea otter recovery buffers century-scale declines in California kelp forests. PLOS Clim 3:e0000290. https://doi.org/10.1371/journal.pclm.0000290
NOAA (2020) Multivariate ENSO Index V2. Accessed March 11, 2021 https://psl.noaa.gov/enso/mei/
Ogden A (1941) The California sea otter trade, 1784–1848 (p 251). University of California Press. http://hdl.handle.net/2027/uc1.31822005660303
Osio AM, Beebe RM, Senkewicz RM (1996) The history of Alta California: a memoir of Mexican California. University of Wisconsin Press, Madison, WI
Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F (1998) Fishing down marine food webs. Science 279:860–863. http://www.ncbi.nlm.nih.gov/pubmed/9452385
Pearse JS, Hines AH (1979) Expansion of a central California kelp forest following the mass mortality of sea urchins. Mar Biol 51:83–91. https://doi.org/10.1007/BF00389034
Pearse JS, Hines AH (1987) Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. Mar Ecol Prog Ser 39:275–283. https://doi.org/10.3354/meps039275
Platt JR (1964) Strong inference. Science 146:347–353. https://doi.org/10.1017/CBO9781107415324.004
Quinn WH, Neal VT, Antunez de Mayolo SE (1987) El Niño occurrences over the past four and a half centuries. J Geophys Res 92:14449–14461. https://doi.org/10.1029/JC092iC13p14449
R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.r-project.org/
Rhemtulla JM, Mladenoff DJ (2007) Why history matters in landscape ecology. Landsc Ecol 22:1–3. https://doi.org/10.1007/s10980-007-9163-x
Ricketts EF, Calvin J, Hedgpeth JW, Phillips DW (1985) Between Pacific tides. Stanford Univ. Press, Stanford, CA
Ripple WJ, Estes JA, Schmitz OJ, Constant V, Kaylor MJ et al (2016) What is a trophic cascade? Trends Ecol Evol 31:842–849. https://doi.org/10.1016/j.tree.2016.08.010
Rogers-Bennett L (2013) *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus*. In: Lawrence JM (ed) Sea urchins: biology and ecology. Elsevier, pp 413–435
Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Sci Rep 9:1–9. https://doi.org/10.1038/s41598-019-51114-y
Santana-Cordero AM, Szabó P (2019). Exploring qualitative methods of historical ecology and their links with qualitative research. Int J Qual Methods 18:1–11. https://doi.org/10.1177/1609406919872112
Satterthwaite EV, Bax NJ, Miloslavich P, Ratnarajah L, C anonico G (2021) Establishing the foundation for the global observing system for marine life. Front Mar Sci 8. https://doi.org/10.3389/fmars.2021.737416
Schiel DR, Foster MS (2015). The Biology and Ecology of Giant Kelp Forests. https://doi.org/10.1525/california/9780520278868.001.0001
Selgrath JC, Gergel SE (2019) How much is enough? Improving participatory mapping using area rarefaction curves. Land 8(11):166-1–14. https://doi.org/10.3390/land8110166
Selgrath JC, Roelfsema C, Gergel SE, Vincent ACJ (2016) Mapping for coral reef conservation: comparing the value of participatory and remote sensing approaches. Ecosphere 7(5):e01325. https://doi.org/10.1002/ecs2.1325
Selgrath JC, Gergel SE, Vincent ACJ (2018) Shifting gears: diversification, intensification, and effort increases in small-scale fisheries (1950–2010). PLoS ONE 13(3):e0190232. https://doi.org/10.1371/journal.pone.0190232
Shears NT, Babcock RC, Salomon AK (2008) Context-dependent effects of fishing: variation in trophic cascades across environmental gradients. Ecol Appl 18:1860–1873. https://doi.org/10.1890/07-1776.1
Shelton AO, Harvey CJ, Samhouri JF, Andrews KS, Feist BE et al (2018) From the predictable to the unexpected: kelp forest and benthic invertebrate community dynamics following decades of sea otter expansion. Oecologia 188:1105–1119. https://doi.org/10.1007/s00442-018-4263-7
Smith JG, Tomoleoni JA, Staedler M, Lyon S, Fujii J et al (2021) Behavioral responses across a mosaic of ecosystem states restructure a sea otter-urchin trophic cascade. Proc Natl Acad Sci 118:e2012493118. https://doi.org/10.1073/pnas.2012493118
Steneck RS, Erlandson JM, Graham MH, Bourque BJ, Corbett D et al (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436–459. https://doi.org/10.1017/S0376892902000322
Strain EMA, Thomson RJ, Micheli F, Mancuso FP, Airoldi L (2014) Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. Glob Chang Biol 20(11):3300–3312. https://doi.org/10.1111/gcb.1261
Tegner MJ, Dayton PK (1991) Sea urchins, El Ninos, and the long term stability of southern California kelp forest communities. Mar Ecol Prog Ser 77:49–63. https://doi.org/10.3354/meps077049
Thurstan RH, McClenachan LE, Crowder LB, Drew JA, Kittinger JN et al (2015) Filling historical data gaps to foster solutions in marine conservation. Ocean Coast Manag 115:31–40. https://doi.org/10.1016/j.ocecoaman.2015.04.019
Tomašových A, Kidwell SM. 2017 Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf. Proc R Soc B 284:20170328. https://doi.org/10.1098/rspb.2017.0328
Tomscha SA, Gergel SE (2014) Historic land surveys present opportunities for reconstructing frontier settlement patterns in North America. Landsc Ecol. https://doi.org/10.1007/s10980-014-0124-x
Vileisis A (2020) Abalone: the remarkable history and uncertain future of California's iconic shellfish. Oregon State University Press, Corvallis
Wernberg T, Bennett S, Babcock RC, De Bettignies T, Cure K et al (2016) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169–172. https://doi.org/10.1126/science.aad8745
Wing SR, Shears NT, Tait LW, Schiel DR (2022) The legacies of land clearance and trophic downgrading accumulate to affect structure and function of kelp forests. Ecosphere 13:1–21. https://doi.org/10.1002/ecs2.4303
Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2010) Mixed effects models and extensions in ecology with R. Springer-Verlag. https://doi.org/10.1007/978-0-387-87458-6