



# Sea urchin mass mortality rapidly restores kelp forest communities

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**ABSTRACT:** Giant kelp *Macrocystis pyrifera* is a foundational species that forms a 3-dimensional habitat and supports numerous high-value fisheries species. Constant grazing of kelp holdfasts by overabundant sea urchins causes catastrophic ecological and economic impacts on rocky reefs worldwide. Overgrazing creates urchin barrens that persist for decades in the absence of ecological forcing that would shift the ecosystem back to a kelp-dominated state. Annual surveys of kelp forest and urchin barren sites in the Southern California Bight were performed from 2011 to 2020 to assess changes in kelp forest communities as a result of restoration efforts through sea urchin culling. However, that time period also encompassed a sea urchin mass mortality event. Following drastic reductions of sea urchin densities, rocky reefs returned to a kelp-dominated state within approximately 6 mo and remained stable through the remainder of the study. Benthic cover, fish, and kelp and macroinvertebrate communities inside former urchin barrens became more similar to that of kelp forest reference sites and continued to do so for the next 5 yr. Giant kelp density increased significantly compared to existing kelp forests, while benthic indicators of urchin dominance (i.e. crustose coralline algae and bare rock cover) decreased. Kelp restoration through sea urchin culling essentially mimics sea urchin mass mortality events. If culling can produce similar declines in urchin density, it may be a viable management tool to rapidly restore persistent urchin barrens at moderate spatial scales, while a mass mortality event can drive recovery of kelp forest communities at more extensive spatial scales.

**KEY WORDS:** Kelp restoration · *Macrocystis pyrifera* · Urchin barrens · Mass mortality · Rocky reefs · Alternative stable state · Ecological restoration

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## 1. INTRODUCTION

Urchin barrens are created by overabundant sea urchins aggregating in large fronts and grazing entire kelp forests down to bare rock substrate (Dean et al. 1984, Steneck et al. 2002) (Fig. 1). This process can cause catastrophic ecological impacts

and severe economic disruption as is presently occurring in northern California and Oregon, USA (Bonaviri et al. 2017, Rogers-Bennett & Catton 2019), and Tasmania and New South Wales, Australia (Ling et al. 2015). While urchin barrens can be short-lived and localized (Harrold & Reed 1985, Graham 2004), there is worldwide evidence of

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Fig. 1. Examples of typical (left column) giant kelp *Macrocystis pyrifera* forest and (right column) urchin barren states of nearshore rocky reefs in the Southern California Bight (SCB), USA. Photos by J. Williams

urchin barrens persisting for decades in the absence of ecological forcing that would return the ecosystem to a kelp-dominated stable state (Norderhaug & Christie 2009, Baskett & Salomon 2010, Filbee-Dexter & Scheibling 2014a).

Sea urchin grazing can typically be controlled by sea urchin predators and competitors (Nichols et al. 2015). However, many of those species have been overharvested (Tegner 1980, Lafferty 2004, Hamilton & Caselle 2015) or decimated by disease (Schultz et

al. 2016, Harvell et al. 2019). Where kelp has been eliminated, there are fewer fish and macroinvertebrate species and individuals, and less overall biomass than in kelp forests (Graham 2004, Miller et al. 2018). While sea urchins occur in high densities in barrens, with no macroalgae to feed on (Harrold & Reed 1985, Konar & Estes 2003) their growth rate is reduced (Ebert 1967, Lafferty 2004), and they persist only in a weakened state on a diet of mainly diatoms (Chapman 1981) and detritus from adjacent kelp forests (Filbee-Dexter & Scheibling 2014b). Their size structure, gonad production, and therefore ecological (Stewart & Konar 2012) and economic value (Teck et al. 2018) are all suppressed in urchin barrens compared to healthy kelp forests.

In the Southern California Bight (SCB), giant kelp *Macrocystis pyrifera* is a foundational species that increases diversity through physical engineering (Miller et al. 2018). It forms a 3-dimensional habitat that supports more than 700 species, and nearly one-quarter of California marine organisms depend on it for at least a portion of their life history (Graham 2004). This ecosystem serves as a refuge from predation, functions as a nursery for newly settled juveniles (Dayton 1985, Steneck et al. 2002), and supports numerous high-value recreational and commercial fisheries for invertebrates (Zahn et al. 2016) and finfish (Pondella et al. 2019). Like other regions worldwide, one of the most significant present-day causes of kelp forest loss in the SCB is overgrazing of macroalgae, specifically by purple sea urchins *Strongylocentrotus purpuratus* and red sea urchins *Mesocentrotus franciscanus* (Steneck et al. 2002), whose predators have been reduced by strong recreational and commercial fishing pressure (Hamilton & Caselle 2015). Recent ecosystem-based management efforts (e.g. marine protected areas) have yielded increases in abundance of some urchin predators (Hamilton & Caselle 2015, Selden et al. 2017, Eisaguirre et al. 2020), although urchin barrens still persist throughout the SCB. It takes several years before increases in size structures (i.e. predators growing large enough to successfully prey upon sea urchins) and densities of sea urchin predators (Salomon et al. 2010, Leleu et al. 2012) alter ecological function. Additionally, there is a positive feedback mechanism where crustose coralline algae, more commonly found within urchin barrens, facilitates further recruitment of sea urchins, allowing rocky reefs to remain in a barren alternative stable state for decades even with reduced fishing pressure on urchin predators (Baskett & Salomon 2010).

The Palos Verdes Peninsula, a rocky headland located near the center of the SCB mainland (Fig. 2), is

adjacent to the largest urban area on the US west coast and is subject to cumulative anthropogenic impacts associated with urban development, many of which historically impacted growth of kelp forests (Stull et al. 1987). Pollution and nutrification from urban runoff and the installation of major sewage outfalls in Santa Monica Bay during the 1940s nearly eliminated giant kelp from the region by 1958 (Wilson & North 1983). Sedimentation from coastal development on the peninsula, in addition to the expansion of the adjacent Port of Los Angeles, further impacted settlement and growth of giant kelp. While small-scale restoration efforts and improvements to sewage treatment helped restore some giant kelp to the peninsula (Foster & Schiel 2010), the giant kelp canopy cover at the Palos Verdes Peninsula decreased by approximately 80% since the first large-scale survey in 1911 (Pondella et al. 2018). The cumulative ecological and economic losses incurred in places like the Palos Verdes Peninsula as a product of deforestation (Claisse et al. 2013) necessitated the use of more active restoration measures to quickly return urchin barrens to a kelp-dominated stable state (Baskett & Salomon 2010, Layton et al. 2020).

Present-day kelp forest restoration efforts in the SCB were preceded by decades of trial and error. Early restoration efforts in this region attempted to transplant or regrow giant kelp (Wilson & North 1983). These efforts required excessive effort and cost and did not address the problems of constant grazing pressure and facilitation of sea urchin settlement by crustose coralline algae. Restoration efforts found greater success by actively decreasing sea urchin densities either by relocating sea urchins from within urchin barrens to distant, non-barren areas (Ford & Meux 2010), or by culling using quicklime (North & Pearse 1970) or hammers (Wilson & North 1983, House et al. 2018). Multiple small-scale (1–2 ha) restoration efforts in this region demonstrated that reducing urchin density from as high as  $100 \text{ m}^{-2}$  to  $< 2 \text{ m}^{-2}$  enabled the natural settlement and growth of giant kelp and other macroalgae regardless of other present-day anthropogenic impacts. These restored kelp forests have remained intact through several notable disturbances (e.g. 200 yr storm events, red tide, El Niño events) and maintained high kelp densities (Ford & Meux 2010), including 1 site at the Palos Verdes Peninsula restored (in 2005–2008) so successfully that it was used as a kelp reference site in the present study.

For a decade, annual surveys were conducted at the Palos Verdes Peninsula with the intent of determining the effects of kelp forest restoration efforts through urchin culls. However, in January 2015, both red and

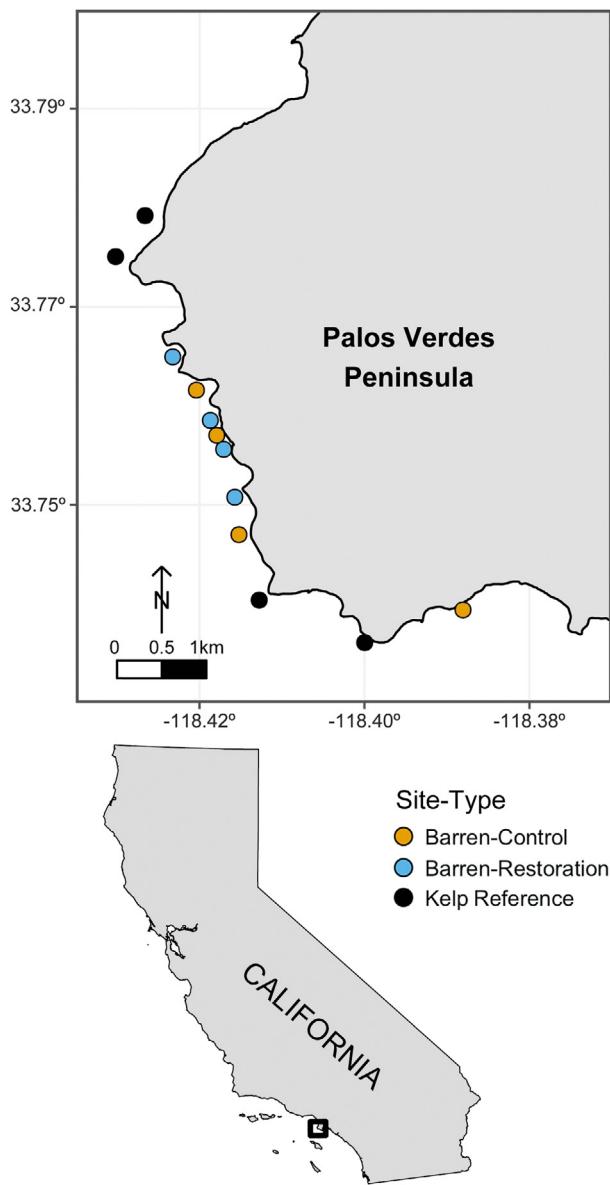


Fig. 2. Survey sites by site type on the western half of Palos Verdes Peninsula, California, USA

purple sea urchins were found at the Palos Verdes Peninsula with lesions characteristic of 'black-ring disease' (Fig. 3), where a bacterial infection causes dark lesions to appear, epidermal tissue degrades, spines drop off, and eventually the test itself is perforated, causing death (Pearse et al. 1977, Lester et al. 2007). Live, emergent sea urchins were rarely observed at monitoring sites along the Palos Verdes Peninsula that summer. This sea urchin mass mortality event occurred nearly concurrently with restoration, and while disease does not always reduce sea urchin densities to levels that occur naturally in predator-rich environments (Lafferty 2004), it obscured long-term ef-

fects of anthropogenic urchin culls. Fortunately, in addition to restoration sites, our long-term monitoring program also surveyed urchin barren control sites and kelp forest reference sites. Here we describe the effects of reducing sea urchin density on temperate rocky reef communities in urchin barren and kelp forest states. Using data from annual surveys conducted before and after the mass mortality event and restoration effort, we evaluated changes in community structure and the extent and magnitude of taxon-specific changes which occurred as a result of these impacts.

## 2. MATERIALS AND METHODS

### 2.1. Site selection and survey methods

After surveying the Palos Verdes Peninsula in 2011 and classifying shallow rocky reefs as either urchin barrens or kelp forest sites (Claisse et al. 2013), we chose monitoring sites at 4 urchin barren reefs that were to be restored (11.1 ha), 4 barren reefs designated as barren-control sites, and 4 kelp forest reefs designated as kelp reference sites (hereafter 'Barren-Restoration', 'Barren-Control', and 'Kelp Reference' site types, respectively; Fig. 1). Scuba divers visually surveyed each site annually from 2011 to 2020 at a depth of ~5 m using modified CRANE survey protocols (described in detail by Zahn et al. 2016, Pondella et al. 2019). Briefly, rocky reef ecosystems were characterized using 4 survey types: (1) 30 m × 2 m band transects to estimate species-specific fish density and size distribution along the reef surface, in the midwater, and through the kelp canopy when it was present; (2) 30 m × 2 m band transects to estimate density of macroinvertebrates and stipitate algae (kelp) on the reef; (3) uniform point contact surveys to determine percent cover of primary reef placeholders, including sessile invertebrates, algae, and abiotic features (e.g. bare sand, bare rock, shell hash); and (4) roving collection and/or measurement of several commercially and ecologically important invertebrate species (e.g. urchins, abalone, lobster).

### 2.2. Restoration methods and timeline

Purple sea urchin density was reduced from ~18 to ~2 m<sup>-2</sup> by divers using rock hammers at the 4 Barren-Restoration sites (House et al. 2018). Divers left red sea urchins in place as they were not overabundant and are economically valuable. Given the large spatial scale of the restoration effort (22.8 ha total target



Fig. 3. (a,b) Lesions on purple sea urchins *Strongylocentrotus purpuratus* and (c,d) red sea urchins *Mesocentrotus franciscanus* collected on 6 January 2015 from Palos Verdes Peninsula. Photos by J. Williams

area), and the nature of the labor force (e.g. multiple individual commercial urchin diver teams, The Bay Foundation non-profit employees, volunteers), restoration of sites was intended to occur sequentially. However, practical considerations resulted in restoration efforts occurring concurrently at some reefs, and divers would often return to sites after a period of months to monitor and cull additional purple urchins in small high-density patches until the entire site was considered 'restored'. One site was restored just before our 2014 survey, prior to any community response to the effort, and represents the only Barren-Restoration site where urchin densities were reduced to the  $\sim 2 \text{ m}^{-2}$  target density prior to the mass mortality event which occurred between our 2014 and 2015 surveys. The other 3 Barren-Restoration sites were restored during the 2015 and/or 2016 surveys, although the majority of restoration work (78% by acreage) was completed at all sites prior to the 2016 survey. For further details, see House et al. (2018).

### 2.3. Data processing

Prior to analysis, pelagic and highly mobile fish species that are not characteristic inhabitants of rocky reef habitats (e.g. mackerel, sardines, silversides) were excluded from the data set, and young-of-the-year were removed prior to density (but not biomass) calculations because they could numerically dominate the assemblage at some sites sampled early during the sampling season but decline later in the year as a result of natural mortality. Total length (TL) estimates were converted to biomass using standard species-specific length-weight conversions from the literature (e.g. Williams et al. 2013). Density and biomass (separately) were then summed across all 3 portions (bottom, midwater, and canopy) of each transect, except for when the water depth was  $< 6 \text{ m}$ , meaning that the coverage of the canopy and mid-water portions would overlap, in which case no mid-water portion was included (Pondella et al. 2019). All

fish, kelp, and macroinvertebrate densities were scaled to number or grams per 100 m<sup>2</sup>, and benthic cover was calculated as a percentage.

#### 2.4. Community analyses

We examined geographical and temporal patterns for specific community types (fishes, kelp and macroinvertebrates, and benthic cover) to help characterize the nearshore rocky reef ecosystems. For each community type, we constructed a Bray-Curtis similarity matrix using the 'vegdist' function in the 'vegan' package (Oksanen et al. 2019) in R version 4.0.2 (R Core Team 2020). The matrix used square root-transformed (for density data) or arcsine root transformed (for percent cover data) taxon-specific values by site and year and the Bray-Curtis similarity coefficient. Two-dimensional, non-metric multidimensional scaling (nMDS) was used to visualize and examine patterns among community types over time using the 'metaMDS' function in the 'vegan' package in R. A separate matrix was created using the mean values among sites for each site type and year, and the nMDS results were overlaid on the site-by-site visualization. Differences in community composition (permutational multivariate analysis of variance, PERMANOVA) and similarity percentages (SIMPER) of before-impact era (2011–2014) and after-impact era (2015–2020) communities were determined using the 'adonis' and 'simper' functions, respectively, in the 'vegan' package in R. PERMANOVAs were also run to identify significant differences between each Barren-Control and Barren-Restoration community type within both eras to determine the efficacy of pooling the 2 site types for further analyses, as sites in both types were originally urchin barrens and then both experienced the urchin mass mortality event. To account for multiple comparisons among eras and communities, significance values were adjusted by controlling for the false discovery rate (FDR, 5%) using the procedure of Benjamini & Hochberg (1995).

#### 2.5. Progressive-change multiple before–after control-impact (PCmBACI)

The spatial scale and amount of effort in this restoration work necessitates multiple points of impact over time. Accordingly, this experiment intended to utilize a staircase design to assess restoration success versus a control, as Barren-Restoration sites were restored sequentially. These staircase experimental

designs are considered robust to time-treatment interactions (Walters et al. 1988). However, the mass mortality event occurred between the 2014 and 2015 sampling events and universally impacted the entire study, including the Kelp Reference and Barren-Control sites. We were still able to perform robust analyses of impact using an mBACI design (Downes et al. 2002). Our design consists of multiple before-and after-impact surveys of each site type, multiple impact sites, and uses multiple Kelp Reference sites as the 'controls'. Further, we used a method which eliminates a perceived flaw in BACI designs, namely the failure to detect non-step-changes, by incorporating a progressive-change aspect to the mBACI design that uses multi-model inference to identify the best model (either step-change or linear) for after-impact change (Thiault et al. 2017).

For this assessment, taxon-specific changes in percent cover or density were compared between site types from the before- and after-impact eras. In order to reduce the number of statistical tests and error associated with multiple analyses, taxa that were examined independently using this modified PCmBACI analysis were limited to those that SIMPER analyses identified as influential to differences in community structure ( $\geq 10\%$  mean contribution to dissimilarity). Our analysis treated all sites independently and selected the model with the highest relative likelihood using estimates derived from weights of Akaike's information criterion corrected for small sample size (AICc) (Akaike 1973). Effect ratios (the after-impact change in density/cover in urchin barrens relative to the change in the Kelp Reference) and 95% confidence intervals were obtained by bootstrapping (9999 permutations), and significance values were adjusted by controlling for the FDR (5%). For reference and visualization, effects within site type and universal before–after effects were analyzed in the same manner for all taxa, including those with significant BACI interactions. Lastly, to identify ecologically important density thresholds and after-impact size trends, we examined the relationship between purple sea urchin size structure and density.

### 3. RESULTS

#### 3.1. Community analyses

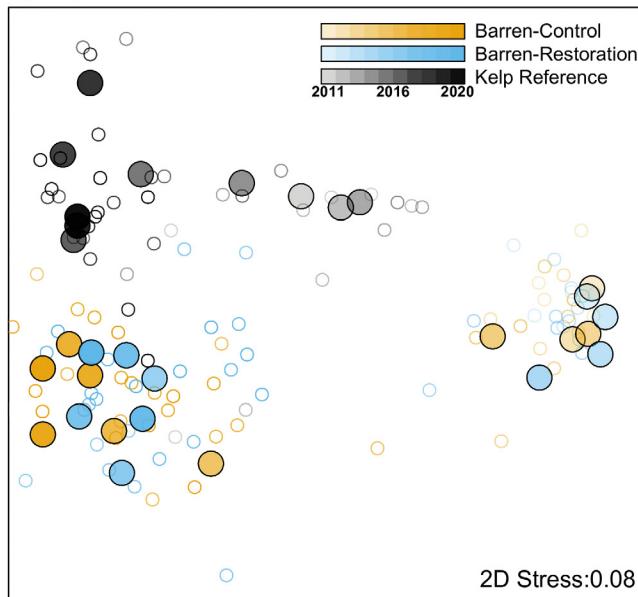
For every community data type (kelp and macroinvertebrates, benthic cover, fish density, fish biomass), the community composition at all 3 site types (Kelp Reference, Barren-Control, Barren-Restoration) be-

came more similar following the impact (i.e. after 2015) (Fig. 4). The Barren-Restoration sites and Barren-Control sites were not significantly different for all community types during both the before-impact and the after-impact eras (Fig. 4, Table 1). As such, sites from Barren-Restoration and Barren-Control site types were pooled as a 'Barren' site type in all further analyses. After pooling, all pairwise PERMANOVA tests were significant when comparing com-

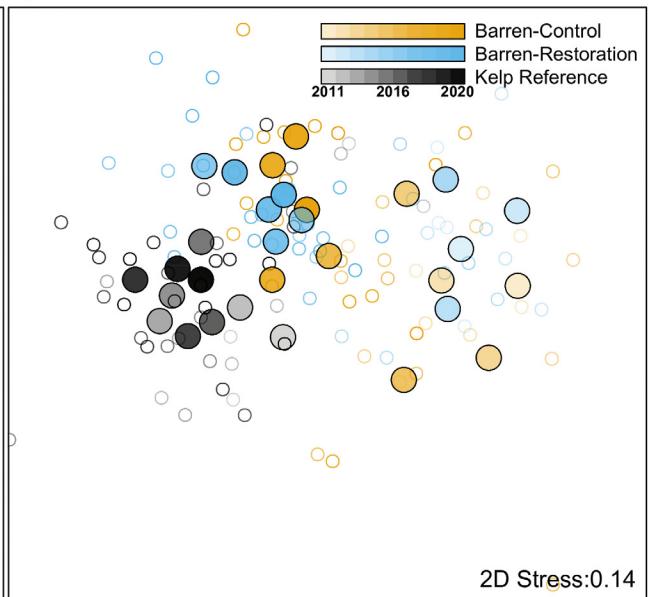
munity structure among site types within era and within site type between eras (Table 2), indicating not only a significant difference in community structures between Barren and Kelp Reference sites during each era, but also a clear shift in community structures for all site types after impact.

The distinct shift in kelp and macroinvertebrate community structures after-impact (Fig. 4a) was generally a result of increased giant kelp, chain-bladder

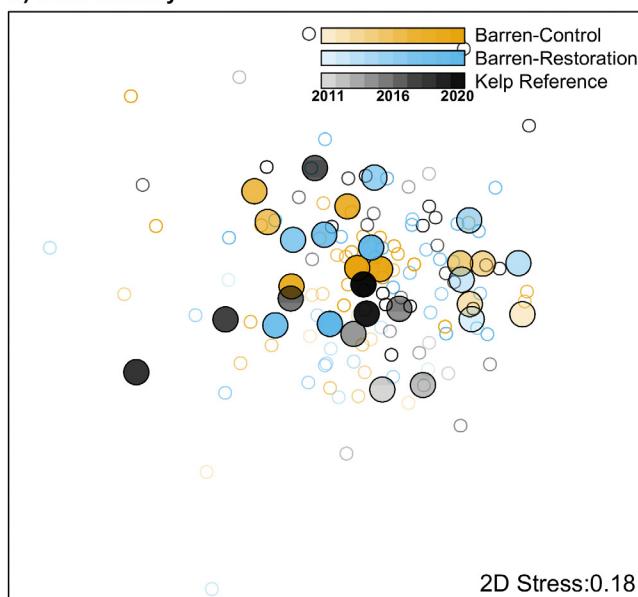
#### a) Kelp and macroinvertebrates



#### b) Benthic cover



#### c) Fish density



#### d) Fish biomass

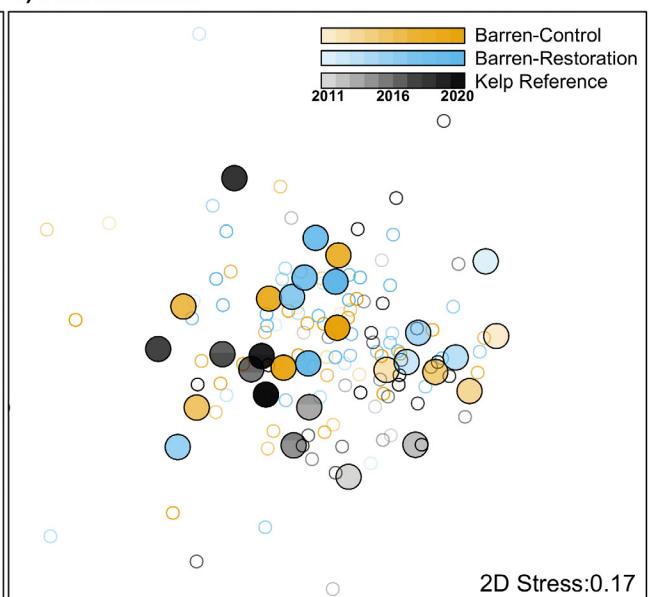


Fig. 4. Two-dimensional nMDS plots of community structure by year (indicated by increased opacity of color over time) and site type for (a) kelp and macroinvertebrates, (b) benthic cover, (c) fish density, and (d) fish biomass. Individual sites are shown as open circles with site type means, indicated by closed circles, overlain in the same 2-dimensional space

Table 1. Pairwise comparisons of each community between Barren-Control and Barren-Restoration site types by site within before- and after-impact eras. p-values were adjusted by controlling for the false discovery rate (5%). No pairs were significantly different (PERMANOVA,  $\alpha < 0.05$ ), therefore Barren-Control and Barren-Restoration communities were pooled for all further analyses. df = 1 for all comparisons

Community	Era:site type pairs		SS	Pseudo- <i>F</i>	R <sup>2</sup>	Adjusted p
Kelp & macro-invertebrates	Before:Barren-Control	Before:Barren-Restoration	0.05	0.81	0.03	0.761
	After:Barren-Control	After:Barren-Restoration	0.10	0.96	0.02	0.761
	Before:Barren-Control	Before:Barren-Restoration	0.12	1.63	0.05	0.456
	After:Barren-Control	After:Barren-Restoration	0.27	3.09	0.08	0.071
Benthic cover	Before:Barren-Control	Before:Barren-Restoration	0.10	0.65	0.02	0.763
	After:Barren-Control	After:Barren-Restoration	0.14	0.96	0.02	0.698
Fish density	Before:Barren-Control	Before:Barren-Restoration	0.13	0.77	0.03	0.761
	After:Barren-Control	After:Barren-Restoration	0.19	1.27	0.03	0.659
Fish biomass	Before:Barren-Control	Before:Barren-Restoration	0.13	0.77	0.03	0.761
	After:Barren-Control	After:Barren-Restoration	0.19	1.27	0.03	0.659

kelp (*Stephanocystis* spp.), and wavy turban snails *Megastraea undosa* (Fig. 5) at Barren sites. Further, this was combined with the near total extirpation of several echinoderms, including red and purple sea urchins, warty sea cucumbers *Apostichopus parvimensis*, and both giant-spined sea stars *Pisaster giganteus* and ochre sea stars *P. ochraceus* at all sites (Fig. 6). Benthic cover communities (Fig. 4b), most evidently at Barren sites, illustrated similar patterns driven by after-impact increases in erect coralline algae and decreases in bare rock and crustose coralline algae cover (Fig. 7). Similar patterns were seen in fish communities (by density and biomass; Fig. 4c,d, respectively), although there was generally more overlap between after-impact fish communities among all site types compared to kelp and macro-invertebrate and benthic cover community types.

Shifts in the fish communities were generally due to increases in numerical densities of garibaldi *Hypsypops rubicundus*, kelp bass *Paralabrax clathratus*, and rock wrasse *Halichoeres semicinctus* (Fig. 8).

### 3.2. PCmBACI and taxon-specific trends

The defined impact in this study was the reduction of sea urchins from the ecosystem, an event that was clearly observed at all sites (Fig. 6). Furthermore, when relating density by mean test sizes of purple sea urchins, patterns emerged suggesting that mean test sizes rarely exceeded 40 mm (35.0 ± 1.3 mm, 95 % CI) once densities were above approximately 3 m<sup>-2</sup> (Fig. 9). Thirteen other taxa were identified by the SIMPER procedure as contributors

Table 2. Pairwise comparisons of each community between Barren and Kelp Reference site types by site within before- and after-impact eras, and within site types among eras. p-values were adjusted by controlling for the false discovery rate (5%); \* indicates significantly different communities (PERMANOVA;  $\alpha < 0.05$ ). df = 1 for all comparisons

Community	Era:site type pairs		SS	Pseudo- <i>F</i>	R <sup>2</sup>	Adjusted p
Kelp & macro-invertebrates	Before:Barren	Before:Kelp Reference	2.87	34.6	0.43	<0.001*
	After:Barren	After:Kelp Reference	2.19	20.2	0.25	<0.001*
	Before:Barren	After:Barren	9.16	103.2	0.57	<0.001*
	Before:Kelp Reference	After:Kelp Reference	1.02	11.0	0.22	<0.001*
Benthic cover	Before:Barren	Before:Kelp Reference	1.38	16.8	0.27	<0.001*
	After:Barren	After:Kelp Reference	0.91	11.27	0.14	<0.001*
	Before:Barren	After:Barren	1.66	20.0	0.20	<0.001*
	Before:Kelp Reference	After:Kelp Reference	0.18	2.33	0.06	0.025*
Fish density	Before:Barren	Before:Kelp Reference	0.84	5.43	0.11	<0.001*
	After:Barren	After:Kelp Reference	0.51	3.43	0.05	<0.001*
	Before:Barren	After:Barren	1.57	10.7	0.12	<0.001*
	Before:Kelp Reference	After:Kelp Reference	0.47	2.93	0.07	0.001*
Fish biomass	Before:Barren	Before:Kelp Reference	0.45	2.70	0.08	<0.001*
	After:Barren	After:Kelp Reference	0.64	4.05	0.05	<0.001*
	Before:Barren	After:Barren	1.14	7.21	0.09	<0.001*
	Before:Kelp Reference	After:Kelp Reference	0.42	2.54	0.06	0.006*

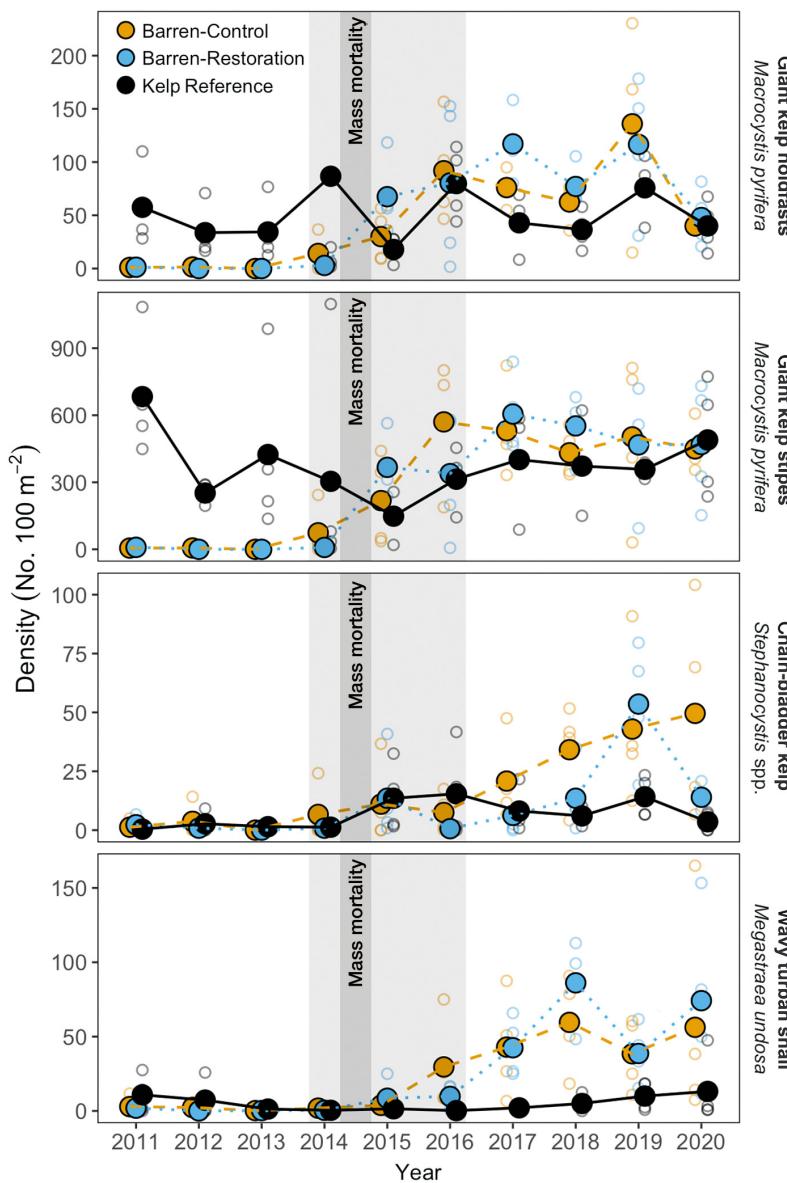


Fig. 5. Density (by year and site type) of kelp and macroinvertebrates that increased in density following the mass mortality and/or restoration events. Site type means are indicated by closed circles, individual sites are shown as open circles. Light gray shading indicates active restoration years; the darker gray bar indicates the mass mortality event and analyzed point of impact

to shifts in community structure, and these were then examined for changes in percent cover or density between site types from before- to after-impact using the PCmBACI approach. Giant kelp holdfast and stipe density were both tested independently. Densities of each of the 3 fish species were tested in terms of both abundance and biomass, bringing the total number of tests to 18. Eleven of these tests showed a significant BACI effect (Fig. 10), 7 of which showed an increase in density or cover following urchin removal at

Barren sites in comparison with Kelp Reference sites, and 4 showed a decrease. A step-change model, indicating an immediate after-impact change, best described the relative changes over time for all taxa. Linear models, indicating more gradual change after-impact, were not selected for any taxa in the PCmBACI model selection procedure.

Taxon-specific temporal shifts generally grouped into 4 categories: (1) taxa that were initially more abundant at Barren sites than Kelp Reference sites but universally decreased, including echinoderms that were nearly extirpated from all monitoring sites after impact (Fig. 6) and bare rock and crustose coralline algae cover (Fig. 7); (2) taxa that were initially less abundant in Barren sites than Kelp Reference sites but increased in Barren sites to levels similar to that of Kelp Reference sites after impact (giant kelp, erect coralline algae, and kelp bass density; Figs. 5, 7, & 8); and (3) taxa that were universally infrequent prior to impact and either universally increased after impact (chain bladder kelp, rock wrasse density and biomass, kelp bass biomass; Figs. 5 & 8); or (4) increased only in Barren sites after impact (wavy turban snails and garibaldi density and biomass; Figs. 5 & 8).

#### 4. DISCUSSION

Following drastic reductions of sea urchin densities in barrens, rocky reefs rapidly returned to a kelp-dominated

state by the first annual survey, approximately 6 mo following the first observed sign of a sea urchin mass mortality event, and remained stable through the remaining 5 yr of this study. While this effect has been noted following previous sea urchin mass mortality events (Pearse & Hines 1979, Feehan & Scheibling 2014), this is even more remarkable given that this period was marked by extended periods of low-nutrient conditions, typically a cause for decreased kelp cover and growth (Reed et al. 2016). Active restoration through culling of purple urchins occurred

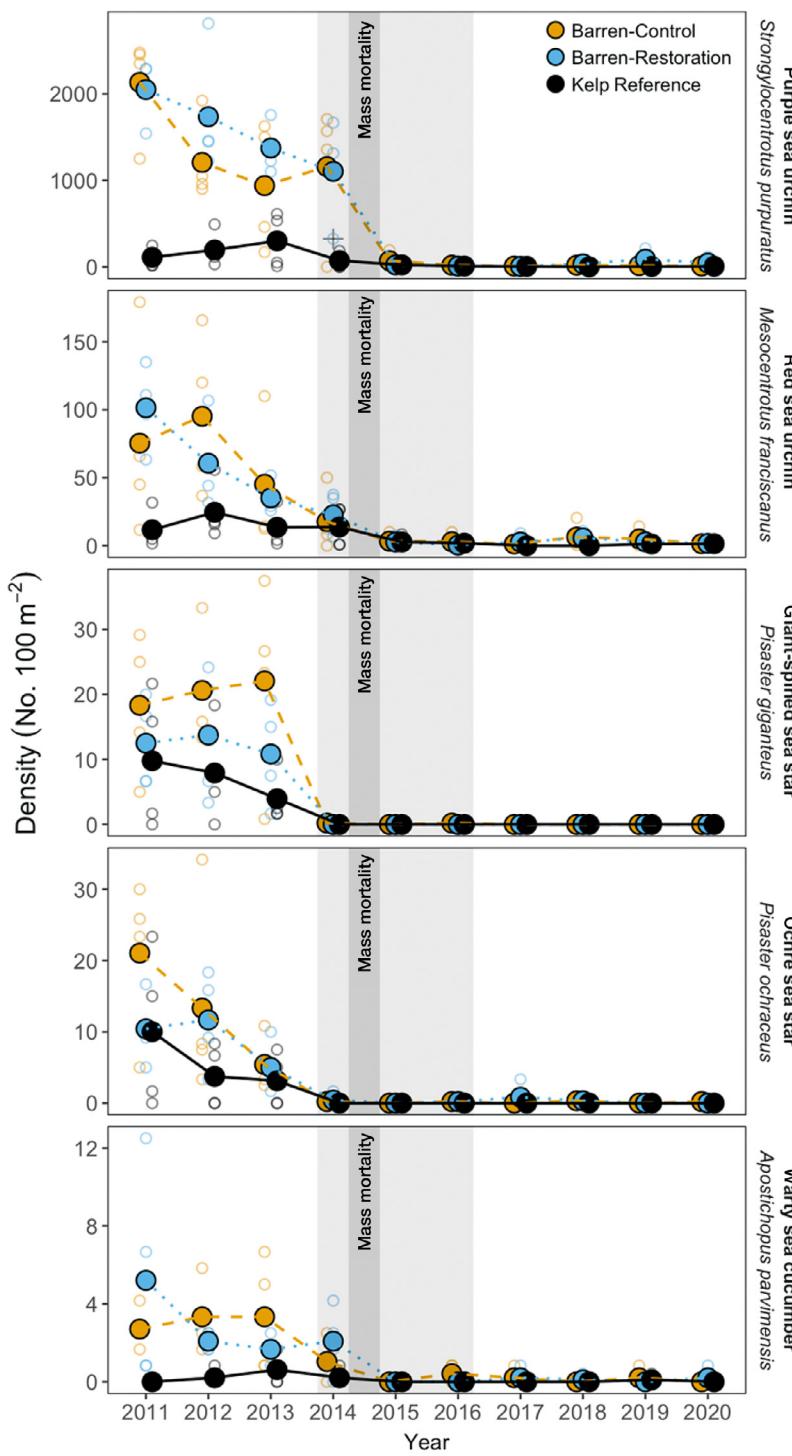


Fig. 6. Density (by year and site type) of kelp and macroinvertebrates that decreased in density following the mass mortality and/or restoration events. The purple sea urchin density at the Barren-Restoration site that was restored prior to the mass mortality event is noted with a cross through the open circle. Other details as in Fig. 5

concurrently at the Barren-Restoration sites, beginning approximately 18 mo before the mass mortality event and continuing afterwards to remove small,

high-density pockets of sea urchins that remained (House et al. 2018). However, we detected few differences in taxon-specific or community changes over time between Barren-Restoration sites that were cleared of sea urchins by hand and disease, and Barren-Control sites that were cleared of sea urchins only by the mass mortality event. Therefore, the overall extent and magnitude of change due to restoration effort could not be separated from that of the mass mortality event. As restoration through urchin culling essentially mimics sea urchin mass mortality events by reducing sea urchin densities and grazing pressure (Pearse & Hines 1979, Scheibling 1986, Feehan & Scheibling 2014), this is not a surprising result. However, it does illustrate that the underlying assumption of this active method of kelp forest restoration is correct, that drastically reducing sea urchin densities can be successful in pushing rocky reef ecosystems back over their ecological tipping point from an urchin barren stable state to a kelp forest stable state.

Following the urchin mass mortality event and concurrent active restoration, kelp forest communities and benthic cover inside former urchin barrens became more similar to that of Kelp Reference sites and continued to do so for the next 5 yr. Giant kelp holdfast density, giant kelp stipe density, and erect coralline algae cover increased significantly following impact compared to existing kelp forests, while telltale benthic indicators of urchin dominance (crustose coralline algae and bare rock cover) decreased. While we included sea stars in the PCMBACI analysis, they were almost completely extirpated from the entire SCB prior to the 2014 survey due to an unrelated sea star wasting disease outbreak (Hewson et al. 2014). Sea cucumbers also declined to near zero

prior to the 2015 surveys, and while sea cucumbers are susceptible to bacterial infections similar to those that cause black-ring disease in sea urchins (Del-

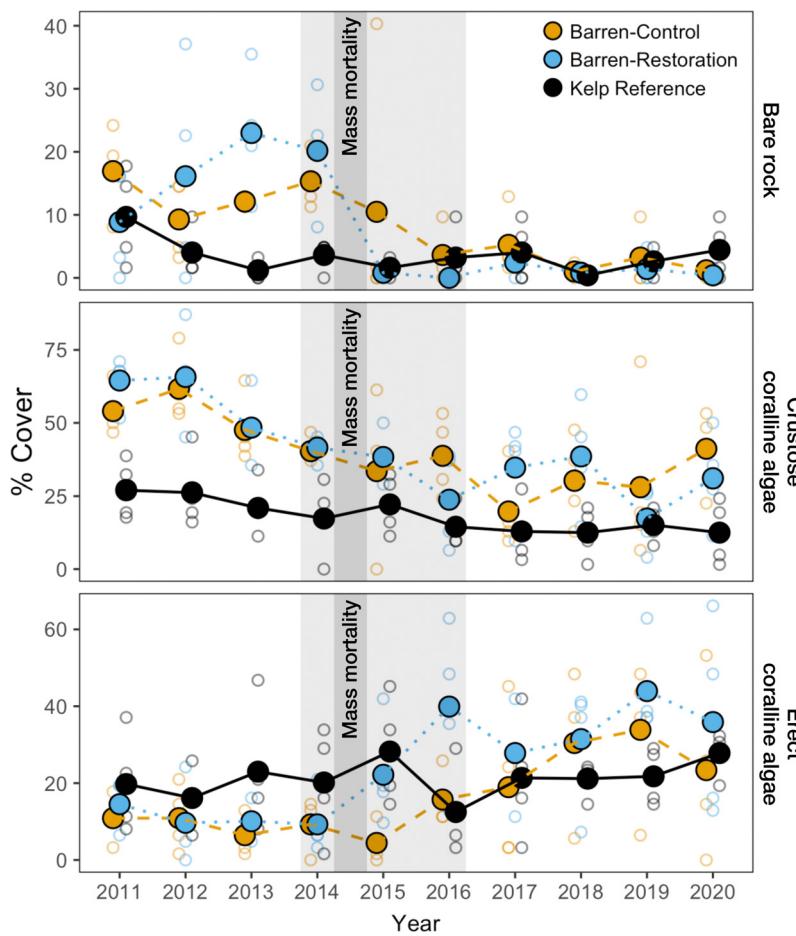


Fig. 7. Percentage (by year and site type) of 3 types of benthic cover impacted by mass mortality and/or restoration events. Other details as in Fig. 5

roisse et al. 2020), we did not observe any diseased or deceased individuals. It is unknown whether this decrease is the result of a third disease-driven mass mortality event for another class of echinoderms, increased fishing pressure on this emerging fishery species, or possibly a previously undocumented result of increased algal cover.

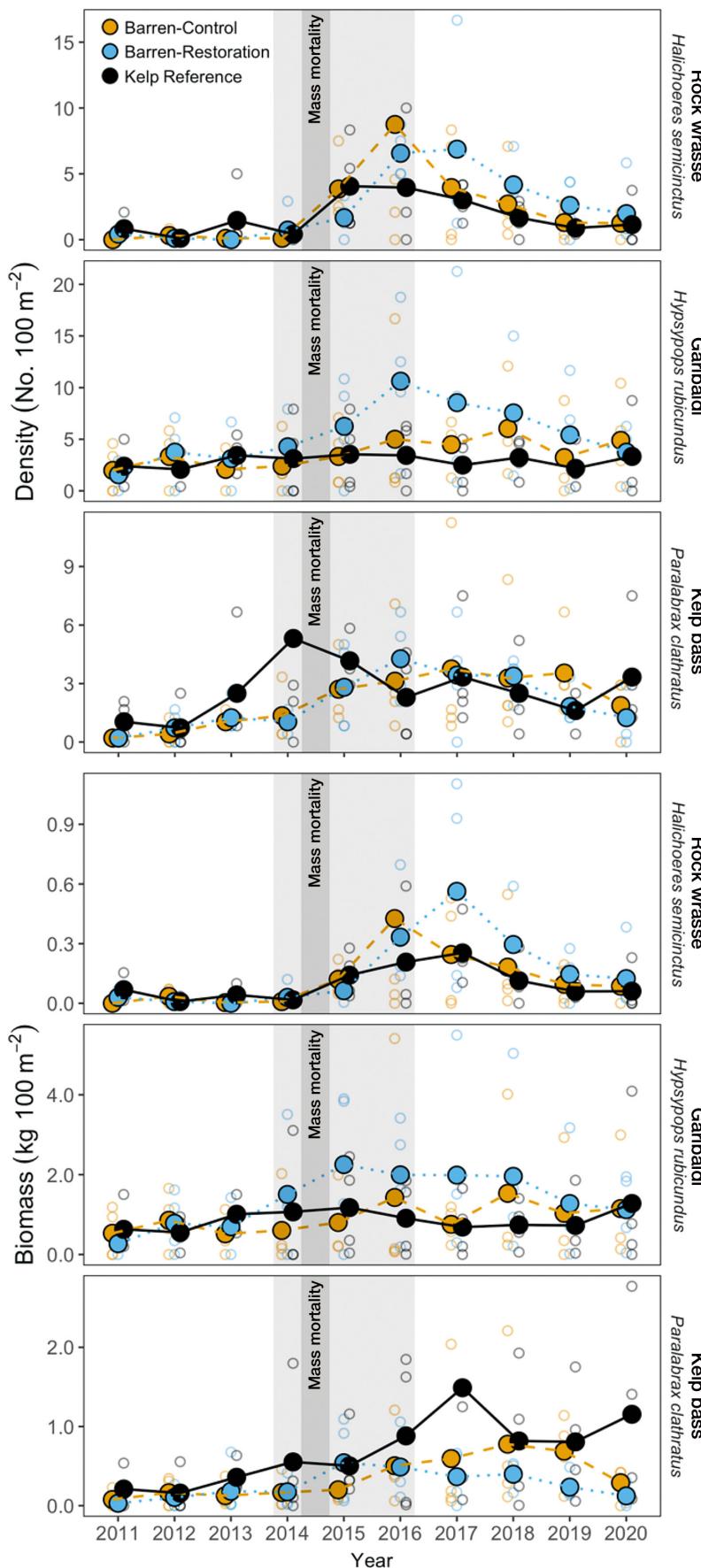
Other taxa increased more inside former Barren sites relative to the Kelp Reference sites, including density of 1 macroinvertebrate (wavy turban snail) and density and biomass 3 fishes (rock wrasse, kelp bass, garibaldi). Given the consistently low densities of wavy turban snails and garibaldi inside Kelp Reference sites throughout time, this may suggest high recruitment and/or survival at these sites in an early successional stage of urchin barrens returning to kelp forests, and these 2 taxa appear to be regressing to the typical kelp forest mean. Garibaldi rapidly increased in density and biomass at Barren-Restoration sites after impact, and this may reflect attraction to feeding on freshly culled urchins (P. House pers.

comm.). Rock wrasse and kelp bass increases were more universal across the ecosystem. Rock wrasse are fish with tropical origins (Adreani & Allen 2008) that likely benefitted from a several-year period of warm-water conditions. Kelp bass increases began prior to the mass mortality event, potentially due to the implementation of marine protected areas in 2012 and more restrictive recreational regulations for this popular game fish in 2013 (Miller & Erisman 2014).

The mean test size of purple sea urchins rarely exceeded 40 mm when densities exceeded  $\sim 3 \text{ m}^{-2}$  across all site types in this study, which is similar to the density ( $3.2 \text{ m}^{-2}$ ) at which Lafferty (2004) noted food scarcity and the emergence of disease epidemics in Channel Islands National Park. Although urchins in low-density areas (e.g. Kelp Reference sites) were also affected by the mass mortality event, this may suggest a crucial density threshold for the health of these urchins. Densities above  $3 \text{ m}^{-2}$ , especially in mature urchin barrens, put sea urchins in a starved state where they are unable to grow or develop gametes (Bishop & Watts 1994, Claisse et al. 2013), and they may shrink in

size to conserve or resorb nutrients and energy (Ebert 1967) leaving them more susceptible to disease transmission (Lafferty 2004). The ability of sea urchins to fight off infection appears to be limited when water temperatures are near the top of their historic range (Gilles & Pearse 1986, Scheibling & Hennigar 1997), and purple sea urchins in particular suffer from abnormal development at higher temperatures ( $>20^\circ\text{C}$ ; Farmanfarmaian & Giese 1963). Due to 'The Blob' and El Niño, the SCB experienced record high sea surface temperatures and sustained low nutrient levels beginning in 2014 (Bond et al. 2015, Jacox et al. 2016, Reed et al. 2016), which likely resulted in further starvation of already starved sea urchins inside urchin barrens and recruitment failure of urchins in kelp forests (Lester et al. 2007).

Causes for sustained urchin barrens can be complicated and cumulative (Graham 2004), and kelp forest restoration likely requires a multi-faceted approach (Claisse et al. 2013). The current approach in the SCB includes indirect management approaches such



as the implementation of marine protected areas to address the loss of top-down control (Hamilton & Caselle 2015, Selden et al. 2017, Eisaguirre et al. 2020) and improvements in water quality (including reducing sedimentation and nutrification) to address the loss of bottom-up control (Foster & Schiel 2010). Culling purple sea urchins from urchin barren reefs to reduce their density can provide a crucial management strategy for shifting persistent urchin barrens on rocky reefs back to a kelp forest state. Further, by not culling red sea urchins and restoring their kelp food source, red sea urchins will produce larger gonads for the commercial fishing industry (Claisse et al. 2013). This has provided motivation for commercial urchin fishermen to become involved in restoration efforts and actively contribute to ecosystem restoration (House et al. 2018). While the mass mortality event removed the sea urchins en masse, the results thus far include rapid recruitment of juvenile kelp to former barrens and resilience over a multiyear period, 2 criteria established for kelp restoration projects (Layton et al. 2020). Kelp forests along the Palos Verdes Peninsula have recovered to the highest aerial coverage in nearly 80 yr (Pondella et al. 2018), several fish species have significantly increased in abundance and biomass throughout the region, red sea urchins in former barrens are increasing in size, and those that remain are producing larger gonads for the fishery (Claisse et al. 2013, House et al. 2018).

If kelp forest restoration through urchin culling can produce similar declines in urchin density to that of a mass mortality event, it may be a viable rocky reef management tool to

Fig. 8. Density and biomass (by year and site type) of fishes impacted by mass mortality and/or restoration events. Other details as in Fig. 5

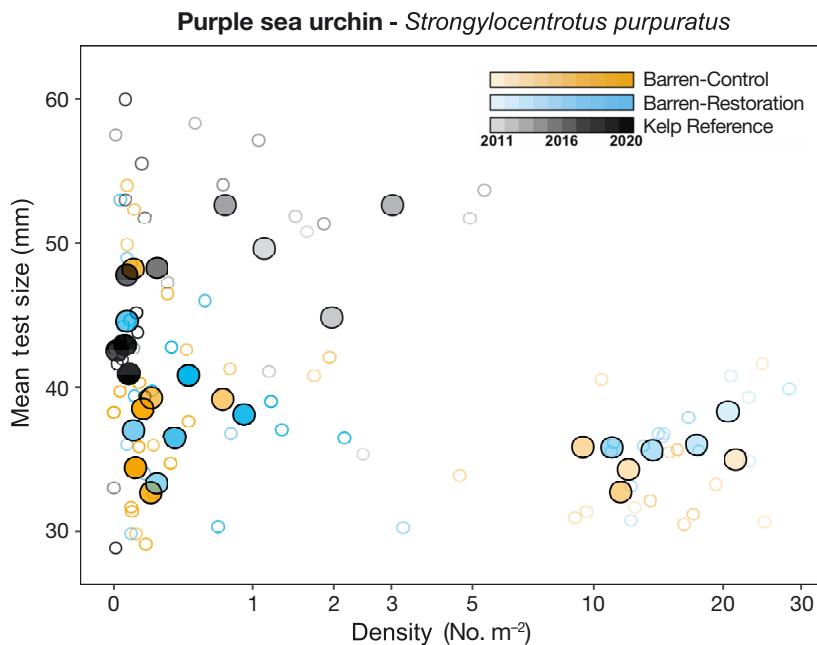


Fig. 9. Mean test size and density (shown on a logarithmic scale) of purple sea urchins. Site type means are indicated by closed circles, individual sites are shown as open circles, and years are indicated by increased opacity of color over time

restore persistent urchin barrens at moderate spatial scales (hundreds of square meters to hectares). At those scales, and especially in conjunction with management efforts that benefit sea urchin predator populations (Hamilton & Caselle 2015, Eisaguirre et al. 2020), this type of restoration can provide long-term ecosystem and fishery benefits. However, given the extreme spatial scale of kelp deforestation and urchin barrens along the coast of northern California and Oregon, USA (>90 % bull kelp canopy reduction along more than 350 km of coastline; Bonaviri et al. 2017, Rogers-Bennett & Catton 2019), an urchin disease mass mortality event like the one documented here may ultimately be a primary driver for re-establishing kelp to those reefs.

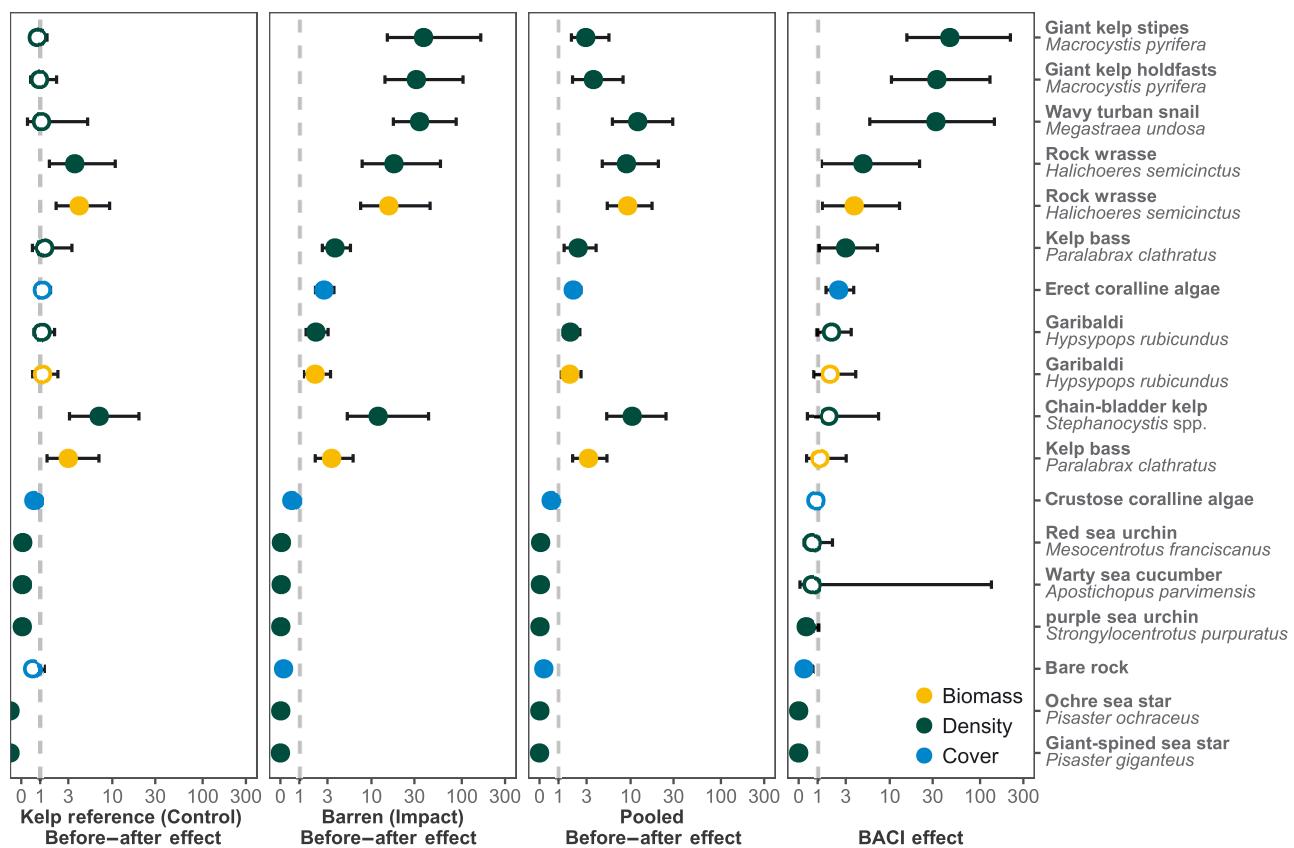


Fig. 10. Mean effect ratios and 95 % confidence intervals for each species examined in the progressive-change multiple before–after control–impact (PCmBACI) analysis. Note: x-axis is log scaled. 'Before–after effect' ratios describe the before–after change in biomass/density/cover at all sites pooled, Barren sites only, and Kelp Reference sites only. Before–After effect ratios >1 (<1) indicate an increase (decrease) following impact. 'BACI effect' describes the ratio of before–after change in biomass/density/cover in urchin barrens relative to the before–after change in the Kelp Reference. BACI effect ratios >1 (<1) indicate a relative increase (decrease) in Barren sites versus Kelp Reference sites following impact. Solid circles indicate significant ( $p < 0.05$ ) step-change impacts after controlling for the false discovery rate (5%); linear models were not selected for any taxa in the PCmBACI procedure

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#### LITERATURE CITED

- Adreani MS, Allen LG (2008) Mating system and reproductive biology of a temperate wrasse, *Halichoeres semicinctus*. *Copeia* 2008:467–475
- Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petran BN, Csaki F (eds) International Symposium on Information Theory. Akademiai Kiado, Budapest, p 267–281
- Baskett ML, Salomon AK (2010) Recruitment facilitation can drive alternative states on temperate reefs. *Ecology* 91: 1763–1773
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc B* 57:289–300
- Bishop CD, Watts SA (1994) Two-stage recovery of gametogenic activity following starvation in *Lytechinus variegatus* Lamarck (Echinodermata: Echinoidea). *J Exp Mar Biol Ecol* 177:27–36
- Bonaviri C, Graham C, Gianguzza P, Shears NT (2017) Warmer temperatures reduce the influence of an important keystone predator. *J Anim Ecol* 86:490–500
- Bond NA, Cronin MF, Freeland H, Mantua N (2015) Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophys Res Lett* 42:3414–3420
- Chapman ARO (1981) Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St Margaret's Bay, Eastern Canada. *Mar Biol* 62: 307–311
- Claisse JT, Williams JP, Ford T, Pondella DJ, Meux B, Protopapadakis L (2013) Kelp forest habitat restoration has the potential to increase sea urchin gonad biomass. *Ecosphere* 4:38
- Dayton PK (1985) Ecology of kelp communities. *Annu Rev Ecol Evol Syst* 16:215–245
- Dean TA, Schroeter SC, Dixon JD (1984) Effects of grazing by two species of sea urchins (*Strongylocentrotus franciscanus* and *Lytechinus anamesus*) on recruitment and survival of two species of kelp (*Macrocystis pyrifera* and *Pterygophora californica*). *Mar Biol* 78: 301–313
- Delroisse J, Van Wayenbergh K, Flammang P, Gillan D and others (2020) Epidemiology of a SKin Ulceration Disease (SKUD) in the sea cucumber *Holothuria scabra* with a review on the SKUDs in Holothuroidea (Echinodermata). *Sci Rep* 10:22150
- Downes BJ, Barmuta LA, Fairweather PG, Faith DP and others (2002) Monitoring ecological impacts: concepts and practice in flowing water. Cambridge University Press, New York, NY
- Ebert TA (1967) Negative growth and longevity in the purple sea urchin *Strongylocentrotus purpuratus* (Stimpson). *Science* 157:557–558
- 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* 101:e02993
- Farmanfarmaian A, Giese AC (1963) Thermal tolerance and acclimation in the western purple sea urchin, *Strongylocentrotus purpuratus*. *Physiol Zool* 36:237–243
- Feehan CJ, Scheibling RE (2014) Effects of sea urchin disease on coastal marine ecosystems. *Mar Biol* 161:1467–1485
- Filbee-Dexter K, Scheibling RE (2014a) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Mar Ecol Prog Ser* 495:1–25
- Filbee-Dexter K, Scheibling RE (2014b) Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin. *Aquat Biol* 23:71–86
- Ford T, Meux B (2010) Giant kelp community restoration in Santa Monica Bay. *Urban Coast* 2:43–46
- Foster MS, Schiel DR (2010) Loss of predators and the collapse of southern California kelp forests (?): alternatives, explanations and generalizations. *J Exp Mar Biol Ecol* 393:59–70
- Gilles KW, Pearse JS (1986) Disease in sea urchins *Strongylocentrotus purpuratus*: experimental infection and bacterial virulence. *Dis Aquat Org* 1:105–114
- Graham MH (2004) Effects of local deforestation on the diversity and structure of southern California giant kelp forest food webs. *Ecosystems* 7:341–357
- Hamilton SL, Caselle JE (2015) Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests. *Proc R Soc B* 282: 20141817
- Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66:1160–1169
- Harvell CD, Montecino-Latorre D, Caldwell JM, Burt JM and others (2019) Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). *Sci Adv* 5:eaau7042
- Hewson I, Button JB, Gudenkauf BM, Miner B and others (2014) Densovirus associated with sea-star wasting disease and mass mortality. *Proc Natl Acad Sci USA* 111: 17278–17283
- House P, Barilotti A, Burdick H, Ford T, Williams J, Williams C, Pondella D (2018) Palos Verdes kelp forest restoration project, Project Year 5: July 2017–June 2018. A report to the Montrose Settlements Restoration Trustee Council Los Angeles CA. The Bay Foundation, Los Angeles, CA
- Jacox MG, Hazen EL, Zaba KD, Rudnick DL, Edwards CA, Moore AM, Bograd SJ (2016) Impacts of the 2015–2016 El Niño on the California Current System: early assessment and comparison to past events. *Geophys Res Lett* 43:7072–7080
- Konar B, Estes JA (2003) The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84: 174–185
- Lafferty KD (2004) Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecol Appl* 14:1566–1573

- Layton C, Coleman MA, Marzinelli EM, Steinberg PD and others (2020) Kelp forest restoration in Australia. *Front Mar Sci* 7:74
- Leleu K, Remy-Zephir B, Grace R, Costello MJ (2012) Mapping habitats in a marine reserve showed how a 30-year trophic cascade altered ecosystem structure. *Biol Conserv* 155:193–201
- Lester SE, Tobin ED, Behrens MD (2007) Disease dynamics and the potential role of thermal stress in the sea urchin, *Strongylocentrotus purpuratus*. *Can J Fish Aquat Sci* 64: 314–323
- Ling SD, Scheibling RE, Rassweiler A, Johnson CR and others (2015) Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philos Trans R Soc B* 370: 20130269
- Miller EF, Erisman B (2014) Long-term trends of southern California's kelp and barred sand bass populations: a fishery-independent assessment. *Calif Coop Ocean Fish Invest Rep* 55:119–127
- Miller RJ, Lafferty DK, Lamy T, Kui L, Rassweiler A, Reed DC (2018) Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. *Proc R Soc B* 285:20172571
- Nichols KD, Segui L, Hovel KA (2015) Effects of predators on sea urchin density and habitat use in a southern California kelp forest. *Mar Biol* 162:1227–1237
- Norderhaug KM, Christie HC (2009) Sea urchin grazing and kelp re-vegetation in the NE Atlantic. *Mar Biol Res* 5: 515–528
- North WJ, Pearse JS (1970) Sea urchin population explosion in southern California coastal waters. *Science* 167:209
- Oksanen J, Blanchet FG, Friendly M, Kindt R and others (2019) vegan: Community Ecology Package. R package version, 2.5-3. <https://cran.r-project.org/package=vegan>
- Pearse JS, Hines AH (1979) Expansion of a central California kelp forest following the mass mortality of sea urchins. *Mar Biol* 51:83–91
- Pearse JS, Costa DP, Yellin MB, Agegian CR (1977) Localized mass mortality of red sea urchin, *Strongylocentrotus franciscanus* near Santa Cruz, California. *Fish Bull* 75: 645–648
- Pondella DJ II, Williams JP, Williams CM, Claisse JT, Witting D (2018) Restoring a nearshore rocky reef ecosystem in the challenge of an urban setting. *Am Fish Soc Symp* 86:165–186
- Pondella DJ II, Piacenza SE, Claisse JT, Williams CM, Williams JP, Zellmer AJ, Caselle JE (2019) Assessing drivers of rocky reef fish biomass density from the Southern California Bight. *Mar Ecol Prog Ser* 628:125–140
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. [www.r-project.org](http://www.r-project.org)
- Reed D, Washburn L, Rassweiler A, Miller R, Bell T, Harrer S (2016) Extreme warming challenges sentinel status of kelp forests as indicators of climate change. *Nat Commun* 7:13757
- Rogers-Bennett L, Catton CA (2019) Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. *Sci Rep* 9:15050
- Salomon AK, Gaichas SK, Shears NT, Smith JE, Madin EMP, Gaines SD (2010) Key features and context-dependence of fishery-induced trophic cascades. *Conserv Biol* 24: 382–394
- Scheibling R (1986) Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. *Oecologia* 68:186–198
- Scheibling RE, Hennigar AW (1997) Recurrent outbreaks of disease in sea urchins *Strongylocentrotus droebachiensis* in Nova Scotia: evidence for a link with large-scale meteorologic and oceanographic events. *Mar Ecol Prog Ser* 152:155–165
- Schultz JA, Cloutier RN, Côté IM (2016) Evidence for a trophic cascade on rocky reefs following sea star mass mortality in British Columbia. *PeerJ* 4:e1980
- Selden RL, Gaines SD, Hamilton SL, Warner RR (2017) Protection of large predators in a marine reserve alters size-dependent prey mortality. *Proc R Soc B* 284:20161936
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459
- Stewart NL, Konar B (2012) Kelp forests versus urchin barrens: alternate stable states and their effect on sea otter prey quality in the Aleutian Islands. *J Mar Biol* 2012: 492308
- Stull JK, Dryden KA, Gregory PA (1987) A historical review of fisheries statistics and environmental and societal influences off the Palos Verdes Peninsula, California. *Calif Coop Ocean Fish Invest Rep* 28:135–154
- Teck SJ, Lorda J, Shears NT, Ben-Horin T and others (2018) Quality of a fished resource: assessing spatial and temporal dynamics. *PLOS ONE* 13:e0196864
- Tegner MJ (1980) Multispecies considerations of resource management in southern California kelp beds. *Can J Fish Aquat Sci* 954:125–143
- Thiault L, Kernalégouen L, Osenberg CW, Claudet J (2017) Progressive-Change BACIPS: a flexible approach for environmental impact assessment. *Methods Ecol Evol* 8: 288–296
- Walters CJ, Collie JS, Webb T (1988) Experimental designs for estimating transient responses to management disturbances. *Can J Fish Aquat Sci* 45:530–538
- Williams CM, Williams JP, Claisse JT, Pondella DJ II, Domeier ML, Zahn LA (2013) Morphometric relationships of marine fishes common to central California and the Southern California Bight. *Bull South Calif Acad Sci* 112:217–227
- Wilson KC, North WJ (1983) A review of kelp bed management in southern California. *J World Maricult Soc* 14: 347–359
- Zahn LA, Claisse JT, Williams JP, Williams CM, Pondella DJ II (2016) The biogeography and community structure of kelp forest macroinvertebrates. *Mar Ecol* 37:770–785

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