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FORUM

Abalone recruitment patterns before and after sea urchin barrens formation in northern California: incorporating climate change

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ABSTRACT
Understanding the recruitment dynamics of invertebrates in kelp forests is critical to informing climate-ready restoration. Here we examine abalone and sea urchin recruitment (3–20 mm in size) patterns in northern California across a period of drastic change. Annual surveys were conducted before, during and after the MHW (2014–2016), the loss of a major predatory sea star (2012–2016) and the collapse of a bull kelp forest in 2014. Divers surveyed artificial reef recruitment modules (n = 12) over 20 years in an area that once supported dense bull kelp, *Nereocystis leutkeana*, forests and the world's largest recreational abalone fishery. From 2016 to 2022, we tracked the decline of red abalone, *Haliotis rufescens*, recruitment and the rise of purple sea urchin, *Strongylocentrotus purpuratus*, recruitment. Adult densities of purple sea urchins increased as did newly settled sea urchins (<3 mm), while adult and newly settled red abalone declined. Eight years after the kelp forest collapse, red abalone recruitment remained low and sea urchin recruitment continued to increase. Recruitment patterns can inform both abalone restoration targets and sea urchin dynamics as part of a more holistic kelp forest recovery plan that is responsive to climate change drivers.

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Introduction

Catastrophic regime shifts or transitions from kelp forest to a sea urchin barren state (Pearse et al. 1970; Lawrence 1975; Rogers-Bennett 2006) can have dramatic impacts on productivity, settlement and recruitment. Sea urchin populations can increase greatly and suddenly (Ling et al. 2009, 2015; Johnson et al. 2011; Wernberg et al. 2016) and have long recovery times, known as 'the hysteresis effect' (Scheffer et al. 2001). The persistence of these alternative states beyond a generation time can then be referred to as a stable states (Connell and Sousa 1983) with negative impacts cascading through the ecosystem (Rogers-Bennett and Catton 2022). Ocean warming may facilitate sea urchin population increases and range extensions (Johnson et al. 2011), negatively

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affecting kelps directly via thermal stress and through sea urchin-mediated herbivory. Quantitative monitoring of invertebrate recruitment and settlement before and after kelp forest transitions may help to identify the mechanism responsible for switches (tipping points) to alternative states (Schröder et al. 2005) with diminished biodiversity and ecosystem services (Filbee-Dexter and Scheibling 2014; Rogers-Bennett and Catton 2019). The transition from kelp forest to sea urchin barrens has been an active field of research for more than 100 years since the Japanese coined the term 'Isoyake' for sea urchin barrens (Fujita 1998) found in many parts of the world including California (North 1971; Rogers-Bennett 2007).

Knowledge of the population dynamics of sea urchins can help elucidate the mechanisms behind such transitions. Northern California is an example of a region which has rapidly and radically transitioned from a relatively stable kelp forest to domination by sea urchins (Rogers-Bennett and Catton 2019; McPherson et al. 2021). This demise of bull kelp forests led to mass abalone mortalities, increased vulnerabilities to anthropogenic and environmental stressors (Rogers-Bennett and Catton 2022) and reduced primary productivity (Rogers-Bennett et al. 2021). As a result, the decline of the red abalone stock in northern California and southern Oregon (Rogers-Bennett and Catton 2022) led to the state of California's and Oregon's Fish and Game Commission's closure of the socio-economically valuable fishery. The recreational fishery in northern California was valued at >$44 M per year (Reid et al. 2016) and then closed in 2018.

Surveys eight years after the collapse of the kelp forest show that sea urchin barrens continue to dominate the north coast region. To better understand the transition to sea urchin barrens, researchers have been investigating the abundance of drift kelp (detrital kelp) as well as the abundance of herbivores (Rennick et al. 2022). In some cases, herbivore abundances changed little yet destructive grazing occurs while in other cases herbivore numbers rise sharply to reach outbreak conditions (Klemmer et al. 2012; Kautz et al. 2016). In some cases, trophic cascades mediated by predatory fishes and sea stars can also control sea urchin foraging, particularly in local kelp-rich patches where sea urchins are high in calories (Rogers-Bennett 2007; Smith et al. 2021). Clearly, the human management response to barrens conditions could differ depending on the mechanism of action responsible for the shift. Therefore, there is a need to explore if changes in kelp or herbivores or predator abundance or some combination has resulted in kelp deforestation. In northern California, temporal patterns of juvenile sea urchin abundance can be used to examine the strength of future year classes entering the population to inform kelp forest restoration efforts in the region.

Recruitment of sea urchins and abalone (3–20 mm) is, however, difficult to measure because they reside on complex rocky reefs and are small and cryptic (McShane and Smith 1988; Sasaki and Shepherd 1995), making them challenging to find without destructive sampling of the natural reef. With advances in methods, the number of recruitment studies for abalone (McShane and Smith 1991; Sasaki and Shepherd 2001; Bouma et al. 2012; Rogers-Bennett et al. 2016; Hart et al. 2020; Estrada et al. 2021) and sea urchins (Rowley 1990; Ebert et al. 1994; McNaught 1999; Norderhaug and Christie 2013; Carson and Ulrich 2019) have increased. Pinto abalone, *Haliotis kamtschatkana*, are listed as a 'species of concern' in the United States, (Species of Concern 79 FR 77998) and endangered on the international red list (https://www.iucnredlist.org/); while flat, *H. walallensis*, and red abalone, *H. rufescens*, are internationally listed as critically endangered. In contrast, pinto abalone in Canada have been shown to have had robust recruitment in modules placed in southern (Defreitas 2003) and northern British Columbia (Okamoto, unpublished data). Recruitment modules in southern California, have been used to show temporal patterns, with warm-water years favouring recruitment of green abalone (*H. fulgens*) and Coronado sea urchins (*Centrostephanus coronatus*), while cold-water species did not do as well (Kawana et al. 2019).

Here, we examine settlement, juvenile recruitment and adult density patterns of red abalone and sea urchins before, during and after the marine heatwave (MHW) which precipitated the collapse of the bull kelp forest in 2014 and the subsequent rise in purple sea urchins, using a 20-year time series (2001–2022) in northern California. Recruitment modules were placed in a highly productive red abalone site, Van Damme in Mendocino County, northern California with seasonally abundant *Nereocystis luetkeana* (bull kelp) canopy cover, and a subcanopy of the stipitate kelp *Pterogophora californica* and numerous subtidal red algae, including upright and encrusting corallines. Annual settlement was investigated by quantifying the number and sizes of newly settled (260 um-3 mm) abalone and sea urchins on natural coralline-covered cobbles. The numbers of juvenile red abalone and purple sea urchins (4–20 mm) were assessed inside recruitment modules with 2.6 m^2 of cryptic area and adult abalone and sea urchin densities were determined along transects (30 × 2 m). The time series encompassed two periods; (1) years with extensive bull kelp forest (2001–2013) and (2) years dominated by sea urchin barrens (2015–2022; no data 2020–2021) (Rogers-Bennett and Catton 2019). We discuss the shift observed from high densities of abalone when the bull kelp canopy was abundant to the dramatic increases in sea urchin densities, which occurred in the years after the MHW when the bull kelp collapsed in 2014. We explore baseline levels of abalone and sea urchin recruitment when the bull kelp forest was robust to inform conservation goals for kelp forests in northern California and worldwide.

Materials and methods

In this study, we examine red abalone, purple and red sea urchins at Van Damme State Park in Mendocino County, northern California. We examine three life history classes: newly settled 280 um to 3 mm, juveniles from 3 to 20 mm and subadults and adults >21 mm.

Sea urchin settlement

Annual settlement was investigated by counting and measuring newly settled (260 μm-3 mm) sea urchins on natural crustose coralline algae (CCA) on benthic cobbles. Selected cobbles were collected and ranged in size from 5 to 30 cm in length. Cobbles were collected from depths ranging from 2 to 20 m (for more methods information see Rogers-Bennett et al. 2016). Divers searched each area for the cobbles of the appropriate size with the highest per cent of CCA and placed them carefully in large zip locked plastic bags. Once on the deck of the boat cobbles were kept in cold seawater and processed in <3 h to search for newly settled abalone and sea urchins. For each cobble, the depth, cobble greatest diameter, width and height as well as per cent cover of CCA were recorded. Approximately, 80 cobbles were sampled from Van Damme State Park in August of each year from 2007 to 2022 (excluding 2020 and 2021 due to COVID-19 restrictions in sampling). Sea urchins were removed from the cobbles by placing each cobble individually in buckets in seawater with 5% ethanol and allowing the ethanol to anaesthetise the sea urchins for 10 min. Cobbles were gently and thoroughly brushed in the seawater using soft dish brushes sweeping from the top to the bottom of each cobble across each surface. The sea urchins were collected on a 150 µm mesh sieve, rinsed into a sample jar, and fixed in 90% ethanol. Samples were later examined microscopically in a lab, counted by species/taxa and measured with an ocular micrometer.

Recruitment modules

Larger juvenile abalone and sea urchins, ranging from 3 to 20 mm, were examined inside recruitment modules (RMs) bolted onto rocky subtidal reefs. These RMs provided a standard surface area and were deployed at Van Damme State Park (VDSP) (lat. $39^0$16’08”N, long. $123^0$47’58”W), a site which is about 3 miles of coastline in northern California in August 2000. RMs were made of stainless steel cages filled with concrete cinder blocks cut lengthwise resembling the letter M (rectangles measuring 813 mm x 610 mm x 305 mm high) and stacked three blocks tall (Davis 1995). Each RM had a surface area of approximately 4.8 m^2, of which 2.6 m^2 was a sheltered area created by the sides, top and bottom of each M-shape. Twelve RMs were deployed between 10 and 12 m depth in three groups of four. The modules were placed 3–6 m apart within the cluster of four. The northern cluster was approximately 140 m from the central cluster, and the southern cluster was 710 m from the central cluster. Each RM was bolted to the reef with five stainless lag bolts6 inches in length in each of the four corners and one in the centre of the module. Surveys involved one dive team for each RM, opening the lid and carefully removing each block, then counting and measuring abalone and sea urchins inside the RMs. Abalone and sea urchins outside the RMs were not sampled. If abalone and sea urchins within RMs were too abundant to count reliably in the underwater, they were gently swept into fine mesh bags (2 mm) to be counted and measured back on the boat. After sampling, each block was set to the side while the next block was removed. When a survey was completed, divers re-assembled each RM and secured its lid with cable ties. Each RM took two divers approximately 40–50 min to survey.

RMs were deployed and left to season for one year before the first surveys began in August 2001. In August each year thereafter RMs were surveyed and any cinder blocks that were missing were replaced. In 2014, 6 of the 12 RM modules were replaced with new steel cages, and in 2015 the remaining six steel cages were replaced. In each case, the existing bricks were re-used in the same module. In some years fewer than 12 RM were surveyed due to older RM cages being damaged by winter storms. The numbers of urchins and abalone are reported per module, for each year. RM surveys were conducted every year starting in 2001 with the exception of 2020 and 2021 due to COVID-19 constraints on field work.

Density of subadult and adult abalone and sea urchins

The density of adult red abalone, *Haliotis rufescens*, (>80 mm in shell length) and both purple (*Strongylocentrotus purpuratus*) and red (*Mesocentrotus franciscanus*) sea urchins (>50 mm test diameter) were collected from subtidal surveys at Van Damme State Park periodically from 1999 to 2022 as part of the Kelp Forest Monitoring

Program of the California Department of Fish and Wildlife and UC Davis, Bodega Marine Lab. Surveys at Van Damme were located on rocky reef kelp forest habitat. Prior to the decline of kelp (in 2014) at least 30 transects were sampled overall. After 2014, surveys were reduced to at least 12 transects per site. In all cases, transects were evenly distributed among the depth strata. Each transect was 30 m x 2 m (60 m^2) and were located within each of four depth strata: 1–5 m, 6–10 m, 11–15 m, and 16–20 m. Abalone and urchins were quantified along each transect. Most subadult and adult abalone and sea urchin surveys at Van Damme were conducted in August but surveys at this site were not conducted every year (with 11 years sampled out of 22 years).

Statistical analyses

To estimate whether densities (e.g. recruitment into RMS or benthic density of adults) for each species differed in the years leading up to versus following the MHW, we used a Bayesian negative binomial generalised linear mixed model with a log-link. Specifically, we estimated the proportional change in density from before to after the MHW (2014) for each analyses as well as the posterior probability of an increase or decrease. Because our goal was to estimate before/after trends rather than effects that may result from contributions from individual years, we accounted for variation among years by treating year as a random effect. Because each recruitment module (RM in the case of recruitment) or stratum (in the case of adult densities) was surveyed repeatedly over time this also accounted for potential variation including RM or stratum as a random effect for recruitment and adult analyses, respectively. Because some years included singular observations, we included an informative prior for the dispersion term (folded normal with mean of zero and standard deviation of .01). For all other parameters we included vague priors (wide variance relative to the scales of inference – folded student-t with 3 degrees of freedom and standard deviation of 3) for intercepts and before/after effects on the log-scale. Changes in scales and shape of these priors had no qualitative impact on results (e.g. expanding sd or formulating as student-t with longer tail, for example).

Temperature

Temperature loggers (n = 3) were used to track subtidal seawater temperatures in the rocky reef habitat at VDSP. Hobo® loggers made by Onset were set at 10 m depth to record temperature once hourly from August 2001–2022. Loggers were wrapped in electrical tape and placed inside plastic housings to minimise fouling. Loggers were affixed outside of one stainless steel RM at each site (north, central and south) and were downloaded and changed on subsequent surveys in August of each year. Loggers failed from August 2004 to October 2005. Temperature data are used to detect the magnitude, frequency and duration of temperatures exceeding 12 °C. This temperature is an important metric for bull kelp growth, signalling a transition to decreases in NO_3 concentrations (García-Reyes et al. 2014).

Kelp time series

Landsat satellite imagery was used to track changes in the extent of bull kelp canopy (Bell et al. 2022 Bell et al. 2023, Kelpwatch.org) from 2001 to 2022 at Van Damme State Park. We use only the data from Van Damme. Kelp data used atmospherically corrected 30 m resolution multispectral imagery from five Landsat sensors: Landsat 4, 5, 7, 8 and 9. Data are averaged per season and we show the peak season for kelp in northern California (Q3: July, Aug. and September) during which benthic surveys were conducted. For each frame, if bull kelp occurred in a 30 m x 30 m pixel, the multiple endmember spectral mixture analysis (MESMA, Roberts et al. 1998) was used to estimate the fraction of that pixel covered by kelp canopy. MESMA estimates the fractional cover of two or more 'endmembers' within a pixel. To obtain estimates of canopy area, the canopy fraction of each pixel was then multiplied by the pixel area (~ 900 m^2). Data shown are in hectares of bull kelp canopy cover. The methods used to transform these data into seasonal measurements of canopy area are described (see Bell et al. 2020 for more details on methods and Hamilton et al. 2020 for more details on application of methods to bull kelp).

Results

Recruitment of juvenile sea urchins

Following the collapse of the kelp forest in northern California, there was a shift in the number of juvenile abalone and sea urchins. There was a decline in the abundance of juvenile red abalone in 2016 comparing the early portion of the time series with the later portion of the time series (Figure 1A). There was initially high variability between years for red abalone recruitment but over a 15 year period before the MHW there were only three years of poor recruitment. After the MHW, we see that every year had poor recruitment (no data 2020 and 2021). Specifically, there was a significant decline in density following the MHW (2015 onward) compared to the prior 15 years. Using before-after comparison of the negative binomial General Linear Mixed Model (GLMM), we estimate a high posterior probability ($P = 98.4\%$) of a decrease post vs pre MHW. This decline in recruitment in 2015 onward is estimated to be, on average, 32% of the recruitment prior to the collapse (95% uncertainty interval: 13–98%). This decline is illustrated by the fact that recruitment of juvenile red abalone (<21 mm) dropped below 0.28 per module which is 20th percentile of our time series from 2001 to 2015 prior to the collapse of the kelp forest.

In contrast to juvenile red abalone, an examination of coralline-covered cobbles from the site showed newly settled sea urchins (<3 mm) were rare earlier in the samples (2007–2014) and then high in abundance in the most recent years from 2015 to 2022 (Figure 1B). We did not distinguish between red and purple sea urchins in these samples as this can be subjective at this early life history stage; despite red sea urchins frequently having more prominent pedicellaria. The smallest sea urchins found in the samples came from the recent two years, 2018 and 2022 indicating recruitment is ongoing (Figure 1B). Previous work has shown that newly settled abalone were rare in the samples after 2015 when sea urchins are abundant in the samples (Rogers-Bennett and Catton 2022).

Similarly, to newly settled sea urchins, there was a significant *increase* in the numbers of juvenile purple and red sea urchins from 2014 onwards (Figure 1C,D). Before-after comparison using the negative binomial GLMM yields a high posterior probability (>99%) of an increase in 2014 onward relative to the prior period for both species.

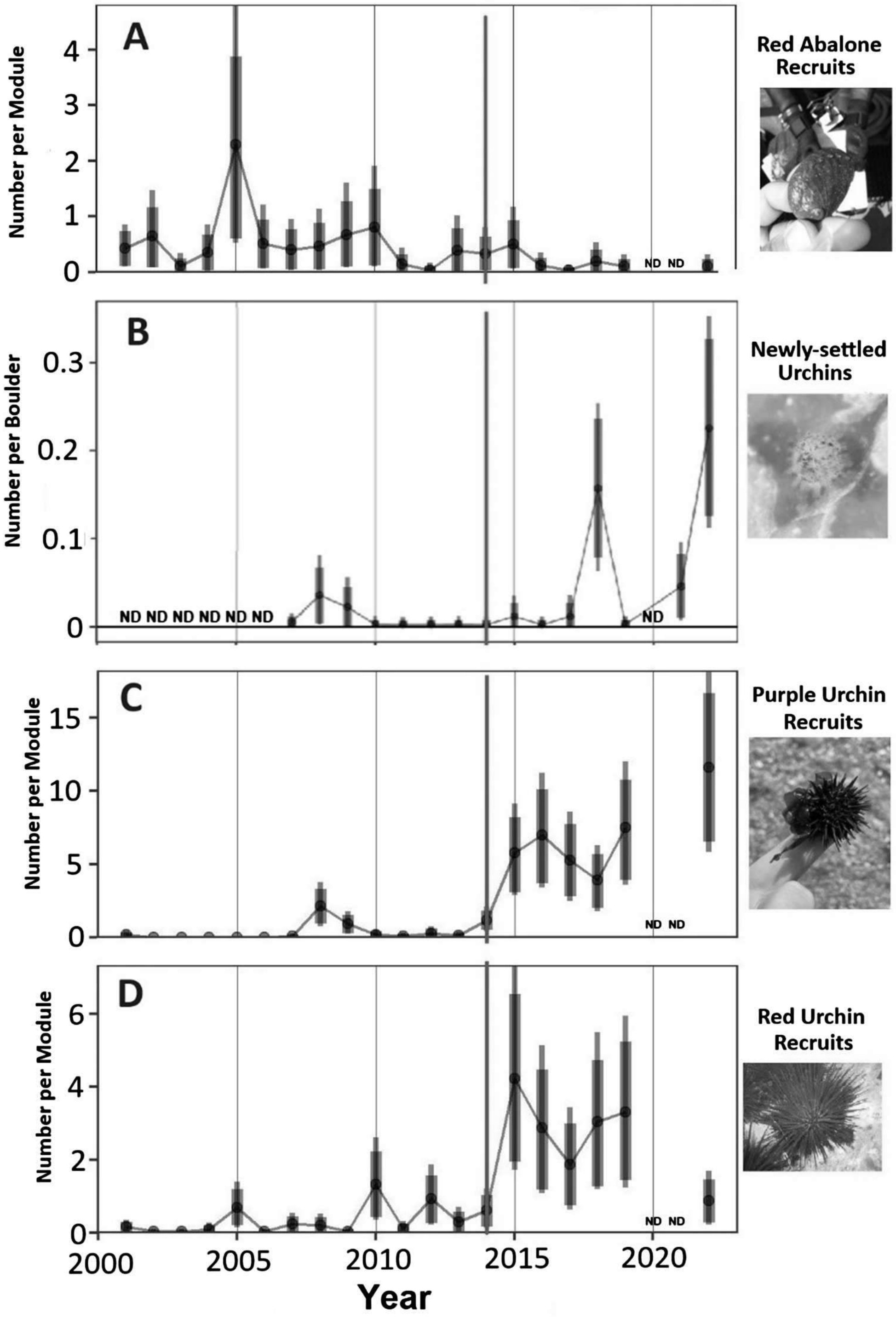

Figure 1. Recruitment of young of the year (<21 mm) red abalone (*Haliotis rufescens*), newly settled sea urchins of purple (*Strongylocentrotus purpuratus*) or red sea urchins (*Mesocentrotus franciscanus*) (<3 mm) and purple and red sea urchins mean in recruitment modules with 90% and 95% confidence intervals before and after kelp forest collapse in 2014 (vertical red line). Photo credits: red abalone (A. Maguire), newly settled sea urchin (S. Karlitz), juvenile purple sea urchin (L. Rogers-Bennett) and juvenile red sea urchin (L. Rogers-Bennett).

On average, juvenile purple sea urchin recruitment after 2014 was over 39 times the recruitment prior to 2014 (95% uncertainty interval: 11.4- 153 x increase). Juvenile purple sea urchin (<21 mm) abundances increased after the start of the warm water in 2014. Prior to 2014, purple sea urchin juveniles never exceeded three juveniles per module. In 2015, there were 5.8 juvenile purple sea urchins per module, far more than had ever been recorded in the previous 15 years (Figure 1C). Like juvenile purple urchins, densities of juvenile red sea urchins increased during and immediately after the marine heatwave (2015–2019) (Figure 1D). Specifically, recruitment densities increased substantially as estimated under the negative binomial GLMM. We estimate that, on average, red sea urchin recruitment after the kelp forest collapse was over nine times the recruitment before 2014 (an estimated increase of 1.7–58.4% at a 95% HPD uncertainty level, >99% posterior probability of an increase post vs pre heatwave).

Densities of subadult and adult abalone and sea urchins

In the years prior to the collapse in kelp, adult and adult red abalone were abundant on transects at densities of more than 0.47 red abalone per m^2 (Figure 2). We see that densities of red abalone declined in the years after 2016 and most recently in 2022 were at their lowest density of 0.05 red abalone per m^2 with continuing observations of fresh shells suggesting mortality remains high (L. Rogers-Bennett pers. comm.). On average, red abalone transect densities after 2014 were 20%of densities prior to 2014 (95% uncertainty interval: 9%—46%, >99% posterior probability of a decline pre vs post heatwave). Meanwhile, subadult and adult purple urchin numbers increased more than 41 times (95% uncertainty level 16.7–96.2 x, >99% posterior probability of an increase pre vs post heatwave) from a maximum of 7.7 purple urchin per m^2 pre-2016 to a maximum of >43 purple urchin per m^2 after 2016. The increase in purple sea urchins occurs in 2015 in shallow habitats. Van Damme had not experienced purple sea urchin densities >4.3 per m^2 prior to 2013 and then they jumped to >39 per m^2 in 2016. This past year, in 2022, has been the highest densities for adult purple sea urchins ever recorded in the region at a maximum of 43.2 per m^2.

In the early years of the time series when kelp was abundant, adult purple sea urchins were more abundant in the deeper depths 10–20 m as compared with the shallow depths <10 m. In 2013, the maximum density of purple sea urchins in the deep stratum was 2.3 per m^2 while in the shallows it was 1.1 per m^2. In the period following the loss of the kelp, from 2016 to 2022, the patterns reversed with the maximum observed density for purple sea urchins reaching an average of >50 m^2 at 5 m (15 feet) depth and 25 m^2 at 15 m (45 feet) depth. In contrast to purple urchins (increase) or abalone (decrease), there did not appear to be a dramatic or significant change in adult red sea urchin densities over the time series.

Purple sea urchin dynamics

To examine the dynamics of the increases in purple sea urchins, we quantified abundances and densities of different life history stages of purple sea urchins over time. Adult purple sea urchins increased in 2015 a year following the start of the MHW and the decline in kelp (Figure 2). At the same time, juvenile purple sea urchin

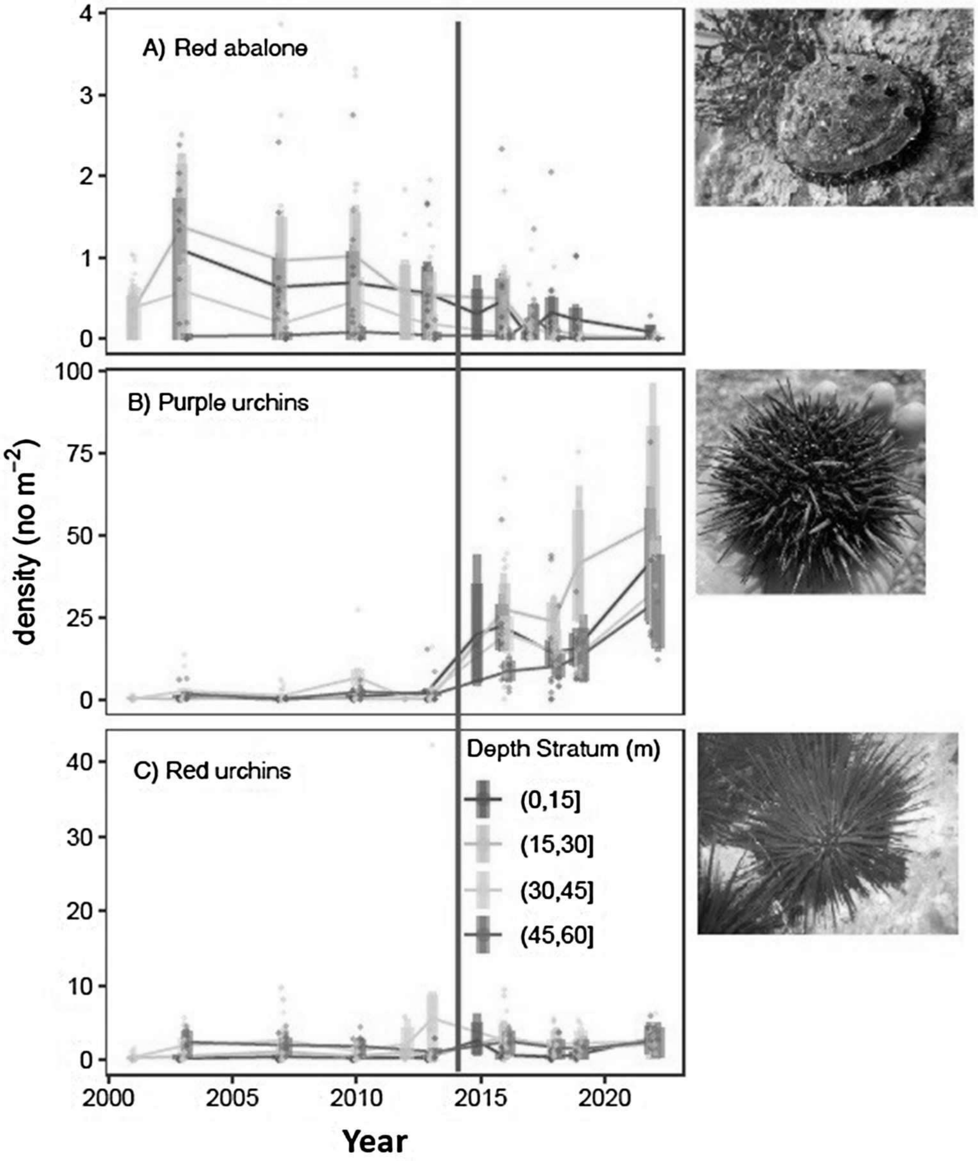

Figure 2. Densities of adult red abalone, red sea urchins and purple sea urchins found along transects at four depth strata (1–5 m, 5–10 m, 10–15 m and 15–20 m) prior to and after the kelp forest collapse (2014 – red vertical line). Purple urchin plot includes 90% and 95% confidence intervals. Only shallow depths were surveyed for purple sea urchins in 2015.

recruitment (<21 mm) began to increase (Figure 1C). We see a large increase in newly settled sea urchins (<3 mm) in the coralline covered in 2018 after the MHW has subsided (Figure 1B). During the marine heatwave years only juveniles and adult purple sea urchins increased in abundance while newly settled purple sea urchins did not in these samples. Since then all three life history stages of purple sea urchins have increased dramatically and have remained high despite the lack of kelp and other algal species (from 2015 to 2022) (Figures 1BC and 2B). During the latest sampling year in 2022, juvenile purple sea urchins were the highest in the time series. The last year 2022, was also the highest for newly settled and adult purple sea urchins indicating the increase in purple sea urchins is continuing.

Kelp and temperature dynamics at Van Damme

The warmest year 2014 with peak water temperatures in September (Figure 3) was the first year of the loss of bull kelp that has thus far persisted for a decade. Peaks in kelp abundance at Van Damme occurred in 2008 and again 2013 however we saw no relationship with red abalone recruitment and kelp (Figure 4). Over the past decade, 2021 had cold water temperatures (Figure 3) and was a year when kelp should have been abundant the following summer, but there was only a very small increase because herbivory remained intense with high densities of sea urchins (Figure 2BC).

Discussion

Changes in abalone and sea urchin recruitment patterns

The transition in the ecosystem from kelp forest to sea urchin barrens was mirrored by a shift from red abalone to sea urchin recruitment to the recruitment modules. We see that following the collapse of the kelp forest and the rise of sea urchin barrens in northern California, the number of juvenile abalone declined while the juvenile purple sea urchins rose to very high levels at Van Damme (Figure 1). In northern California at Van Damme, we see in 2015 the marked increase in adult purple sea urchins and these high densities have persisted (Figure 2B) despite the lack of kelp and other algal species. Meanwhile, the density of adult red sea urchins appears to have remained fairly stable over time (Figure 2C).

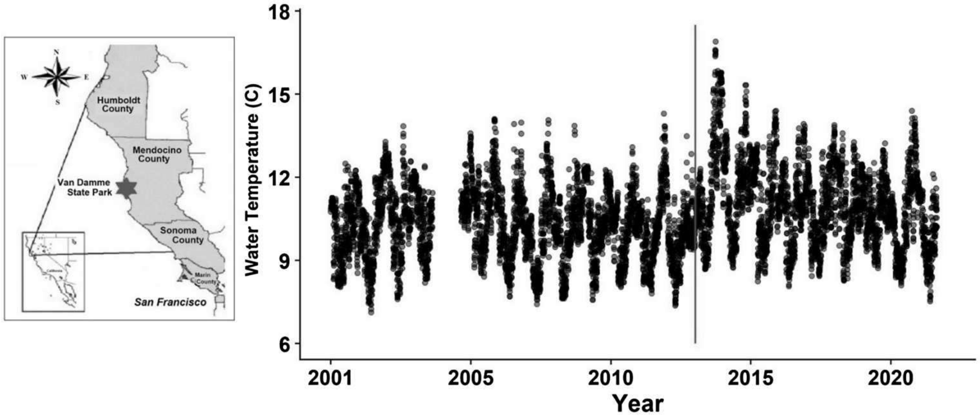

Figure 3. Seawater temperature time series (2001–2022) collected from Hobo® temperature loggers set at 10 m depth on rocky reef in Van Damme State Park, Mendocino County, CA. The highest temperatures occurred between September 20 and 26, 2014. Dots are daily averages. The red vertical line is set at the year 2014 when the kelp forest collapsed.

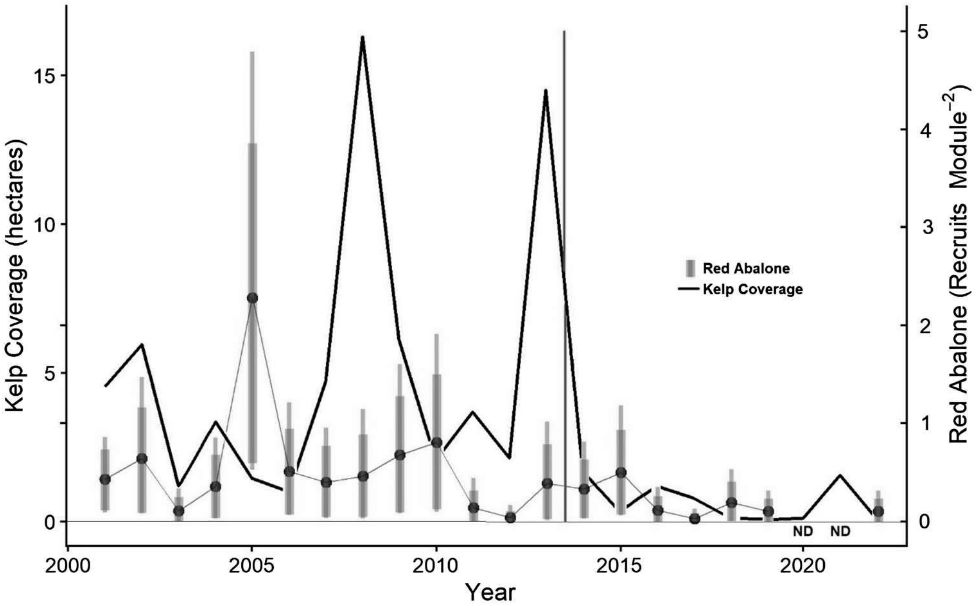

Figure 4. Surface kelp coverage (hectares) (black line) at Van Damme State Park and juvenile red abalone recruitment (mean #/module) (black dots) with 90% and 95% confidence intervals (purple bars) from 2001 to 2022. The red vertical line is set at 2014, when the kelp forest collapsed.

In some regions, the presence of adult sea urchins and their spine canopy can benefit abalone recruitment (Tegner and Dayton 1977; Day and Branch 2000; Rogers-Bennett and Pearse 2001) but we show this is not the case when sea urchin densities are extremely high or if the morphology of the dominant sea urchin species (purple sea urchins) have short spines limiting the spine canopy area.

There was no pattern of higher abalone recruitment (<21 mm) in years with more kelp (NS. $r^2 = 0.004$) nor in the following year (Figure 4) suggesting variables other than local bull kelp canopy abundance, may be more important for abalone reproduction and recruitment. This may be the result of adult red abalone eating subcanopy of brown algae or benthic red algae which prior to 2015 were all abundant even in years when the surface canopy was not. The number of newly settled abalone and larval abalone was variable prior to the collapse of the kelp forest (2007–2013) but during and after the marine heatwave (2014–2018) newly settled and larval abalones were almost absent at Van Damme (Rogers-Bennett and Catton 2022). In the Monterey area in central California, newly settled abalones were found consistently over a 5-year period with the exception of 2015 during the peak of the marine heatwave (Hart et al. 2020).

Dynamics of sea urchin barrens formation

The formation of sea urchin barrens in the north coastal region began in 2015 with an increase in juveniles, and adult purple sea urchins. In our previous work, we also examined the settlement of sea urchins (<3 mm) in northern California at a nearby site and found a peak in purple sea urchins settlement in 2015 during the MHW (Okamoto et al. 2020). This pattern of sea urchin settlement (Okamoto et al. 2020) closely mimics that of the juvenile data in the recruitment modules (RM) reported on here. This may be that in the north, the MHW was not warm enough to produce thermal stress suppressing sea urchin gonad development and spawning as has been shown in laboratory experiments at warm temperatures (in excess of those found in the field) (Okamoto et al. 2023). We suggest that it is still unknown how adult purple sea urchin densities increased so rapidly since there did not appear to be large reserves of adults in the deeper water or in crevice habitat in this region as has been suggested as a possible mechanism for areas in Monterey (Smith et al. 2021; Smith and Tinker 2022).

This could be interpreted as multiple factors operating at the same time during the MHW. There could have been some movement of sub adult and adult sea urchins into shallow habitats (<20 m) at the same time as an increase in the survival of newly settled sea urchins to the juvenile stage. This could have been coupled with an increase in spawning and newly settled sea urchins as detected by Okamoto et al. (2020). In this sampling of the cobbles we did not see an increase in newly settled sea urchins on the until a few years later in 2018 (Figure 1B). It is possible that purple sea urchins benefited from the MHW by increases in survival during the early life history stages along with reduced predation. Many small predators (both small adults and juveniles of larger bodied invertebrates) may have been killed during the MHW. An important large predator, the sunflower star, has been missing from the system for many years starting prior to the MHW (McPherson et al. 2021).

Given that sea urchins are free-spawning organisms, high densities of individuals in close proximity to one another can lead to enhanced fertilisation success which could lead to massive recruitment events (Pennington 1985; Levitan et al. 1992). High densities of purple sea urchins are now spreading south into central California (K. Rootsaert pers. comm.) and north into southern Oregon (Galloway et al. 2023). In contrast, in central California, the behaviour of the sea urchins initially was thought to be precipitated by the movement and feeding of existing adults rather than a major recruitment event (Smith et al. 2021; Smith and Tinker 2022).

Even though there has been some cooling, kelp abundances have not rebounded even after the cool year of 2021 when we would have expected good recovery (Figure 4). There seems little doubt that, at least for this study area, intense grazing by sea urchins has suppressed bull kelp recovery in Van Damme and more generally in northern California. It seems unlikely, therefore, that bull kelp will flourish again unless cool seawater temperatures prevail for the critical winter period (García-Reyes et al. 2022) and more importantly, sea urchin grazing is reduced (McPherson et al. 2021).

Abalone and ecosystem restoration planning

Abalone restoration will depend on the recovery of the kelp forests and algal communities, but this requires a deeper understanding of the mechanisms that promote resilience and persistence in the ecosystem. This climate-driven MHW and sea urchin impact on abalone resources (Rogers-Bennett and Catton 2019) highlights the importance of long time series in providing the context for kelp forest ecosystem and key species' restoration. To adapt to a changing environment and inform abalone management and restoration there needs to be understanding of what conditions were like prior to the transition to the alternative state; in this case transition to a sea urchin barren. Here we see that under starvation conditions red abalone populations are continuing to decline despite the closure of the fishery due to extreme natural mortality and the loss of the kelp forest habitat. Purple sea urchins are dominating the system and thriving despite the lack of kelp forest from 2014 to 2022.

Knowledge of abalone recruitment patterns are critical for marine resource restoration as populations that have reduced recruitment levels may recover slowly and may not be able to sustain fishing mortality in addition to natural mortality. A robust recruitment monitoring programme needs to be in place to support management and restoration efforts, specifically informing practitioners as to what baseline levels of recruitment were like during the sustainable period and what the speed of abalone recovery might be. At the same time, quantifying recruitment patterns of purple sea urchins will be critical to know if sea urchin populations are starting to decline indicating kelps can recover. In this case, purple sea urchin recruitment is higher than it has been in the last 8 years showing no signs of slowing down.

Ecosystem and resource assessment requires knowledge of current and baseline recruitment rates. These data can be used to establish targets and understand when populations may be in need of restoration or on the verge of population expansions (as was the case of sea urchins as early as 2015). Our 20-year time series for red abalone shows that recruitment is <0.28 per module, that this is <20th percentile of the recruitment of juvenile through time, and can be used to define a population in need of restoration. We would expect then that when the red abalone populations in northern California is recruiting and self-sustaining, as it had been prior to 2015, then recruitment will be >0.28 per module. Other regions which have experienced kelp forest collapse or decline, such as along the western coast of Australia in 2011 (Caputi et al. 2019), have also used recruitment information to establish targets and make decisions about whether stocks are rebounding or in need of restoration. In these ways, a time series of recruitment as measured in RM can be used to help establish quantifiable metrics for abalone recovery. Abalone inside Marine Protected Areas may be more resilient to climate change impacts such as MHW (Micheli et al. 2012).

Similarly, when purple sea urchin recruitment rates increase this can be used as an early warning indicator of a transition in the ecosystem. Here it was clear that sea urchin recruitment exceeding the levels observed in the past began to occur in 2015. The average number of juvenile purple sea urchins before the collapse of the kelp forest was 0.1 per module and this increased nearly 40-fold with 16 or more per module in the years after the collapse. In this case, we saw >5 per module (roughly $> 1/\text{m}^2$ in the RM) which could be used to trigger management restoration actions. Therefore, one can use these levels as warning indicators of an impending 10 or 20-fold increase in recruitment of juvenile sea urchins, which should trigger more work to monitor sea urchins in the system. Monitoring predators of sea urchins can also help predict outbreaks since sea urchin predators such as sunflower sea stars play a significant role in limiting sea urchin herbivory and maintaining kelp forests (Galloway et al. 2023). An outbreak of grazers can potentially trigger a switch from kelp forest to sea urchin barren conditions which can have cascading trophic impacts on the community as a whole (Ling et al. 2015; Rogers-Bennett and Catton 2019, 2022).

We make the case here that recruitment monitoring should be a part of any sampling programme to track the health of kelp forest ecosystems. This monitoring needs to encompass multiple years so that there is some knowledge of the average recruitment since recruitment of marine invertebrates is known to be highly temporally variable (Menge et al. 2011). Recruitment is extremely vulnerable to warm water, low oxygen and a suite of herbivores. These ecosystem drivers of recruitment need to be better quantified if ecosystem-based management is to be put into practice. We suggest that it will be important to develop recruitment indicators as measures of ecosystem health to inform management and establish restoration targets for recovery to manage resources, ecosystem and the critical ecosystem services they provide (Smale et al. 2019).

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Data availability statement

Data from this paper will be available at the following NSF data management link: https://www.bco-dmo.org/award/818928

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References

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. doi:10.1016/j.rse.2018.06.039.

Bell TW, Cavanaugh KC, Saccomanno VR, Cavanaugh KC, Houskeeper HF, Eddy N, Schuetzenmeister F, Rindlaub N, Gleason M. 2023. Kelpwatch: a new visualization and analysis tool to explore kelp canopy dynamics reveals variable response to and recovery from marine heatwaves. PLoS One. 18(3):e0271477.

Bell TW, Cavanaugh KC, Siegel DA. 2022. SBC LTER: time series of quarterly NetCDF files of kelp biomass in the canopy from Landsat 5, 7 and 8, since 1984 (ongoing). Environ Data Initiat. ver 16. https://doi.org/https://doi.org/10.6073pasta/93b47266b20bc1782c8df9c36169e372.

Bouma JV, Rothaus DP, Straus KM, Vadopalas B, Friedman CS. 2012. Low juvenile pinto abalone *Haliotis kamtschatkana kamtschatkana* abundance in the San Juan Archipelago, Washington State. Trans Am Fisheries Soc. 141:76–83. doi:10.1080/00028487.2011.651551.

Caputi N, Kangas M, Chandrapavan A, Hart A, Feng M, Marin M, Lestang SD. 2019. Factors affecting the recovery of invertebrate stocks from the 2011 Western Australian extreme marine heatwave. Frontiers in Marine Science. 6:484. doi:10.3389/fmars.2019.00484.

Carson HS, Ulrich M. 2019. Status report for the pinto abalone in Washington. Olympia: Washington Department of Fish and Wildlife. iii + 25 pp.

Connell JH, Sousa WP. 1983. On the evidence needed to judge ecological stability or persistence. The Am Naturalist. 121(6):789–824. doi:10.1086/284105.

Davis GE. 1995. Recruitment of juvenile abalone (*Haliotis* spp.) measured in artificial habitats. Mar Freshwat Res. 46:549–554. doi:10.1071/MF9950549.

Day E, Branch GM. 2000. Evidence for a positive relationship between juvenile abalone *Haliotis midae* and the sea urchin *Parechinus angulosus* in the south-western Cape, South Africa. African J Mar Sci. 22:458.

Defreitas B. 2003. Estimating juvenile northern abalone (*Haliotis kamtschatkana*) abundance using artificial habitats. J Shellfish Res. 22:819–823.. 461.

Ebert TA, Schroeter SC, Dixon JD, Kalvass P. 1994. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. Mar Ecol Prog Ser. 111:41–52. 465. doi:10.3354/meps111041.

Estrada AC, Rogers-Bennett L, Steele MA. 2021. Recruitment of postlarval abalone *Haliotis* spp. at Santa Catalina Island: quantifying natural recovery. J Shellfish Res. 40(1):137–144.

Filbee-Dexter K, Scheibling RE. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar Ecol Prog Series. 495:1–25. doi:10.3354/meps10573.

Fujita D. 1998. Strongylocentrotid sea urchin-dominated barren grounds on the Sea of Japan coast of northern Japan. In: Mooi R, Telford M, editors. Echinoderms: San Francisco. Rotterdam: A.A. Balkema Publishers; p. 659–664.

Galloway AWE, Gravem SA, Kobelt JN, Heady WN, Okamoto DK, Sivitilli DM, Saccomanno VR, Hodin J, Whippo R. 2023. Sunflower sea star predation on urchins can facilitate kelp forest recovery. Proc Roy Soc B. 290(1993):20221897–476. doi:10.1098/rspb.2022.1897.

García-Reyes M, Largier JL, Sydeman WJ. 2014. Synoptic-scale upwelling indices and predictions of phyto-and zooplankton populations. Progress Oceanog. 120:177–188. doi:10.1016/j.pocean.2013.08.004.

García-Reyes M, Thompson SA, Rogers-Bennett L, Sydeman WJ. 2022. Winter oceanographic conditions predict summer bull kelp canopy cover in northern California. PLoS One. 17(5): e0267737. doi:10.1371/journal.pone.0267737.

Hamilton SL, Bell TW, Watson JR, Grorud-Colvert KA, Menge BA. 2020. Remote sensing: generation of long-term kelp bed data sets for evaluation of impacts of climatic variation. Ecology. 101(7):e03031. doi:10.1002/ecy.3031.

Hart LC, Goodman MC, Walter RK, Rogers-Bennett L, Shum P, Garrett AD, Watanabe JM, O'leary JK. 2020. Abalone recruitment in low-density and aggregated populations facing climatic stress. J Shellfish Res. 39(2):359–373.. 484. doi:10.2983/035.039.0218.

Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, Edgar GJ, Frusher SD, Gardner C, Haddon M, Helidoniotis F, et al. 2011. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. J Exp Mar Bio Ecol. 400:17–32. doi:10.1016/j.jembe.2011.02.032.

Kautz M, Meddens AJ, Hall RJ, Arneth A. 2016. Biotic disturbances in northern hemisphere forests–a synthesis of recent data, uncertainties and implications for forest monitoring and modelling. Global Ecol Biogeo. 26:533–552. doi:10.1111/geb.12558.

Kawana SK, Catton CA, Hofmeister JK, Juhasz CI, Taniguchi IK, Stein DM, Rogers-Bennett L. 2019. Warm water shifts abalone recruitment and sea urchin diversity in southern California:

implications for climate-ready abalone restoration planning. J Shellfish Res. 38(2):475–484. doi:10.2983/035.038.0231.

Klemmer AJ, Wissinger SA, Greig HS, Ostrofsky ML. 2012. Nonlinear effects of consumer density on multiple ecosystem processes. J An Ecol. 81:770–780. 504 doi:10.1111/j.1365-2656.2012.01966.x

Lawrence JM. 1975. On the relationship between marine plants and sea urchins. Oceanogr Mar Biol Ann Rev. 13:213–286.

Levitan DR, Sewell MA, Chia FS. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. Ecol. 73:248–254. doi:10.2307/1938736.

Ling SD, Johnson CR, Frusher SD, Ridgway K. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proc Nat Acad Sci. 106(52):22341–22345. doi:10.1073/pnas.0907529106.

Ling SD, Scheibling RE, Rassweiler A, Johnson CR, Shears N, Connell SD, Salomon AK, Norderhaug KM, Pérez-Matus A, Hernández JC, Clemente S. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. Phil Trans Royal Society B: Bio Sci. 370 (1659):20130269. doi:10.1098/rstb.2013.0269.

McNaught DC. 1999. The indirect effects of macroalgae and micropredation on the postsettlement success of the green sea urchin in Maine [P.h. D thesis]. Orono: University of Maine.

McPherson ML, Finger DJ, Houskeeper HF, Bell TW, Carr MH, Rogers-Bennett L, Kudela RM. 2021. Large-scale shift in the structure of a kelp forest ecosystem co-occurs with an epizootic and marine heatwave. Comm Biol. 4:298–532. doi:10.1038/s42003-021-01827-6.

McShane PE, Smith MG. 1988. Measuring recruitment of abalone *Haliotis rubra* Leach (Gastropoda:Haliotidae) – comparison of a novel method with two other methods. Aust J Mar Freshwat Res. 39:331–336. 536 doi:10.1071/MF9880331

McShane PE, Smith MG. 1991. Recruitment variation in sympatric populations of *Haliotis rubra* (Mollusca: Gastropoda) in southeast Australian waters. Mar Ecol Prog Series. 73:203–210. doi:10.3354/meps073203.

Menge BA, Gouhier TC, Freidenburg T, Lubchenco J. 2011. Linking explain kelp forest recovery in overgrazed areas in Norway. Mar Ecol Prog Series. 488:119–132.

Micheli F, Saenz-Arroyo A, Greenley A, Vazquez L, Espinoza Montes JA, Rossetto M, De Leo GA. 2012. Evidence that marine reserves enhance resilience to climatic impacts. PLoS One. 7(7): e40832. doi:10.1371/journal.pone.0040832.

Norderhaug KM, Christie HC. 2013. Lack of sea urchin settlement may explain kelp forest recovery in overgrazed areas in Norway. Pasadena: California Institute of Technology.

North WJ. 1971. The biology of giant kelp beds (Macrocystis) in California: introduction and background. Nova Hedwigia. 32:1.

Okamoto D, Spindel N, Collicutt B, Munstermann M, Karelitz S, Gimenez I, Rolheiser K, Cronmiller E, Foss M, Mahara N, Swezey D. 2023. Thermal suppression of gametogenesis explains historical collapses in larval recruitment. *bioRxiv*, 2023-09.

Okamoto DK, Schroeter SC, Reed DC. 2020. Effects of ocean climate on spatiotemporal variation in sea urchin settlement and recruitment. Limnol Ocean. 65(9):2076–2091. doi:10.1002/lno.11440.

Pearse JS, Clark ME, Leighton DL, Mitchell CI, North WJ. 1970. Marine waste disposal and sea urchin ecology. p. I- 93 in Kelp Habitat Improvement Project, Annual Report. (I July. 30-June, 1970), appendix, long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: toward explaining "unexplained" variation. J Exp Mar Biol Ecol. 400(1-2):236–249.

Pennington JT. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. Biol Bull. 169(2):417–430. doi:10.2307/1541492.

Reid J, Rogers-Bennett L, Vasquez F, Pace M, Catton CA, Kashiwada JV, Taniguchi L. 2016. The economic value of the recreational red abalone fishery. Cal Fish and Game. 102(3):119–130.

Rennick M, DiFiore BP, Curtis J, Reed DC, Stier AC. 2022. Detrital supply suppresses deforestation to maintain healthy kelp forest ecosystems. Ecol. 103(5):e3673. 568. doi:10.1002/ecy.3673.

Roberts DA, Gardner M, Church R, Ustin S, Scheer G, Green RO. 1998. Mapping chaparral in the Santa Monica Mountains using multiple endmember spectral mixture models. Remote Sensing of Environment. 65(3):267–279. doi:10.1016/S0034-4257(98)00037-6.

Rogers-Bennett L. 2006. The ecology of Strongylocentrotus franciscanus and Strongylocentrotus purpuratus Chapt 19. In: Lawrence JM, editor. *Edible sea urchins: biology and ecology*. Elsevier.

Rogers-Bennett L. 2007. Is climate change contributing to range reductions and localized extinctions in northern (*Haliotis kamtschatkana*) and flat (*Haliotis walallensis*) abalones? Bulletin of Marine Science. 81(2):283–296.

Rogers-Bennett L, Catton C. 2022. Cascading impacts of a climate-driven ecosystem transition intensifies population vulnerabilities and fishery collapse. Front. Clim. 4:908708. doi:10.3389/fclim.2022.908708.

Rogers-Bennett L, Catton CA. 2019. Marine heat wave and multiple stressors tip bull kelp forest to sea urchin barrens. Scientific Reports. 9(1):15050. doi:10.1038/s41598-019-51114-y.

Rogers-Bennett L, Dondanville RF, Catton CA, Juhasz CI, Horii T, Hamaguchi M. 2016. Tracking larval, newly settled, and juvenile red abalone (*Haliotis rufescens*) recruitment in Northern California. J Shellfish Res. 35(3):601–609. 575 doi:10.2983/035.035.0305

Rogers-Bennett L, Klamt R, Catton CA. 2021. Survivors of climate driven abalone mass mortality exhibit declines in health and reproduction following kelp forest collapse. Frontiers Mar Sci. 8:725134. doi:10.3389/fmars.2021.725134.

Rogers-Bennett L, Pearse JS. 2001. Indirect benefits of marine protected areas for juvenile abalone. Cons Biol. 15(3):642–647. doi:10.1046/j.1523-1739.2001.015003642.x.

Rowley RJ. 1990. Newly settled sea urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality. Mar Ecol Prog Series. 62:229–240. doi:10.3354/meps062229.

Sasaki R, Shepherd SA. 1995. Larval dispersal and recruitment of *Haliotis discus hannai* and *Tegula* spp. on Miyagi coasts of Japan. Mar Freshwat Res. 46:519–529. 589 doi:10.1071/MF9950519

Sasaki R, Shepherd SA. 2001. Ecology and post-settlement survival of the Ezo abalone *Haliotis discus hannai*, on Miyagi coasts of Japan. J Shellfish Res. 20:619–626. 592

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B. 2001. Catastrophic shifts in ecosystems. Nature. 413(6856):591–596. doi:10.1038/35098000.

Schröder A, Persson L, De Roos AM. 2005. Direct experimental evidence for alternative stable states: a review. Oikos. 110:3–19. doi:10.1111/j.0030-1299.2005.13962.x.

Smale DA, Wernberg T, Oliver EC, Thomsen M, Harvey BP, Straub SC, Burrows MT, Alexander LV, Benthuysen JA, Donat MG. 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Change. 9:306–312. doi:10.1038/s41558-019-0412-1.

Smith JG, Tinker MT. 2022. Alterations in the foraging behaviour of a primary consumer drive patch transition dynamics in a temperate rocky reef ecosystem. Ecol Letters. 25(8):1827–1838. doi:10.1111/ele.14064.

Smith JG, Tomoleoni J, Staedler M, Lyon S, Fujii J, Tinker MT. 2021. Behavioral responses across a mosaic of ecosystem states restructure a sea otter–urchin trophic cascade. Proc Natl Acad Sci. 118(11):e2012493118. doi:10.1073/pnas.2012493118.

Tegner MJ, Dayton PK. 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science. 196(4287):324–326. doi:10.1126/science.847476.

Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F, Fromont J, Fulton CJ, Hovey RK, et al. 2016. Climate-driven regime shift of a temperate marine ecosystem. Science. 353:169–172. doi:10.1126/science.aad8745.