

Appendix A

**Evaluation of Anthropogenic Impacts on the San Diego
Coastal Kelp Forest Ecosystem (Biennial Project Report)**

2020 – 2021

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EXECUTIVE SUMMARY

Kelp forests are among the most charismatic marine communities off the southern California coast. They are highly productive, characterized by the rapid growth of their structural species, *Macrocystis pyrifera* (commonly referred to as giant kelp), whose areal rate of primary production can exceed that of tropical rain forests (Towle and Pearse, 1973). Giant kelp forests provide habitat, food and shelter for a host of fishes and invertebrates, and competes with many other algal species. Kelp forests occupy the inner margins of the southern California continental shelf and offshore islands extending from the offshore edge of tidepools to depths as great as thirty meters off the mainland of southern California. Kelp forests also host a range of economically and aesthetically important consumptive and non-consumptive human activities including boating, recreational fishing, spearfishing, SCUBA diving, and the commercial harvest of finfishes, invertebrates, and algae. The kelp forests off Point Loma and La Jolla are among the most important commercial fishing grounds for the red sea urchin (*Mesocentrotus franciscanus*) and spiny lobster (*Panulirus interruptus*) fisheries off California. The kelp forests of La Jolla and Point Loma are the largest contiguous kelp forests off the western coast of the US.

Kelp forests off southern California are affected by both natural and human disturbances. The El Niño Southern Oscillation (ENSO) is the primary ocean climate mode that affects kelp abundance, growth, and reproduction along the west coast of the Americas. Positive ENSO's, known as El Niños, are associated with warm water, depressed concentrations of nitrate, the principal nutrient limiting giant kelp, and a more energetic storm environment off southern California. Both phenomenon can severely stress giant kelp and accompanying species of algae. The opposite conditions occur during negative ENSO events, termed La Niñas, enhancing both the growth and reproduction of kelps. Together, the two ocean climate modes drive the greatest amount of annual variability in surface canopy cover of *M. pyrifera* off southern and Baja California. The periodicity of El Niño is variable, typically occurring at 3-5 year intervals and persisting for <1 year. Kelp forests wax and wane over these cycles, experiencing high mortality during El Niños with recovery afterwards. Rates of recovery depend on growth conditions after an El Niño ebbs. The kelp forests off San Diego have been studied by researchers at the Scripps Institution of Oceanography (SIO) since the 1950's, and baseline data collection began in the 1970's. Currently, kelps and associated animals are monitored at twenty permanent study sites located among the Pt. Loma, La Jolla, and North County kelp forests.

During the current reporting period (2020-2021), the kelp forests off southern California are experiencing a stalled recovery from a marine heat wave that began in 2014 and persisted until the spring of 2017. This lengthened period of heat stress was due to the combination of two consecutive ocean climate events. An anomalous warm pool extended across much of the NE Pacific from 2014-2015. This warm pool, unique in the climate record of the NE Pacific, was coined the BLOB and resulted from decreased wind mixing in the NE Pacific. The climatic forcing of the NE Pacific warm pool is different in nature and scale than ENSO cycles which are caused by anomalous winds along the equatorial Pacific. A strong El Niño occurred during fall of 2015 and the winter of 2016 just as the BLOB was dissipating along the US west coast. Together these consecutive warm events are now referred to as the NE Pacific marine heat wave (MHW) which was the longest and warmest heat event ever observed in the 110 year record of sea surface temperature at the Scripps Institution of Oceanography (SIO) pier. Cooler conditions returned to the equatorial eastern Pacific and the Southern California Bight by late 2016. The spring upwelling seasons of 2017-2021 brought cool nutrient-laden waters up onto the inner continental shelf of southern California creating favorable conditions for giant kelp recovery. However, this cooling is superimposed onto a larger scale trend of increasing ocean temperatures within the California Current System and the global ocean generally. As the ocean

absorbs ever more heat it becomes increasingly likely that conditions supportive of giant kelp growth and reproduction will decrease in frequency and duration over the next century. Because of this, risks to *M. pyrifera* persistence in southern California will likely increase. In fact, the failure of giant kelp to recover over much of its former range off San Diego despite favorable ocean conditions may be evidence that this risk is now manifest.

The marine heat wave and associated depressed nutrient conditions decimated *M. pyrifera* and cohabiting algae off San Diego. Pooled across 20 kelp forest sites, densities of adult *M. pyrifera* were reduced >90%. Unlike previous warm events attributed to El Niño, the coupled marine heat wave resulted in warming and low nutrient exposure of understory kelp species for prolonged periods of time leading to dramatic reductions of those species in addition to giant kelp. The BLOB persisted longer than a typical El Niño and kelps did not recover after the warm pool dissipated as a result of the stress induced by the following El Niño of 2016. The two events affected kelps at the study sites differently, and the historic pattern of areal synchronized mortality and recovery was disrupted. Growth conditions returned to normal with the onset of mild La Niña conditions in the spring of 2017. Rates of giant kelp recovery since then have been variable among study sites and were initially slower than previous recovery periods and non-existent at some study sites. Surface canopy cover in some areas was precluded by increases in understory species density. Some of these areas will likely remain devoid of giant kelp canopy for years since understory species are long-lived and competitively interfere with giant kelp recruitment. Favorable conditions for kelp growth and reproduction returned with the 2018 spring upwelling season and continued through 2021. Numerous study sites experienced significant giant kelp recruitment that successfully matured and became reproductive. However, the giant kelp canopy off San Diego County remains patchy due to a combination of competition with understory species in the shallower margins of the kelp forests and a lack of recruitment in many deeper areas through early 2018. The lack of recruitment in areas deeper than 18 m is possibly a result of decreased light levels caused by phytoplankton blooms. Giant kelp abundances and stipe densities are presently very low relative to historical levels, and recovery from the MHW persists at only five of our 20 study sites. Most other sites are now dominated by space-competitive understory species or are highly disturbed with very little algae.

An anomalously warm surface layer, limited to the upper 3-5 meters of the ocean's surface, bathed much of the southern California coast during the summer of 2018. Sea surface temperatures reached 27°C, exceeding the all time high temperature record for the SIO Pier sea surface temperature series by ~2°C. Summer surface temperature maxima in this record are typically ~23°C. This surface warm pool degraded the giant kelp canopy tissue which was mostly lost from the offshore forests and drifted onto nearby beaches. However, cooler temperatures persisted closer to the bottom, and most of the giant kelp plants in the initial recovery cohorts of 2017 and 2018 survived and regrew to the surface when the warm pool dissipated by the fall of 2018. However, the marine heat wave decimated what remained of the North County kelp forests and the warm surface anomaly resulted in almost total loss of giant kelp within these forests. Recruitment in these forests has been extremely limited and unsuccessful. Similar near-surface warming events have occurred over the last two summers but were not as strong as the 2018 event. The combination of understory overgrowth and summer surface warming may be leading to reduced giant kelp abundances over the long term where it will be limited to smaller patches within its historical footprint. This pattern may herald the eventual loss of giant kelp canopy throughout much of southern California as warming conditions increasingly favor understory kelps such that kelp forests off San Diego mirror those of central Baja California where giant kelp canopy cover is greatly reduced to ephemeral patches. Such a change reflects the initial stages of a poleward biogeographical shift for *M. pyrifera*.

Diseases in many invertebrates, including sea urchins (echinoids) and predatory seastars (asteroids), are common during warm events. Mass mortality of red (*Mesocentrotus franciscanus*) and purple sea urchins (*Strongylocentrotus purpuratus*) and seastars in the genus *Pisaster*, began off San Diego in 2014 and extended through 2017. Sea urchins are primary grazers of many kelp species, and can overgraze giant kelp and associated algal species given the right conditions. They are capable of limiting or even precluding giant kelp recovery, and overgrazed areas known as barrens, can persist in some areas for decades. The echinoderm epidemic associated with the MHW resulted in the disappearance or near-disappearance of seastars and the decimation of sea urchins at our study sites and from all San Diego kelp forests generally. Further, little to no recruitment of sea urchins was observed until the fall of 2017 which continued at many sites through the fall of 2021. Despite this recruitment, populations of adult animals have not yet increased and thus sea urchins have not likely contributed to the dampened giant kelp recovery from the MHW. However, these new cohorts of sea urchins may eventually overgraze some areas off San Diego as they emerge from cryptic nursery habitat and begin to actively forage. Sea urchin overgrazing has been a recurring problem off south Pt. Loma where a unique combination of topography and turbidity emanating from San Diego Bay contribute to resilient barrens. Some recruitment of the seastars *Pisaster giganteus* and *Patiria miniata*, two important kelp forest predators, has been observed off Pt. Loma and La Jolla. However, adult densities are presently still very low and it is unknown whether they will recover anytime soon.

Abalone, another important kelp forest grazer and the target of a once extensive fishery, depend primarily on giant kelp for food. Abalone once supported a large recreational and commercial fishery off southern California until all harvest was closed in 1996 due to depletion from overfishing and disease mainly associated with warm events. Abalone off San Diego County suffered further mortality during and after the 2014-2016 MHW due to disease and lack of food. Abundances of all abalone species at the study sites off La Jolla and Pt. Loma have since declined to near zero with the exception of pink abalone (*Haliotis corrugata*) where there has been some recovery at the two shallowest study sites off central Pt. Loma that began around 2010. Presently, pink abalone densities at these sites are at least an order of magnitude lower than their historical highs.

Sargassum horneri, an invasive algal species that has overwhelmed giant kelp in some sheltered forests off southern California, was first observed in the kelp forests off San Diego in 2014. By 2018, this species had been observed at 13 of 20 study sites, but has since not spread to the remaining sites. Densities of *S. horneri* at the sites where it has been observed have actually decreased over time with the exception of one study site off northern La Jolla where it covers ~3% of the bottom. Presently, this species does not appear to pose as great a risk to San Diego County kelp forests that it has to more sheltered kelp forests off the California Channel Islands.

The failed recovery of giant kelp at many of our study sites can not be due to any localized effects of treated wastewater discharge by the City of San Diego through the ocean outfalls offshore of Imperial Beach (South Bay Ocean Outfall) or Pt. Loma (Pt. Loma Ocean Outfall). The present patchy nature of giant kelp canopy cover is not related to any distance gradient from either outfall. The areas that have exhibited the poorest post-MHW recovery and whose algal communities are the most degraded, relative to their historical condition, include northern La Jolla and North County which are the sites furthest from these outfalls.

INTRODUCTION

Kelp forests are susceptible to human disturbance because of their proximity to urbanized coasts exposing them to overfishing, polluted surface and groundwater discharge, as well as the discharge of wastewater. Perhaps the largest effect is that due to increased turbidity which limits light penetration for kelps to grow, germinate, and reproduce (Clendenning and North, 1960). Dramatic reductions in kelp forest canopy off Palos Verdes have been attributed to the combined effects of wastewater disposal and an energetic El Niño in the late 1950's (Grigg, 1978). Nearshore turbidity due to wastewater discharge has since been mitigated by increasing the offshore distances and depths of discharge, and improved outfall design (Roberts, 1991). Beach replenishment can also negatively impact kelp forests via sedimentation and burial. This has been observed at kelp forests off northern San Diego County where replenished sediments erode from beaches and partially bury low relief habitat that forms the foundation for giant kelp.

The Point Loma Ocean Outfall (PLOO) discharges advanced primary treated wastewater through a deep water open ocean outfall. The Outfall was extended and deepened in 1993, and presently discharges treated wastewater ~7.3 km offshore in marine waters ~98 m deep. The PLOO is situated approximately 5 km offshore of the outer edge of the Point Loma kelp forest. Due to its proximity, wastewater discharge through the PLOO presents at least a perceived risk to the health of the nearby kelp forest community off Pt. Loma. Local human risks to kelp forests can magnify risks posed by larger scale natural disturbances by reducing the resilience of kelp forests after episodic natural disturbances.

Kelp forests in southern California are disturbed naturally by ocean climate variability that occurs at interannual (El Niño Southern Oscillation – ENSO; Fig. 1) and decadal (Pacific Decadal Oscillation - PDO) periods. Positive phases of both ocean climate modes are associated with a deepened thermocline limiting nutrient delivery to the inner shelf that is necessary for kelp growth and reproduction. These modes are also associated with increased storm energy which causes giant kelp mortality via plant detachment and abrasion (Seymour et al., 1989). The northeastern Pacific experienced a profound regime shift in the late 1970's in which the main ocean thermocline deepened, resulting in a step reduction in nitrate concentrations along the Southern California Bight (SCB) that persists at present (Parnell et al., 2010 and Fig. 2). Concentrations of nitrate, the main limiting nutrient for kelp growth in southern California switched from being conducive for kelp growth most years prior to the regime shift, with the exception of the most intense El Niños, to being generally less adequate (Parnell et al., 2010) with the exception of strong negative ENSO phases known as La Niñas. The ecology of kelp forests off San Diego has changed fundamentally due to the increased frequency of natural disturbance resulting in a demographic shift towards younger and smaller *Macrocystis pyrifera* individuals (Parnell et al., 2010).

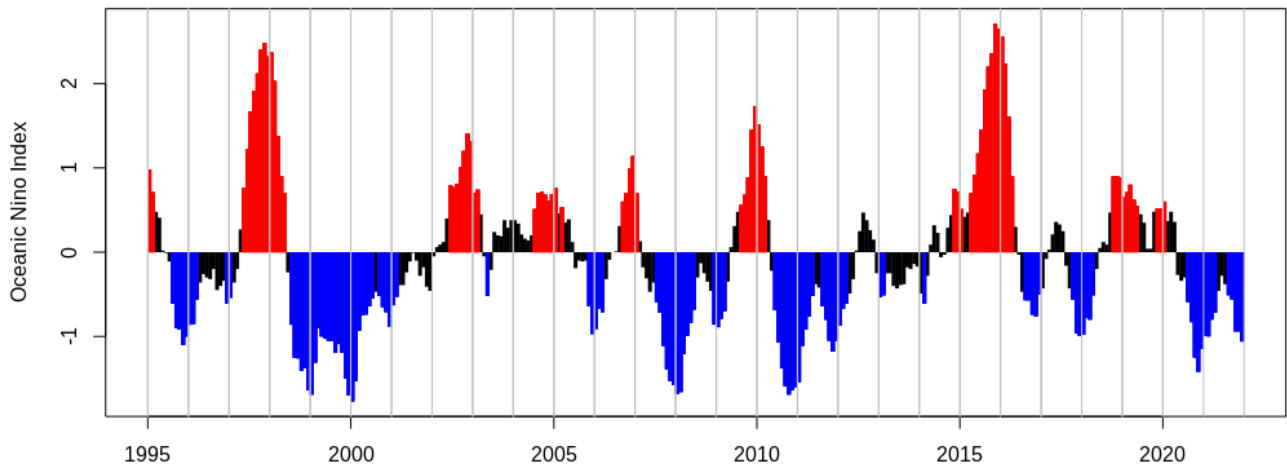


Figure 1. Barplot of the Oceanic Niño Index (ONI) since 1995. Red bars indicate El Niño conditions, blue bars indicate La Niña conditions, and black bars indicate ENSO neutral conditions (data from NOAA, 2022). The ONI index is based on equatorial sea surface temperatures in the Eastern Pacific.

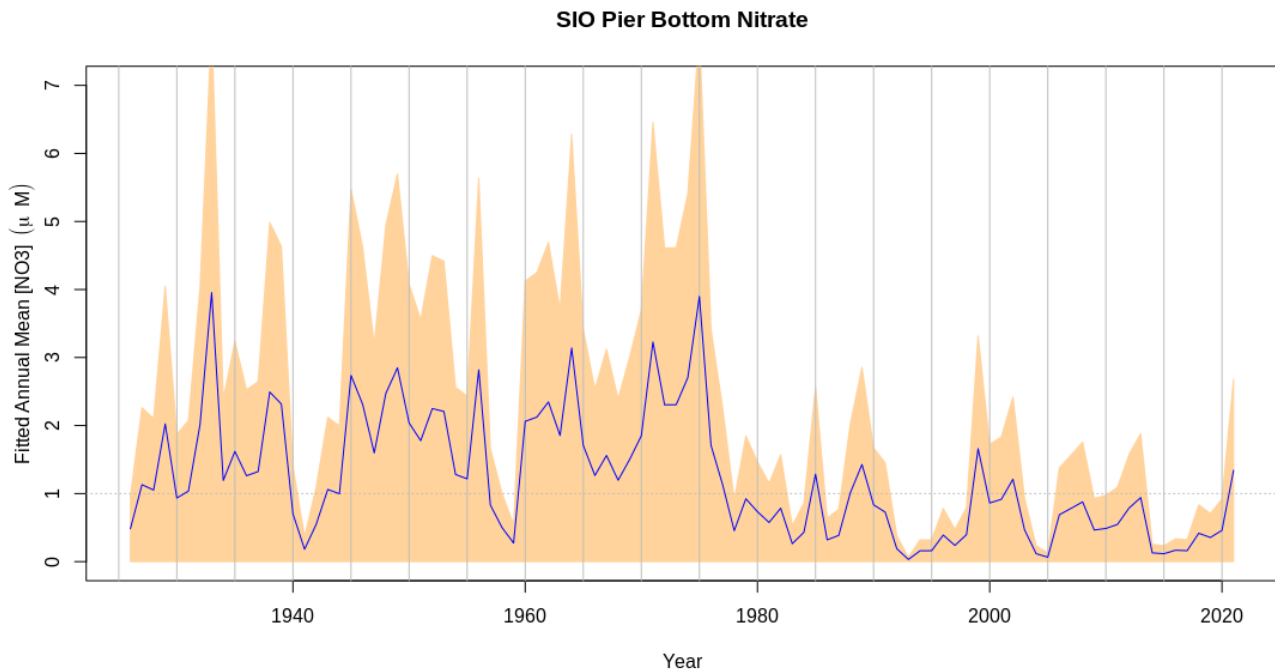


Figure 2. Time series of annual mean nitrate concentrations estimated from daily temperature and salinity sampled at the base of the Scripps Institution of Oceanography Pier (see Parnell et al., 2010 for details). Dotted gray line indicates the minimum nitrate threshold for the growth and reproduction of giant kelp (*M. pyrifera*). Peach area indicates the 95% confidence limits.

Sea urchin overgrazing is another form of natural disturbance within kelp forests (Leighton et al., 1966). Kelps are susceptible to overgrazing when sea urchin densities increase or when sea urchins aggregate into overgrazing fronts. Overgrazing can lead to areas denuded of most or all algae and have been termed barrens. Barrens can be frequent and resilient in some areas including the southern portion of the Pt. Loma kelp forest (Parnell, 2015), or can alternate with forested periods due to external forcing such as reductions in kelp standing stock as a result of El Niño, sea urchin disease epidemics, and indirectly from human activities including the harvest of important sea urchin predators (Steneck et al., 2002). Overfishing of sea urchin predators including spiny lobsters (*Panulirus interruptus*) and sheephead (*Semicossyphus pulcher*) in southern California can lead to outbreaks of sea urchin overgrazing.

A more recent source of disturbance has been the introduction of an invasive alga, *Sargassum horneri*, throughout southern California. This species competes with *Macrocystis pyrifera* for space and light, and is now seasonally dominant in some areas previously dominated by *M. pyrifera*. The most impacted areas include the protected low energy habitats in the lee of islands such as the northern Channel Islands and Santa Catalina Island (Miller et al., 2011). *S. horneri* is now establishing itself in many areas off San Diego County including the kelp forests, bays, and estuaries.

Researchers at the Scripps Institution of Oceanography (SIO) have partnered with the City of San Diego Ocean Monitoring Program to conduct regular surveys of the kelp forests off San Diego County including the kelp forests off Point Loma, La Jolla and North County. These surveys represent a continuation of ecological studies that began at SIO in the Point Loma (PLKF) and La Jolla (LJKF) kelp forests and continue at some of the sites established in the 1970's and 1980's (Dayton and Tegner, 1984). Additional study sites have been established more recently in both kelp forests and in kelp forests off northern San Diego County (North County - NCKF). PLKF and LJKF are the largest contiguous kelp forests off the western United States coast and are historically one of the most studied kelp forest systems in the world.

MATERIALS AND METHODS

Algae, invertebrates and bottom temperatures are monitored at twenty permanently established study sites (Fig. 3). Algae and invertebrates are monitored along four replicate parallel permanent band transects oriented perpendicular to shore (25 x 4 m bands separated 3-5 m apart) except at the DM study site where two sets of band transects are located ~1300 m apart due to the small size and fragmented shape of that forest. The main components of the kelp forest monitoring program include estimation of (1) algal density, growth, reproductive condition and recruitment, (2) invertebrate densities, (3) sea urchin demography (size distributions to monitor for episodic recruitment), and (4) ocean bottom temperature (which is a proxy of ocean nutrient status). The types of data collected and the frequency of collection are listed in Table 1.

Algae

Several life stages of *M. pyrifera* are enumerated to identify recruitment events and follow the fate of recruiting cohorts into adulthood. Survival of recruitment cohorts to adulthood is highly variable and a lack of successful maturation into adulthood indicates changes in the growth environment in the form of stress by temperature and nutrients, grazers, or/ or reduced light. Giant kelp life stages include adults (def., ≥ 4 stipes), pre-adults (def., plants > 1 m tall but with < 4 stipes), bifurcates (a late post recruitment stage indicated by the presence of a split in the apical meristem which represents the primary dichotomous branching event), and pre-bifurcates (very early post

settlement stage lacking the initial dichotomous split). Stipe numbers are counted and recorded for each adult plant each visit.

Conspicuous macroalgal species/groups are enumerated or percent cover is estimated within 5 x 2 m (10 m²) contiguous quadrats along the band transect lines at all sites. Reproduction and growth of *M. pyrifera*, and the understory kelps *Pterygophora californica* and *Laminaria farlowii*, are measured on permanently tagged plants along the central Pt. Loma study sites.

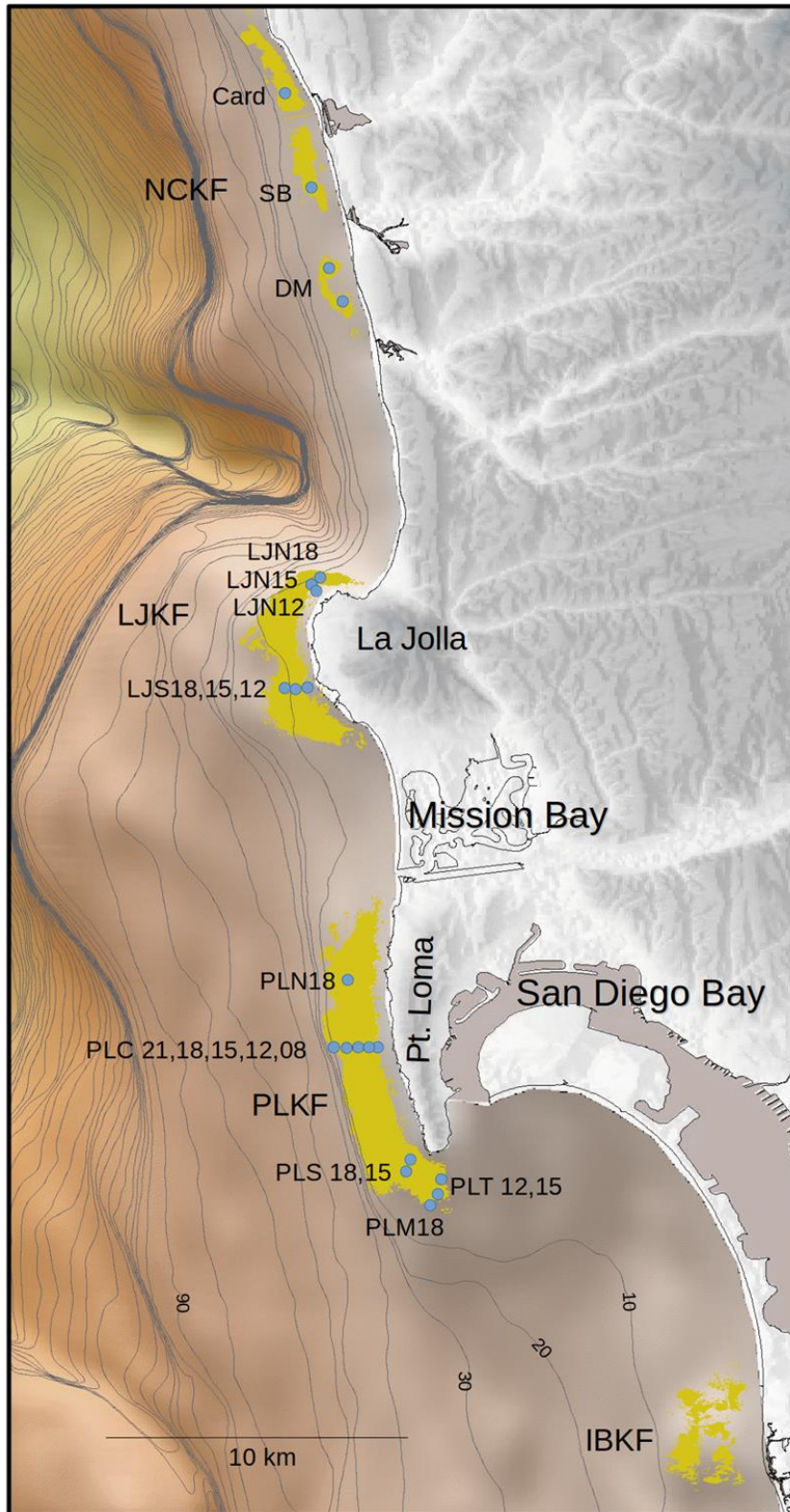


Figure 3. Map of the San Diego inner shelf showing locations of the Point Loma, La Jolla, North County, and Imperial Beach kelp forests (indicated by PLKF, LJKF, NCKF, and IBKF, respectively). Permanent study site locations are indicated by blue circles and corresponding study site names. Depth contour units are meters.

Growth of *M. pyrifera* is monitored by counting the number of stipes on each tagged plant one meter above the substratum. Reproductive state is represented by the size of the sporophyll bundle (germ tissue) at the base of each plant. Sporophyll volume is calculated as a cylinder based on the height and diameter of each bundle. This is an indirect measure of reproductive effort. Reed (1987) has shown that sporophyll biomass is closely related to zoospore production. Reproductive capacity, a derived parameter that represents the relative reproductive potential among plants by coupling sporophyll volume and reproductive state, is calculated as the product of sporophyll volume and squared reproductive state. Reproductive capacity is then standardized by division of each value by the maximal value observed among all sites. Reproductive state for each plant is ranked according to the ordinal scale in Table 2.

Growth of *Pterygophora californica* is determined by the method of DeWreede (1984). A hole (6 mm) is punched into the midrib of the terminal blade ~30 mm from the base of the blade, and another hole is punched monthly at the same location. The distance between the two holes represents the linear growth of each blade. Reproductive effort for *P. californica* is evaluated by a count of the total number of sporophyll blades on each plant and the number with active spore production (def., sori). Growth of *Laminaria farlowii* is determined in a similar manner to *P. californica*. A 13mm diameter hole is punched 100 mm from the base of each blade and is repeated each visit. The distance between the two holes represents the linear growth of each blade. The reproductive status of *L. farlowii* is evaluated as the percent of each blade covered by sori.

The distribution of algal species among all permanent sites was calculated using factor analysis in R (R Core Team, 2018). Factor analysis (Lawley and Maxwell, 1971) was used to reduce the multi-dimensional algal data. This technique facilitates the examination of entire algal communities in two or three dimensions that can then be plotted to assess changes in community composition among study sites and over time. Thirteen algal groups and derived bare space were analyzed among 20 sites. Relative bare space was derived by ranking the sum of rankings for individual algal groups among sampling units. Sampling units (individual 10m² quadrats) with the least amount of total algae (density or percent cover) were ranked highest for bare space.

Invertebrates

All conspicuous sessile and mobile invertebrates are enumerated annually within the 10 m² quadrats during spring. Size frequencies of red (RSU - *Mesocentrotus franciscanus*) and purple (PSU - *Strongylocentrotus purpuratus*) sea urchins are recorded for >100 individuals when possible for each species located near all of the study sites except for the NCKF sites which do not have adequate densities of sea urchins.

Sea urchin recruitment is sampled semi-annually (spring and fall) at all of the Pt. Loma and La Jolla study sites. Sea urchins are exhaustively collected in haphazardly placed 1 m² quadrats in suitable substrate within 50m of each study site. Suitable substrate includes ledges and rocks which can be fully searched for sea urchins as small as 2mm. Sea urchins are measured using calipers and then returned to their place of capture.

Temperature and Sedimentation

Sea bottom temperatures are recorded at 10 min intervals using ONSET Tidbit recorders (accuracy and precision = 0.2°C and 0.3°C (respectively) at the permanent central Pt. Loma study sites

and an additional site located just offshore of PLC21 at a depth of 33 m. Additionally, a water column temperature profile is recorded utilizing a mooring located in south La Jolla at a depth 24 m. Sensors are located at 3 m depth intervals along the mooring.

Sedimentation of the north county kelp forests has historically been problematic at times. The most noticeable burial appeared to be related to beach sand replenishment activities in the early 2000's when large sections of hard bottom substrate supporting the Solana Beach kelp forest was covered by sediments as they migrated offshore from the beach (Parnell, pers. obs.) . With the establishment of kelp forest study sites in the area, sediment depths are monitored along all of the NCKF sites. Sedimentation is tracked by measuring the height of permanently established spikes at replicate locations within each of those forests.

Study Site	Depth (m)	Year Established	Work Conducted (frequency)
Card	17	2006	ABT(q), Inv(a), BT(10min), Sed(q)
SB	16	2006	ABT(q), Inv(a), BT(10min), Sed(q)
DM	16	2007	ABT(q), Inv(a), BT(10min), Sed(q)
LJN18	18	2004	ABT(q), Inv(a), USF(sa), BT(10 min)
LJN15	15	2004	ABT(q), USF(sa), Inv(a), BT(10 min)
LJN12	12	2004	ABT(q), USF(sa), Inv(a), BT(10 min)
LJS18	18	2004	ABT(q), USF(sa), Inv(a), BT(10 min)
LJS15	15	1992	ABT(q), USF(sa), Inv(a), BT(10 min)
LJS12	12	2004	ABT(q), USF(sa), Inv(a), BT(10 min)
PLN18	18	1983	ABT(q), USF(sa), Inv(a), BT(10 min)
PLC21	21	1995	ABT(q), USF(sa), Inv(a), AR(m), BT(10 min)
PLC18	18	1983	ABT(q), USF(sa), Inv(a), AR(m), BT(10 min)
PLC15	15	1983	ABT(q), USF(sa), Inv(a), AR(m), BT(10 min)
PLC12	12	1983	ABT(q), USF(sa), Inv(a), AR(m), BT(10 min)
PLC08	8	1997	ABT(q), USF(sa), Inv(a), AR(m), BT(10 min)
PLS18	18	1983	ABT(q), USF(sa), Inv(a), BT(10 min)
PLS15	15	1992	ABT(q), USF(sa), Inv(a), BT(10 min)
PLT12	12	1997	ABT(q), USF(sa), Inv(a), BT(10 min)
PLT15	15	1997	ABT(q), USF(sa), Inv(a), BT(10 min)
PLM18	18	1996	ABT(q), USF(sa), Inv(a), BT(10 min)

Table 1. List of study sites including year of establishment and work conducted at each site. *ABT* = algal band transects, *USF* = sea urchin size frequency, *Inv* = Invertebrate censuses, *AR* = algal reproduction and growth measurements, and *BT* = bottom temperature. Frequencies are noted in parenthesis: *a* = annual, *sa* = semi-annual, *q* = quarterly, *m* = monthly.

Reproductive Score	Description
0	No sporophylls present
1	Sporophylls present but no sori (sites of active reproduction) development
2	Sporophylls with sori only at the base of sporophylls
3	Sporophylls with sori over most of the sporophylls surface
4	Sporophylls with sori over all of the sporophylls surface
5	Sporophylls with sori over all of the sporophylls surface releasing zoospore

Table 2. Ordinal ranking criteria for *Macrocystis pyrifera* reproductive state.

Finfishes

Fish surveys were initiated in the fall of 2019 and continue semi-annually (fall/spring) at four sites within the LJKF and three sites within the PLKF (Figs. 4 and 5, respectively). Sites were chosen based on topographic features that fish are known to prefer and are as similar as possible in reef size and rugosity based on previously collected bathymetric data (Parnell, 2015). Sites were paired within the LJKF where a large marine protected area (MPA, South La Jolla State Marine Reserve) is located in the southern half (Fig. 4). The take of all species is prohibited within the MPA which went into effect in 2012. Study sites within the LJKF and PLKF were paired by depth (21 and 15 m) to facilitate comparisons of the fish communities inside and outside the MPA (Table 3). Fish counts are conducted along replicate 30x4 m band transects (up to 3 meters off the bottom) which include an initial swimming count for conspicuous species followed by a thorough search for cryptic species using a dive light. The 'UrFL' was discontinued in 2020 due to chronically poor visibility and was replaced by station 'VR' located at the same depth and situated just to the west of our permanent PLC15 algal study site.

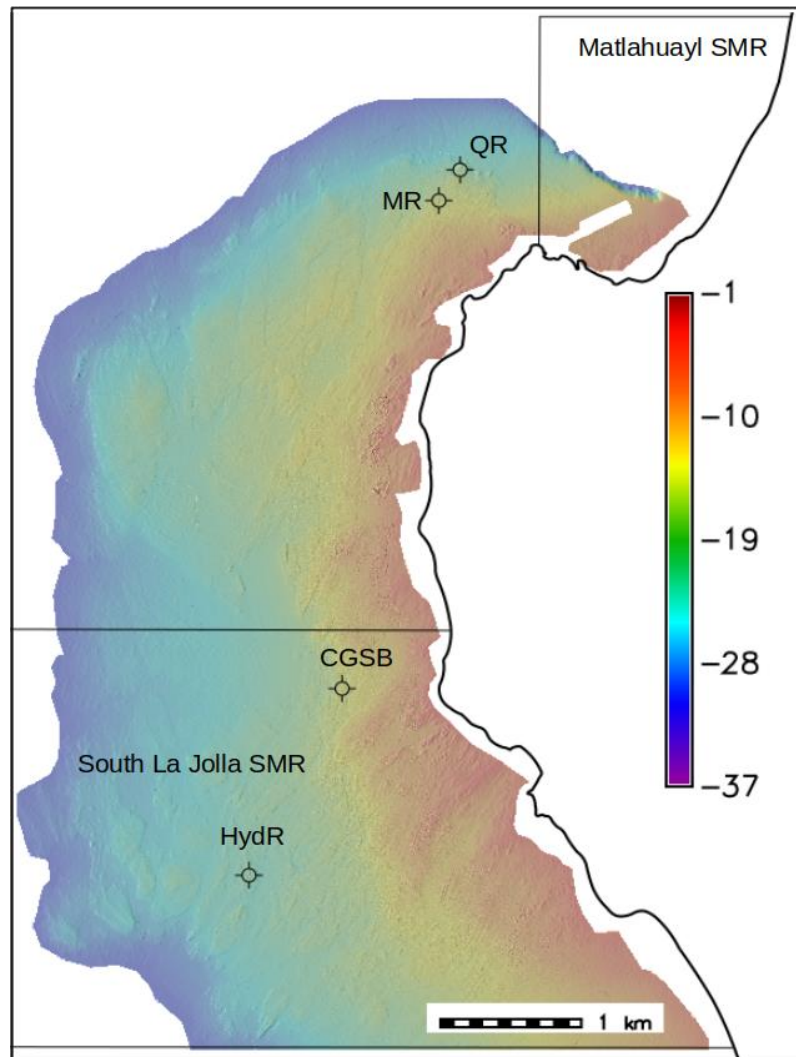


Figure 4. Locations of fish survey study sites within the La Jolla kelp forest. Color legend indicates depth in meters.

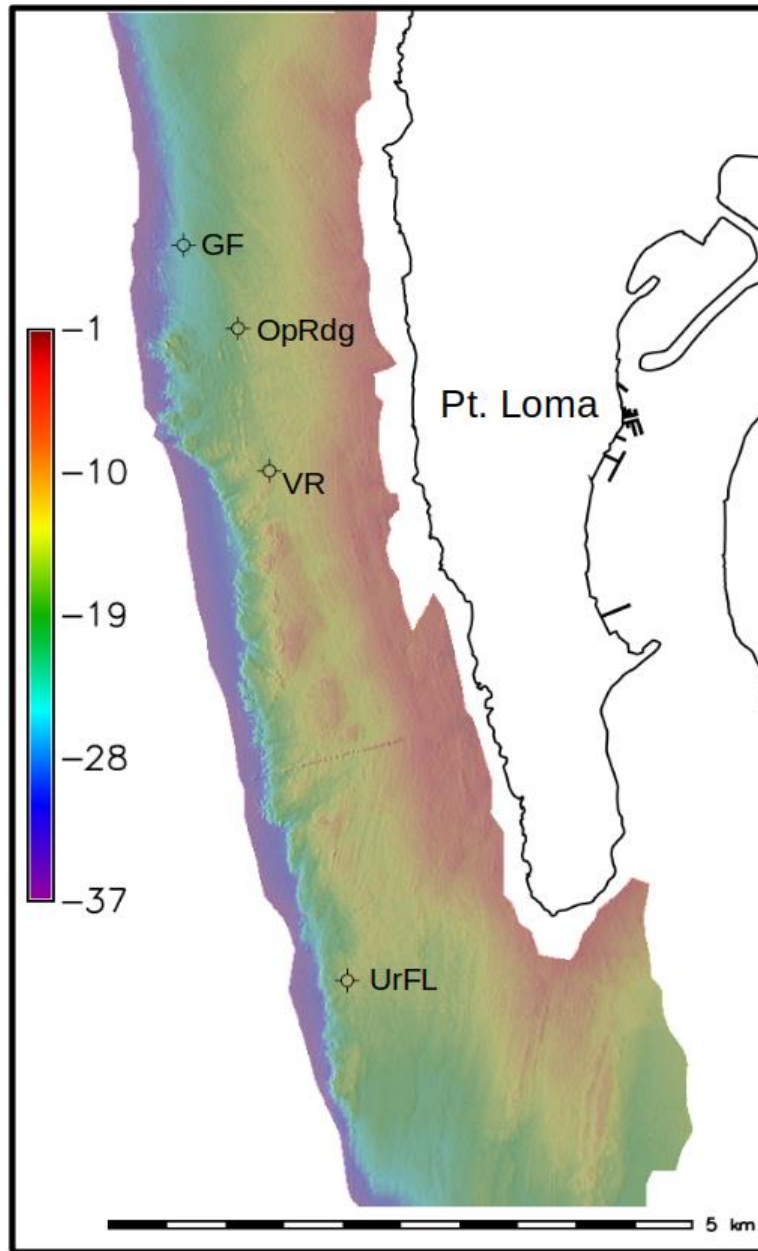


Figure 5. Locations of fish survey study sites within the Pt. Loma kelp forest. Color legend indicates depth in meters. Site 'UrFL' was replaced by 'VR' in 2020 (see text).

Site	Kelp Forest	Depth (m)	MPA	MPA Pairings	Species Richness
QR	La Jolla	21	No	A	27
HydR	La Jolla	21	Matlahuayl SMR	A	39
MR	La Jolla	15	No	B	30
CGSB	La Jolla	15	Matlahuayl SMR	B	23
VR	Pt. Loma	15	No	A	33
OpRdg	Pt. Loma	15	No	A	37
GF	Pt. Loma	21	No	B	33

Table 3. Site details and species richness for fish surveys.

Light

Marine algae are dependent on ambient light to support photosynthetic production enabling growth, reproduction, and recruitment. The aerial extent of where giant kelp can be found is mainly controlled by the availability of hard substrate at depths where light penetration is adequate for gametogenesis and growth since the plants must all recruit and begin growth at the bottom. Light is attenuated in a logarithmic fashion with ocean depth, and various wavelengths are attenuated differentially. Photosynthesis is facilitated by visible light having wavelengths between 400 and 700 nanometers. Light energy within this bandwidth is generally considered to be of primary importance for photosynthesis and is termed Photosynthetic Active Radiation (PAR). Longer wavelength red light is most rapidly attenuated with depth, while shorter wavelength blue light, most important for gametogenesis in Laminarian kelps including *M. pyrifera* (Lüning and Dring, 1975), penetrates further into the water column. Light availability limits the deepest depths that giant kelp can exist along the mainland shelf of southern California to ~25 m. The clearer offshore waters bathing many of the Channel Islands support kelp stands as deep as ~35 m. The main limiting factor for kelp recruitment at depth is the availability of light for gametogenesis, the lower limit of which has been estimated as a quantum dose of ~0.4 mol of photons m⁻²d⁻¹ (Deysler and Dean, 1984), and ~0.7 mol of photons m⁻²d⁻¹ for early sporophyte growth (Dean and Jacobsen, 1984). As light becomes more limiting with depth, the recovery of giant kelp from disturbances such as a MHW, is more limited due to the limited periods that bottom illumination is adequate for gametogenesis and the growth of the early sporophytes.

Bottom PAR was measured at three depths off central Pt. Loma along a cross-shore transect near the permanent algal study sites but in areas without giant kelp canopy. These areas are dominated by low growing understory algae thus precluding shading by nearby giant kelp canopy. The measurement sites off Pt. Loma are located at 24, 15, and 9 m deep. Submarine light is also measured off southern La Jolla at a depth of 24 m. PME miniPAR loggers equipped with LICOR LI-192 quantum sensors are used to measure bottom PAR. Sampling was conducted at 1 minute intervals and the sensors were wiped at 4 hour intervals using a PME miniWIPER to keep the sensor surface clear of marine growth.

RESULTS AND DISCUSSION

Ocean Climate

The ENSO index (ONI – Oceanic Niño Index, Fig. 1) is based on equatorial sea surface temperatures in the eastern Pacific Ocean. ENSO warming and cooling of the west coast of the Americas propagates poleward from the tropics, and the extent that individual El Niño or La Niña events propagate to higher latitudes varies greatly. Therefore, while correlated, the magnitudes of ENSO events at the equator and temperatures along the SCB can be somewhat decoupled.

The bottom temperature record along the central Pt. Loma study sites extends back to 1983 when the strong 1982/1983 El Niño was ebbing. Since then, the largest temperature signals in the time series include the 1997/98 El Niño and the extended warm period of 2014-2016 that was associated with a large scale anomalous NE Pacific warm event (DiLorenzo and Mantua, 2016) termed the BLOB but more recently referred to as a marine heat wave (MHW). This was immediately followed by a strong El Niño in 2015/2016 (Figs. 1, 6, and 7). The ONI (Fig. 1) and the Pt. Loma bottom temperature time series (Fig. 6) are highly concordant for the largest ocean climate events including the onset of the coupled BLOB/El Niño warm event beginning in late 2014 which began to ebb by the spring of 2016 and was immediately followed by cooler La Niña conditions in late 2016. Another cool period occurred between fall 2018 and summer of 2019 that continues to the present (through winter 2022). An anomalous warm event occurred during the summer of 2018 during which surface waters (upper 3-5 m) exceeded 27°C and stayed warm through most of the summer. This event was not observed at the bottom at any of the study sites as it was limited to near surface waters, but was evident in the Scripps Pier temperature time series (Fig. 7) and included the warmest temperatures ever observed in the time series. This warm event caused significant deterioration of the giant kelp surface canopy which virtually disappeared over the summer. However, most plants were still growing and healthy beneath the warm surface layer at the study sites where recovery from the MHW had occurred, because bottom temperatures remained relatively cool during the summer of 2018. Surface warming also occurred during the summers of 2020 and 2021 (Fig. 8, top panel). The recent trend of record and near-record surface temperatures and concomitant near-surface thermocline strengthening poses yet another risk to the health of giant kelp since most canopy biomass is located within the upper 3 meters of the water column. The bottom panel of Figure 8 shows the strength of stratification within the upper 5 meters of the water column. Recent increased near-surface stratification has been attributed to surface warming and exacerbates nutrient limitation as mixing of cooler more nutrient rich waters from below is weakened.

Less pronounced warm periods occurred between the 1997/98 and 2016/17 El Niños. Most notable was the 2005/2006 El Niño when much of the giant kelp canopy disappeared at the surface but plants still grew below the thermocline where nutrients were more abundant. Because bottom temperatures decrease with depth, nutrient stress during warming events also decreases with depth. This physical forcing is a fundamental mechanism that controls space competition between understory and canopy kelps. Strong El Niños such as the 1997/98 El Niño and the 2014-2016 marine heat wave penetrated to the bottom for extended periods even at the offshore edge of the forest stressing all kelps including understory species. By contrast, milder El Niños do not typically penetrate to the bottom of the forests for extended periods (e.g., >1 month), and therefore primarily stress the surface canopy kelps (mainly *M. pyrifera*) more than the understory kelps where temperatures are cooler. Repeated cycles of mild to moderate El Niño events over many years in the absence of large storm waves can lead to understory domination at the expense of giant kelp canopy cover.

Bottom temperatures have been cool since the spring of 2018 (<15°C at all sites except for the central Pt. Loma 8 m site) leading to recruitment and growth at many of the study sites. Warming occurred during the fall and winter of 2018/2019 but temperatures have since cooled with bottom temperatures at study sites deeper than 12 m typically <13°C much of the time. La Niña or near La Niña conditions have dominated the eastern equatorial Pacific since summer of 2020 and southern California by extension. La Niña conditions are predicted to ebb this spring (2022) when ENSO neutral conditions will dominate along the equator and spread to southern California by summer (NOAA, 2022). However, as of this writing, a NE Pacific warm pool is developing that is similar to the BLOB of 2016, and if it continues to develop, it could encroach upon the western U.S. coast by fall. This will likely be deleterious to the giant kelp of southern California if it develops into a major MHW. Giant kelp recovery at the few sites where it has persisted since the last MHW will once again decline precipitously.

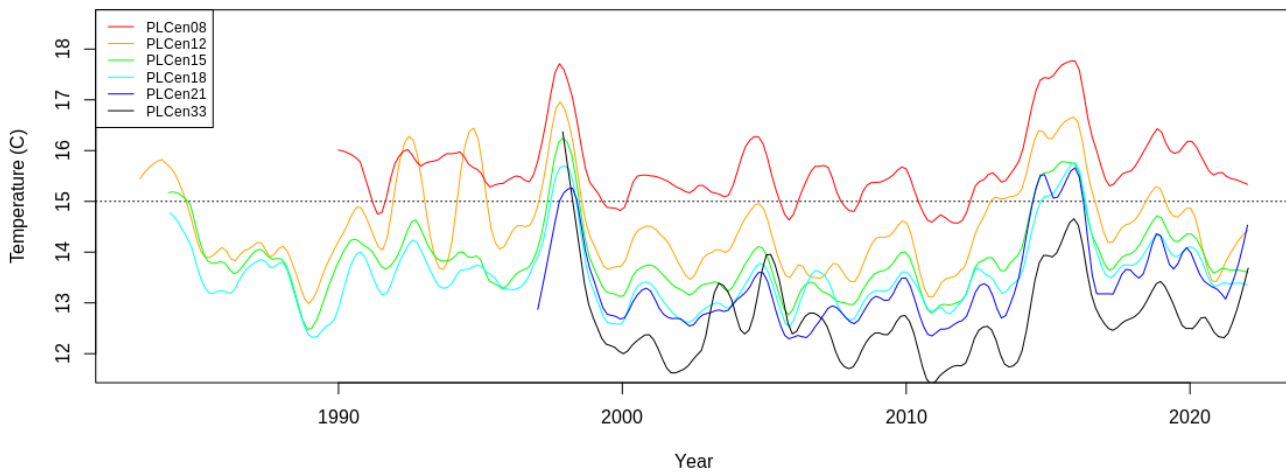


Figure 6. Ocean bottom temperature trends along the central Pt. Loma study sites. Horizontal gray line indicates the temperature above which nitrate concentrations are typically limiting for giant kelp growth.

SIO Pier Surface Temperature

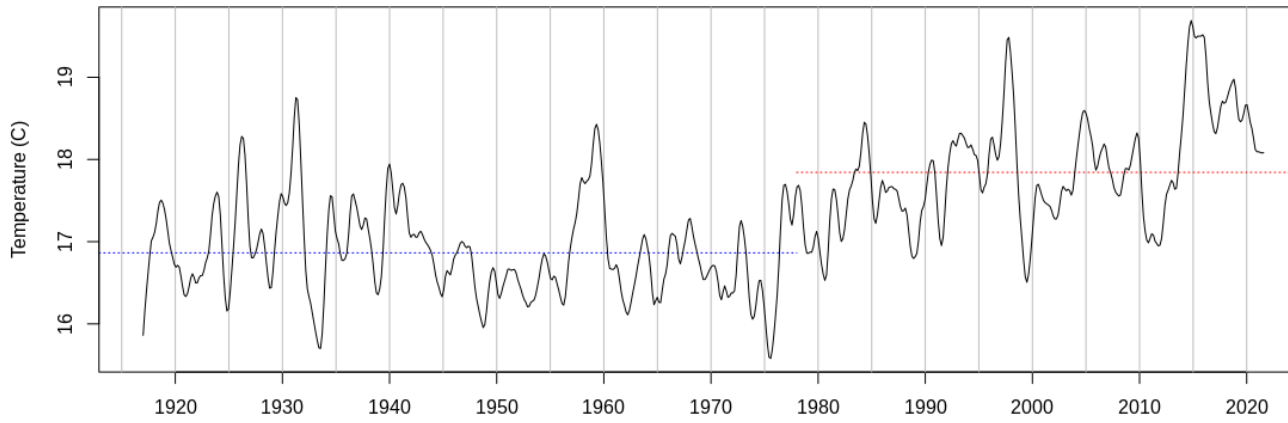


Fig. 7. Trend of surface temperature at the Scripps Institution of Oceanography Pier. Data inclusive through Fall 2021. Dotted blue/red line indicates mean temperature prior/after to regime shift of the late 70's.

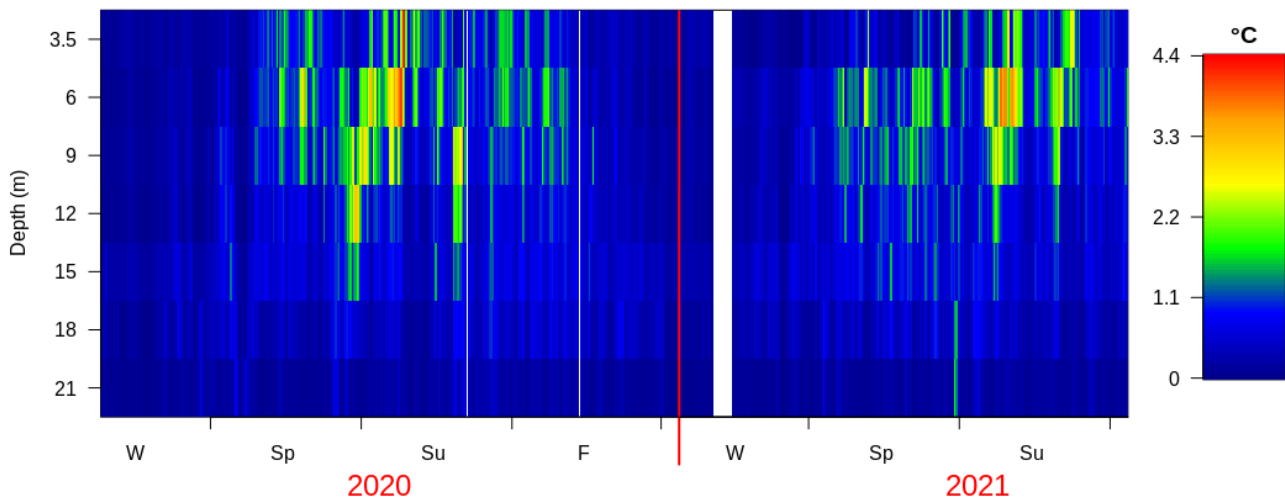
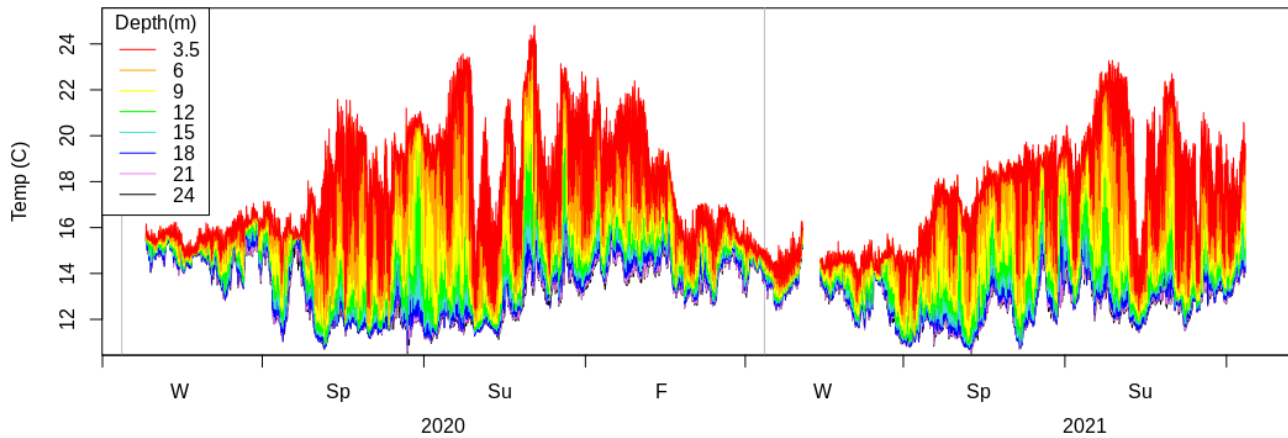


Figure 8. Time series of temperature profiles off south La Jolla (top panel). Bottom panel shows near-surface temperature stratification (temperature difference among thermistors by depth) during spring and summer of 2020 and 2021.

Light

Integrated daily PAR values for the three cross-shore study sites offshore of central Pt. Loma are shown in Fig. 9. Light levels were saturating at the 9m site most of the time with the exception of an intense red tide that dominated the coast of southern California during May of 2020. In contrast, light at the deeper end of the kelp forest at 24 m was well below the gametogenesis and growth thresholds for most of the time series except for a brief period of increased illumination during late winter early and early spring of 2021. Therefore, further recovery of giant kelp in the deeper portions of the Pt. Loma forest (20-25m) as part of any potential post-MHW recovery continues to be extremely limited. Recruitment periods are further limited by the need for a temporal match between kelp spore availability and periods of greater bottom illumination, a rare coincidence given the lack of kelp in the deeper areas of the kelp shelf off San Diego. The same is true for the La Jolla kelp forest. Light meter data from the southern portion of that forest at 24m (not shown) were similar to the data for the same depth off Pt. Loma.

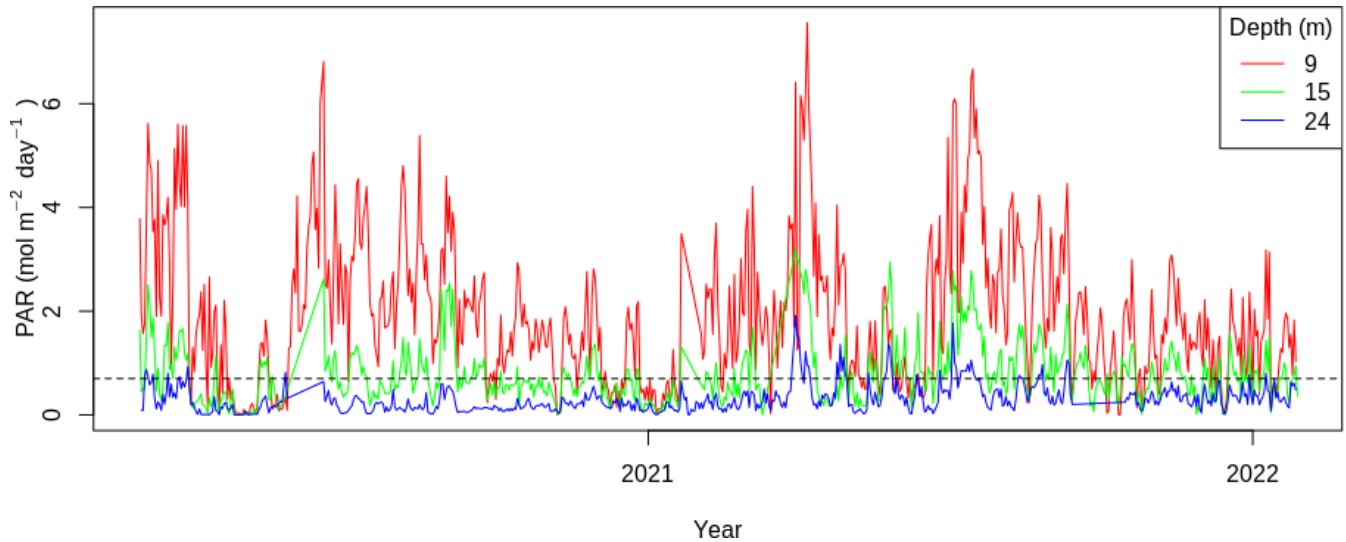


Fig. 9. Daily PAR illuminating the bottom along the central Pt. Loma algal study sites. Horizontal dashed line indicates PAR threshold values for juvenile giant kelp growth (Dean and Jacobsen, 1984).

Giant Kelp Status and Reproduction

The primary abundance pattern for *M. pyrifera* since the 1980's includes rapid declines associated with El Niños (Fig. 10) followed by step increases in plant and stipe density chiefly due to discrete pulses of recruitment leading to varying levels of recovery, or failed recovery if a cohort fails to reach adulthood or succumbs soon afterward. In addition to the temporal variation of regional ocean climate, the recruitment, maturation, and establishment of adult giant kelp plants are highly variable in space even within a single kelp forest. Densities of all life stages and stipes are shown in Figs. 10-13. Densities for these life stages at all of the 18 m deep sites off La Jolla and Pt. Loma are plotted in Fig. 14 for comparisons among the outer kelp forest sites where bottom temperatures are cool relative to shallower sites. Such conditions are typically more conducive for the recruitment and growth of early giant kelp life stages given adequate light.

The 2014-2016 MHW caused massive mortality of giant kelp off San Diego County mainly through a combination of nutrient and temperature stress. Giant kelp surface canopy was nearly entirely lost off most of San Diego, Orange, and Los Angeles counties during 2016 (MBC). Densities of adult *M. pyrifera* plants (Fig. 10) and stipes (Fig. 13) decreased dramatically at all study sites off San Diego. *M. pyrifera* recruited in some areas of the forests beginning as early as 2016 with subsequent recruitment observed in 2017 and 2018. Low levels of recruitment continued into the spring of 2019 (Figs. 11 and 12). Some of the 2016 site cohorts at least partially matured into pre-adults and adults at a subset of the sites.

The basic sawtooth pattern of giant kelp adult and stipe densities after major disturbances appears to have fundamentally changed since the recovery from the 1997 El Niño. Giant kelp recruitment still occurs after such events, but recovery to pre-disturbance densities has since been dampened to various degrees among the study sites. The only site where significant giant kelp recruitment has been observed during this reporting period occurred at PLM18 but is now failing to thrive. Generally, the status of giant kelp among the study sites in relation to the 2014-2016 MHW can be categorized as (1) recovery to giant kelp dominance, (2) recovery followed by collapse, (3) partial

recovery followed by collapse, (4) no recovery, and (5) not kelp dominated prior to the MHW nor afterward. Giant kelp has only maintained recovery at 3 of the 20 sites, all of which are 18 m deep (PLC18, PLS18, and LJS18). Collapsed recovery includes Cardiff, Solana Beach, LJNI2, LJNI5, LJS12, PLN18, PLC08, PLC12, PLC15, PLC21, PLS15, PLT15, and PLM18. LJS15 exhibited some recovery that has since collapsed. There has essentially been no giant kelp recovery at LJNI18 where giant kelp was abundant prior to the MHW and at Del Mar where giant kelp is completely absent and was at very low density prior to the MHW. The reasons for such poor giant kelp performance when growth conditions have been supportive for recovery varies among the study sites, and is not understood at others, particularly LJNI18. A combination of competition with understory species, low light conditions, and the lack of nearby reproductive plants all contribute to this pattern of limited giant kelp recovery. An early colonizing post disturbance brown alga, *Desmarestia ligulata*, dominated the PLT15 and PLM18 study sites until 2019, thus delaying giant kelp recovery via competitive exclusion at those sites.

The poor condition of *M. pyrifera* at most of the study sites is best exemplified in Table 4 which lists the quantiles of stipe sums at each of the sites for the latest sampling bout (Fall, 2021). The site that is currently in the best condition relative to historical data is PLM18 where the quantile for the present stand is ~0.95 for that site. The next greatest quantiles were observed at PLT15 and LJNI18 which each exhibited >0.8 quantiles. These two sites are also doing well by historical standards. This was less true at PLC18 and PLC12 which are presently above the 0.5 quantiles indicating a moderate condition historically. Stipe numbers at the the remaining sites are not doing well, especially PLC21, LJNI12, PLS15, LJNI18, Cardiff, LJS12, PLC15, PLN18 and LJNI15. Quantiles at these sites highlight the present reduced canopy of giant kelp off much of San Diego County despite the recent growth conditions that have now been favorable for nearly four years. This may herald the fundamental shift discussed in Parnell et al., (2010) in which the southern limit of *M. pyrifera* is suddenly shifted northward and kelp forests in southern California begin to mirror algal stands off central Baja California which are typically dominated by understory kelps, particularly *Eisena arborea*. The next El Niño or strong NE Pacific MHW will likely decimate giant kelp even more. One possible mechanism that might reverse this trend would be a very powerful storm effectively eliminating or significantly reducing understory species followed immediately by the onset of good growth conditions such as a La Niña.

Site	Stipe Sum Maximum	Date Maximum Observed	Fall 2021 Stipe Sum	Fall 2021 Stipe Quantile
PLM18	926	2008-12-17	570	0.95
PLT15	770	1999-10-20	245	0.82
LJS18	2114	2009-08-14	1648	0.81
PLC18	3336	1990-10-19	1519	0.66
PLC12	2665	1985-04-11	365	0.53
SB	2933	2011-11-10	574	0.44
LJS15	3341	1994-08-23	82	0.42
PLC08	2454	2018-08-09	294	0.41
PLS18	2483	1994-06-06	214	0.41
DM	519	2010-09-03	0	0.41
PLT12	1952	2008-08-19	0	0.40
PLC21	3274	2013-05-02	116	0.31
LJN12	607	2014-02-11	4	0.28
PLS15	2110	1994-08-25	66	0.17
LJN18	2093	2010-08-04	0	0.16
Card	3341	2014-02-13	8	0.16
LJS12	1013	2018-08-07	66	0.15
PLC15	3819	1989-06-29	114	0.10
PLN18	3083	2013-08-15	0	0.05
LJN15	2161	2013-11-13	0	0.05

Table 4. *Quantiles of giant kelp (M. pyrifera) stipe sums observed during the latest sampling bout (Fall, 2021) for stipe sum distributions over time by individual sites. Date indicates the day that each site maximum was observed. Rows are ordered by decreasing quantile values.*

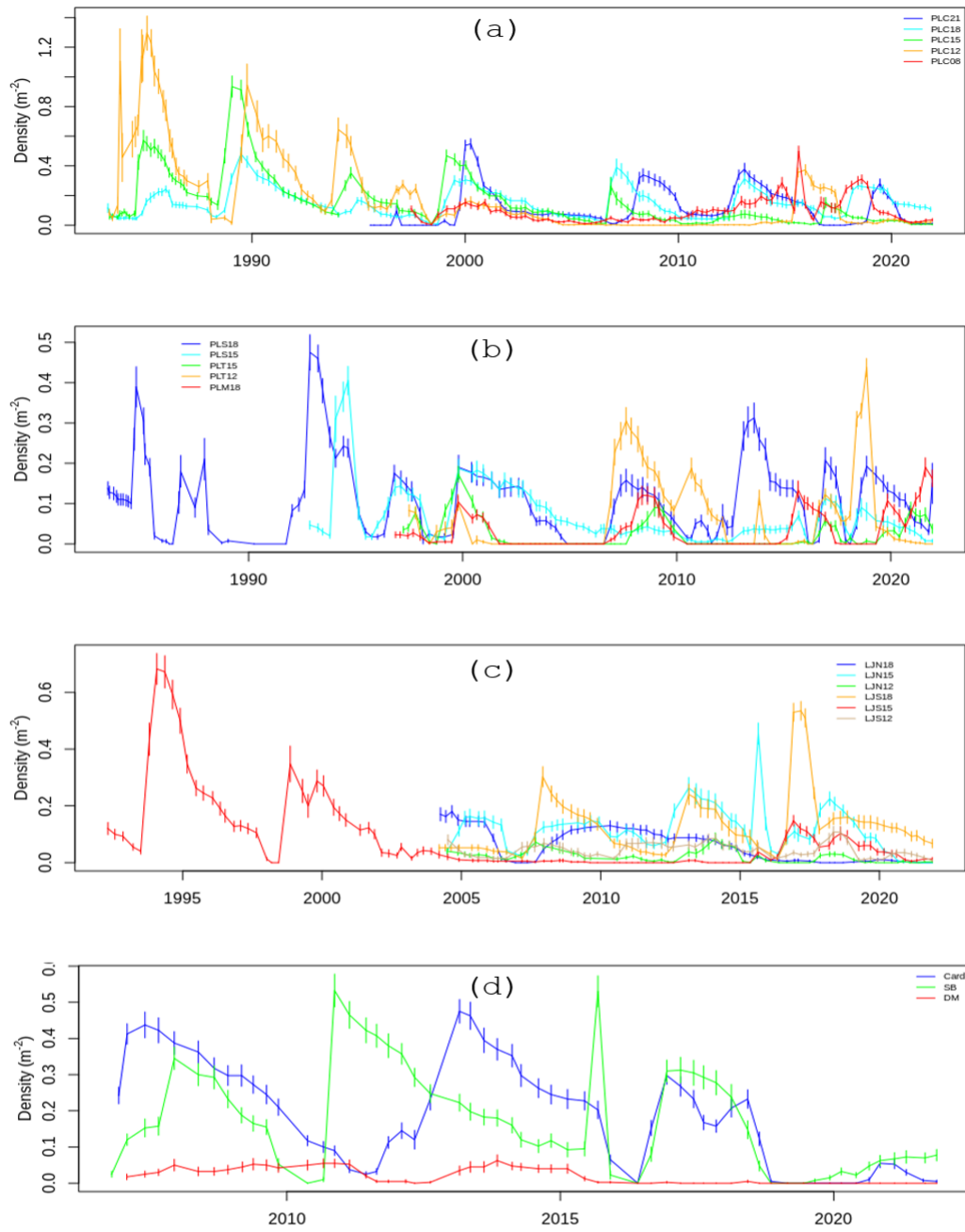


Figure 10. Mean densities of adult *Macrocyctis pyrifera* among study site groups: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County. Error bars indicate standard errors.

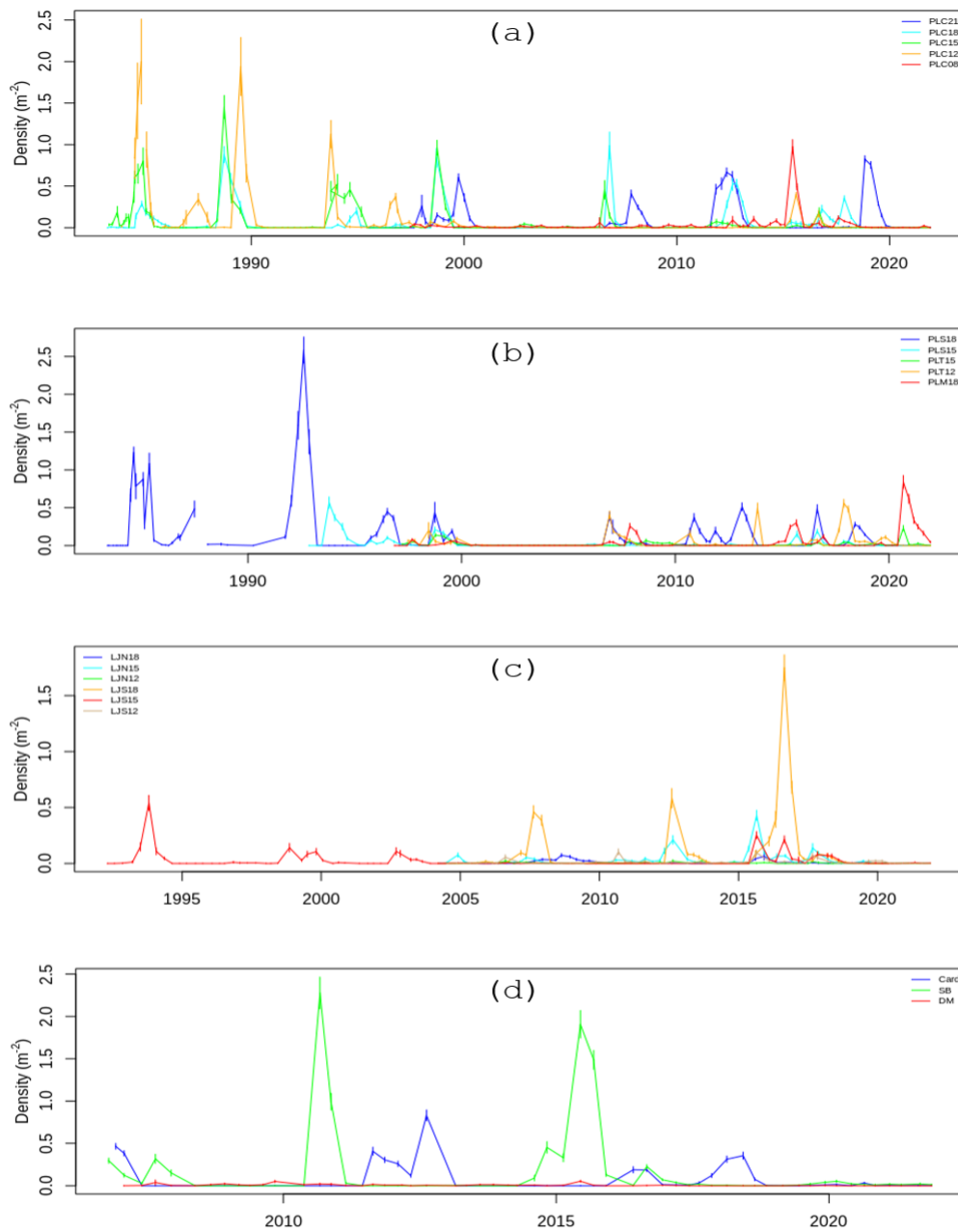


Figure 11. Mean densities of *Macrocystis pyrifera* pre-adults (<4 stipes): (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

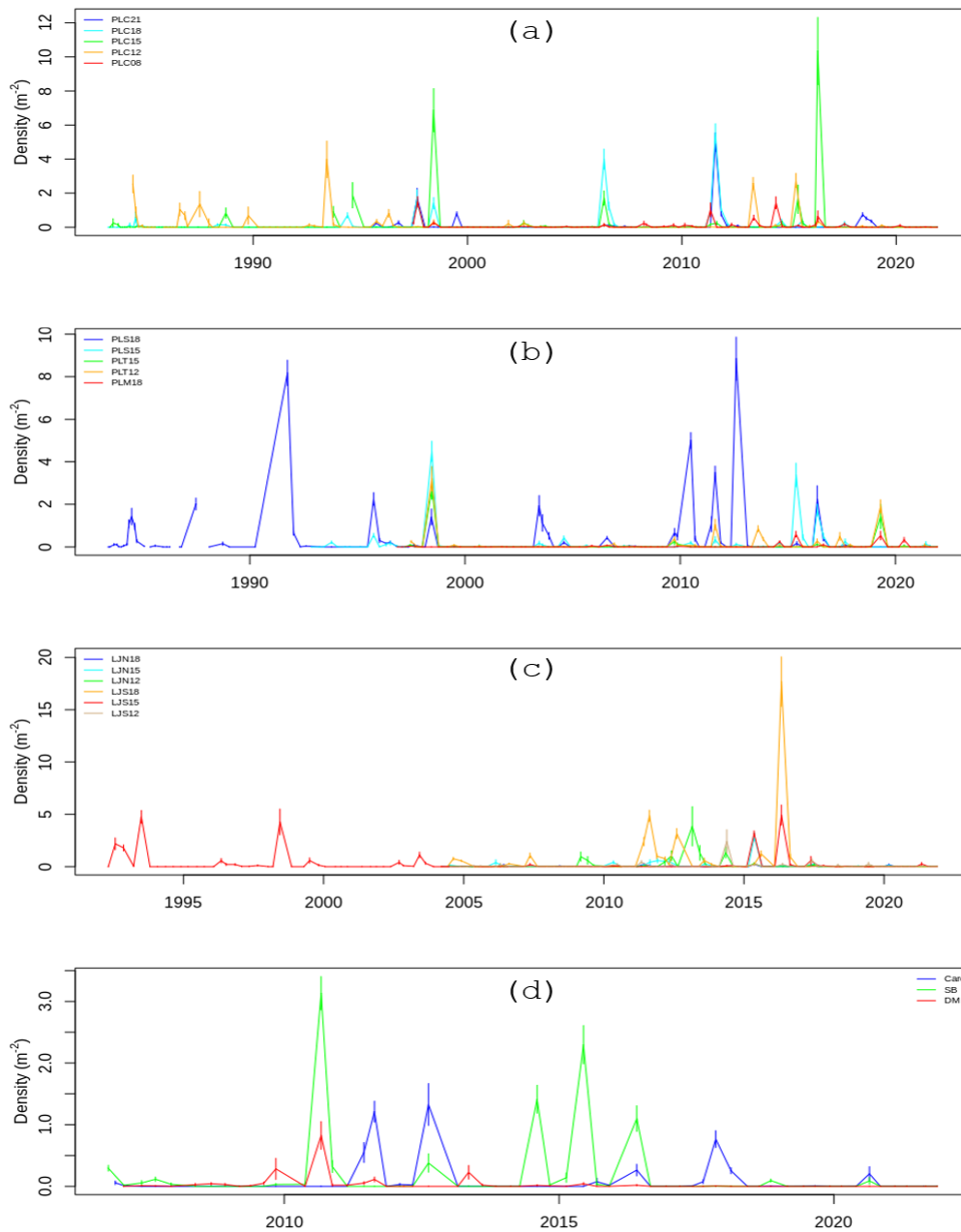


Figure 12. Mean densities of *Macrocyctis pyrifera bifurcates*: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors

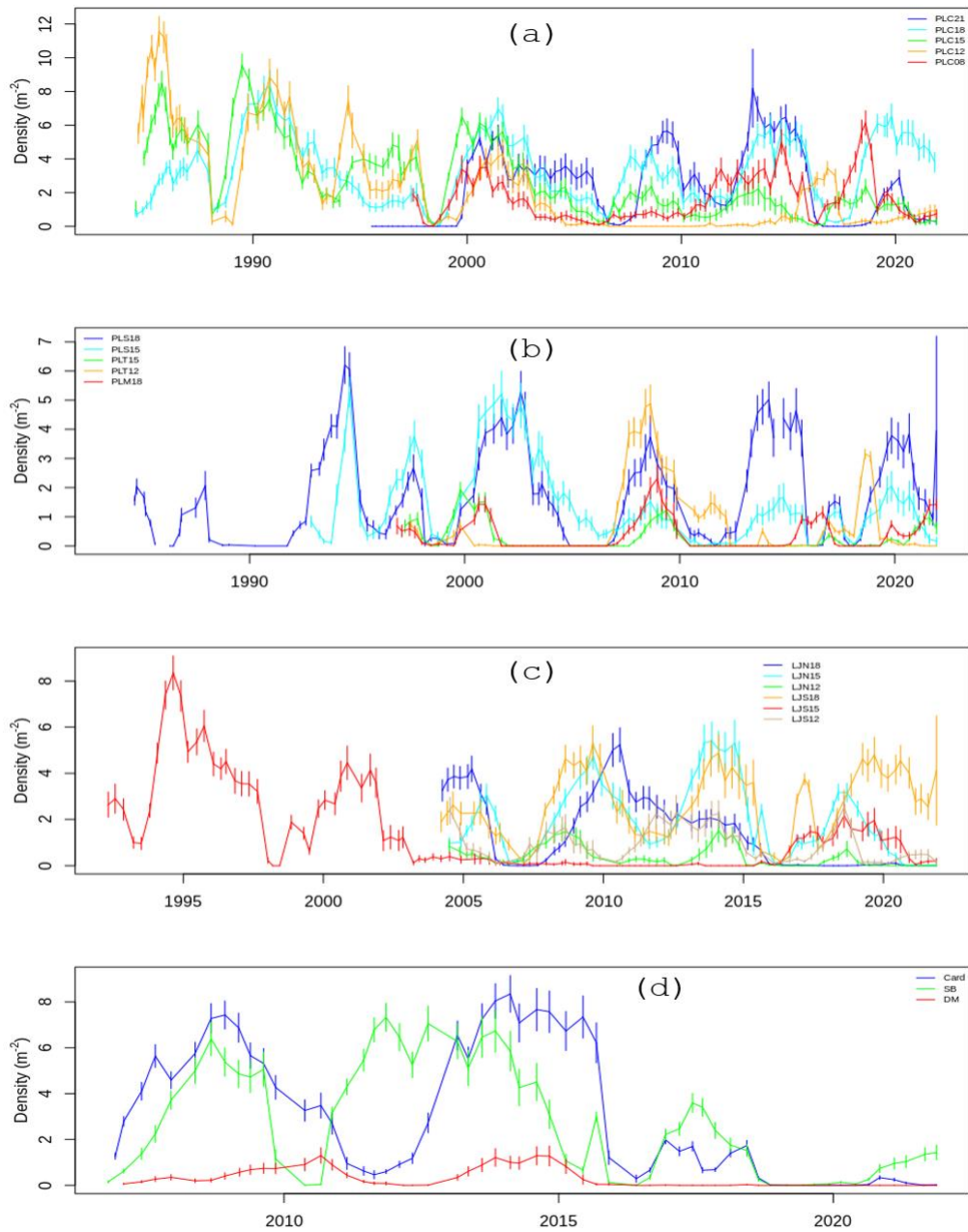


Figure 13. Mean densities of *Macrocystis pyrifera* stipes: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

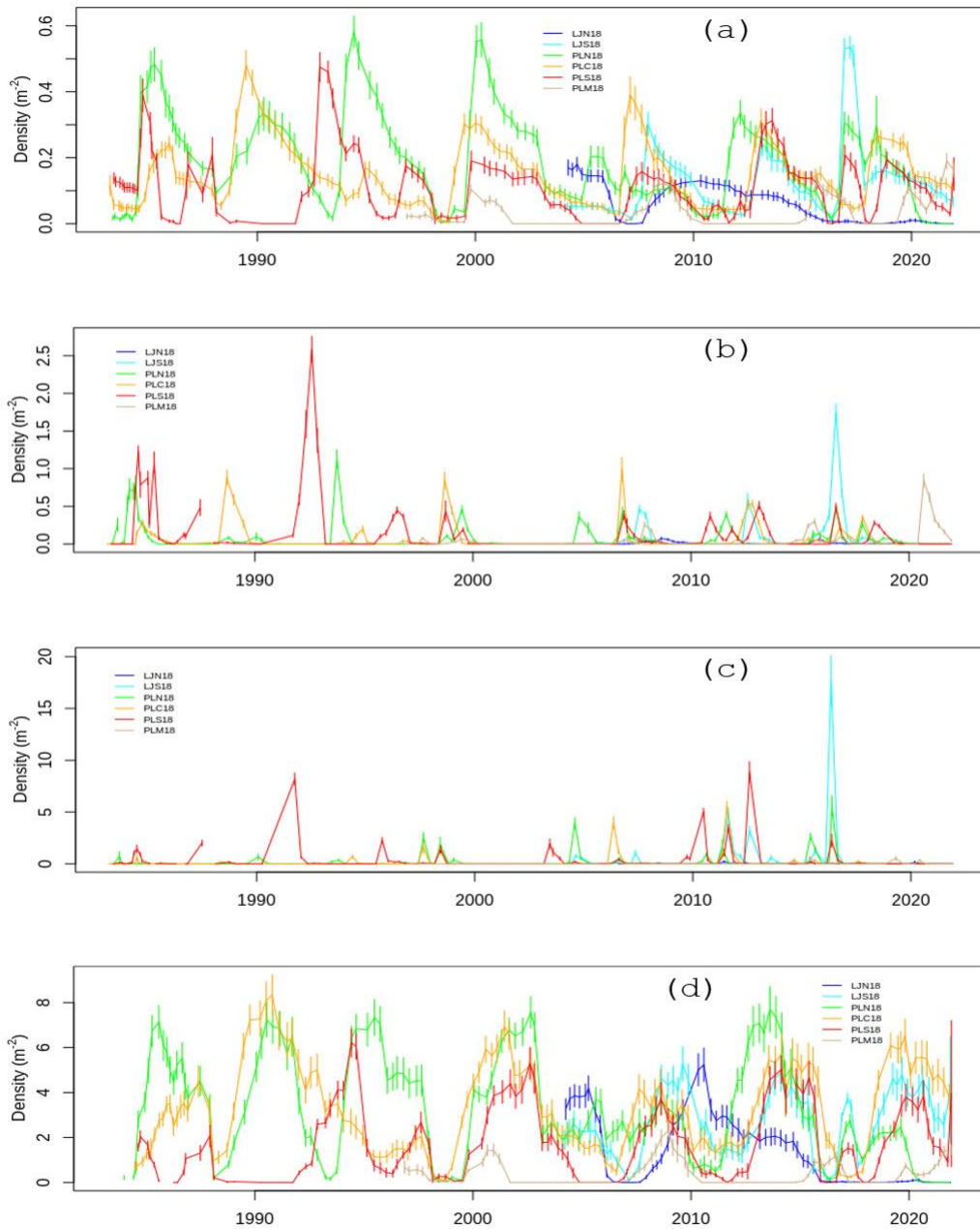


Figure 14. Mean densities of *Macrocyctis pyrifera* (a) adults, (b) pre-adults, (c) pre-bifurcates, and (d) stipes along the 18 m sites off La Jolla and Pt. Loma. Error bars indicate standard errors.

The reproductive condition of giant kelp along the central Pt. Loma study sites was greatly diminished through the MHW and by the end of the 2016 El Niño (Fig. 14). Reproductive capacity was uniformly the lowest among all study sites over the entire time series dating back to before the 1997/98 El Niño. Sporophyll volumes were greatly reduced by the end of the 2016 El Niño and sporophylls were not reproductive at the PLC8 and PLC21 study sites where adult plants were the most abundant. Such greatly diminished reproductive capacity of giant kelp is both an indicator of how stressful the MHW of 2014-2016 was for *M. pyrifera*, but has also likely limited the rate at which giant kelp has been able to recover since that time given the relationship between reproductive capacity as a function of the number of stipes for individual plants (Fig. 15d). Figure 15d indicates that the reproductive output of individual plants relative to their biomass (stipes) has not returned to historical levels suggesting continued stress. The only study site where reproductive capacity has at least briefly recovered is the central Pt. Loma site at 15 m (PLC15) where densities of *M. pyrifera* are low relative to the historical record.

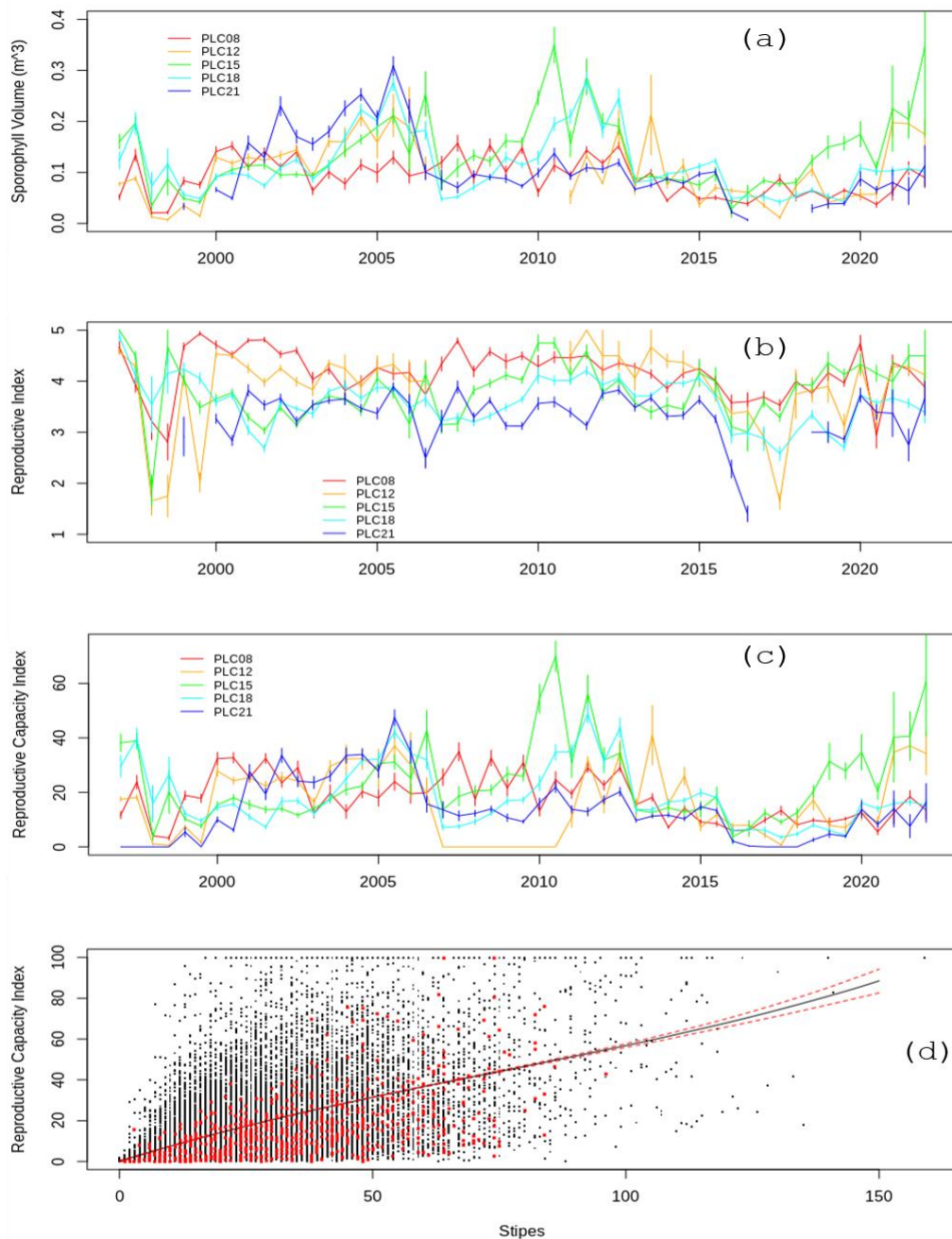


Figure 15. Reproductive states of *Macrocystis pyrifera* at the central Pt. Loma study sites: (a) sporophyll volume, (b) reproductive index (see Table 2), (c) reproductive capacity (derived index of relative among-site reproductive potential - see Methods). Means are plotted and error bars indicate standard errors. (d) Reproductive capacity of *Macrocystis pyrifera* as a function of the number of stipes. Fit is a second order polynomial fit and dashed red curves indicate 95% confidence interval. Data are inclusive between 1997-2021. Red points indicate present study period (2020-2021).

Understory Kelp Status and Reproduction

Understory kelps and turf algae grow close to the bottom, and unlike the local canopy forming kelps (*M. pyrifera*, *Egregia menziesii*, and *Pelagophycus porra*), do not have buoyant pneumatocysts to support photosynthetic tissue up in the water column where light is more abundant. Therefore, high densities of canopy forming kelps outcompete understory kelps and turf algae. El Niño events modulate this competition between the two types of canopy guilds. Buoyant, warm and nutrient depleted water is nearest the surface where most of the photosynthetic and nutrient absorbing tissue for giant kelp is distributed. Therefore, giant kelp is disproportionately stressed by El Niño events. By contrast the understory and turf canopy guilds are exposed to cooler and more nutrient replete waters. As the surface canopy begins to lose tissue and die, the light field for the lower canopy guilds increases leading to rapid growth and reproduction.

Pterygophora californica, a stipitate understory kelp has a central woody stipe that supports photosynthetic blades from below. Stipes can grow up to >2 m in height off the bottom and individuals can persist for decades. The growth form consists of a ribbed terminal blade that grows outward from the end of the stipe. Sporophyll blades grow horizontally outward from the narrowed margins of the stipe. Soral (reproductive) tissue develops on these side branching sporophyll blades. *Laminaria farlowii*, a prostrate understory kelp grows as a long blade along the bottom where it is attached by a small woody stipe and holdfast. Soral tissue develops along the length of the blade. Reproduction and growth is seasonally offset in both species with growth occurring during late spring and summer while reproductive tissue development peaks in winter.

Pterygophora californica and *Laminaria farlowii*, were affected differently by the consecutive warm periods that constituted the 2014-2016 MHW. The main effects on *P. californica* manifested into two groups of sites (Fig. 16). The first group included sites where densities decreased dramatically during the MHW and remained low during and after the 2016 El Niño (PLC21, PLC18, PLC12, PLC08, LJS15, LJS12, LJS12). Densities of *P. californica* at the second set of sites decreased during the BLOB then increased rapidly just after the 2016 El Niño (PLC15, LJS18, LJS15). Densities of *P. californica* at the North County sites have been persistently low and remain low at present with the exception of a 2017 cohort that died by late 2018. Presently, *P. californica* is present in at least moderate density (>1m⁻²) at the LJS15, PLC15, and PLT12 study sites. The 2016 cohort is still thriving at the sites where post El Niño recruitment was greatest (PLC15 and LJS15). *P. californica* at LJS18 has nearly disappeared at LJS18 where *M. pyrifera* has begun to dominate.

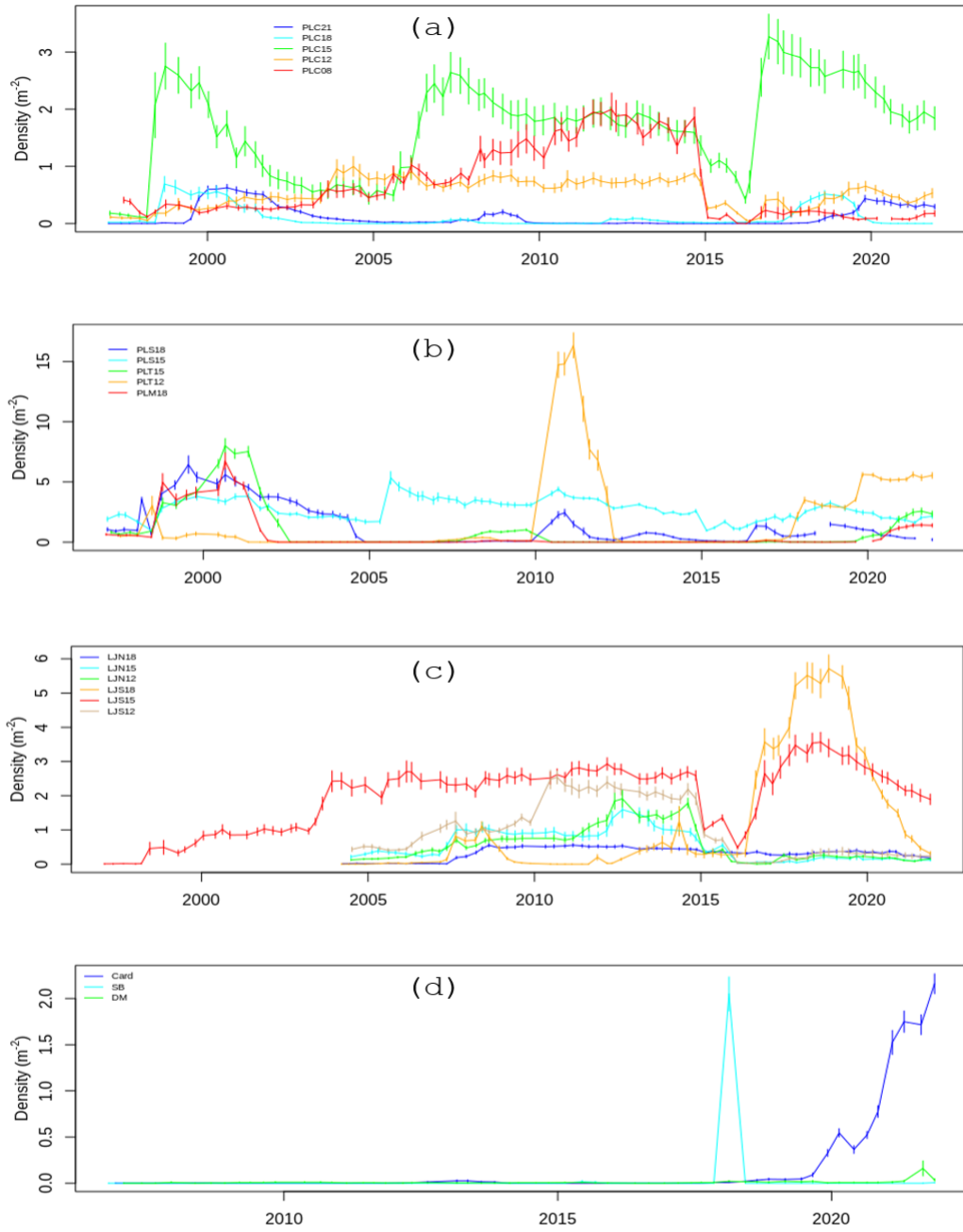


Figure 16. Mean densities of the understory kelp *Pterygophora californica*: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

The response of *L. farlowii* to the MHW also varied among study sites (Fig. 17). The most common pattern has been its increase in cover that was occurring at many sites prior to the MHW. These include all of the central Pt. Loma sites with the exception of PLC18 where *M. pyrifera* is now clearly dominant. *Laminaria farlowii* population trajectories within the south Pt. Loma and La Jolla study sites were generally relatively stable until the MHW but have recovered since with the exception of PLS18, LJNI18, and LJS18. Densities within the north county kelp forests are low by comparison but are increasing, most rapidly at Cardiff.

Densities of *Cystoseira osmundacea* generally increased prior to and during the MHW. Densities have since decreased at some of the sites off La Jolla from their 2018/2019 peak, particularly at the LJNI18 site. This was also true at the PLS15 study site where *C. osmundacea* was increasing prior to and after the MHW, but has since decreased rapidly with a new cohort of recruits leading to increasing densities since late 2020. *C. osmundacea* at PLT12 began to increase through the 2016 El Niño which continues at present. However, densities of *C. osmundacea* at all sites in south Pt. Loma are low in comparison with other areas. The most important pattern among most of the study sites has been the increase in understory, particularly *L. farlowii* and *C. osmundacea*, which has been facilitated, or has directly contributed to declines in *M. pyrifera* at many sites. The general resistance of understory to heat waves and storm disturbance relative to *M. pyrifera*, and their ability to outcompete giant kelp for space, means that this pattern of understory domination will likely continue well into the future barring the occurrence of a really large storm or strong MHW.

The complex trajectories of understory species during and after the consecutive warm periods appear to have switched states. These states can be defined by three canopy/understory modes and are forced by the shading effects of *M. pyrifera* surface canopy. The three modes include (1) lush to moderate surface canopy with less understory, (2) lush understory with reduced surface canopy, and (3) lush to moderate canopy with low fractional cover of understory. A fourth ephemeral mode was also observed during the MHW where both canopy and understory were sparse, forced by the unprecedented duration of nutrient stress during the combined warm periods. In contrast to previous warming events when the shading effect of giant kelp on understory decreases due to thinning of the surface canopy, warm temperatures during the BLOB penetrated to the bottom for an extended period of time (Fig. 6). This resulted in long periods of nutrient stress for these lower canopy species, and delayed their recovery even when bottom light levels increased during periods of low surface canopy.

The growth and reproductive condition of tagged *P. californica* (Figs. 19 and 20) and *L. farlowii* (Figs. 21 and 22) at the central Pt. Loma study sites decreased dramatically during the BLOB but have since increased. Growth and reproduction of *P. californica* remained depressed at the deeper central Pt. Loma sites until 2017 and has since decreased at PLC18. Decreased reproductive output by both species can delay understory recovery after El Niño disturbances (Dayton et al., 1984), and may contribute to the persistence of switched canopy/understory patch modes. Such forcing can result in long term dominance over giant kelp than can persist for several years until the occurrence of a new major disturbance. For both species, growth, and reproduction, to a more limited extent, have recovered at all the study sites off central Pt. Loma. Growth and reproduction of *P. californica* was clearly more affected than *L. farlowii* by the marine heat wave of 2014-2016 and has been somewhat slower to recover.

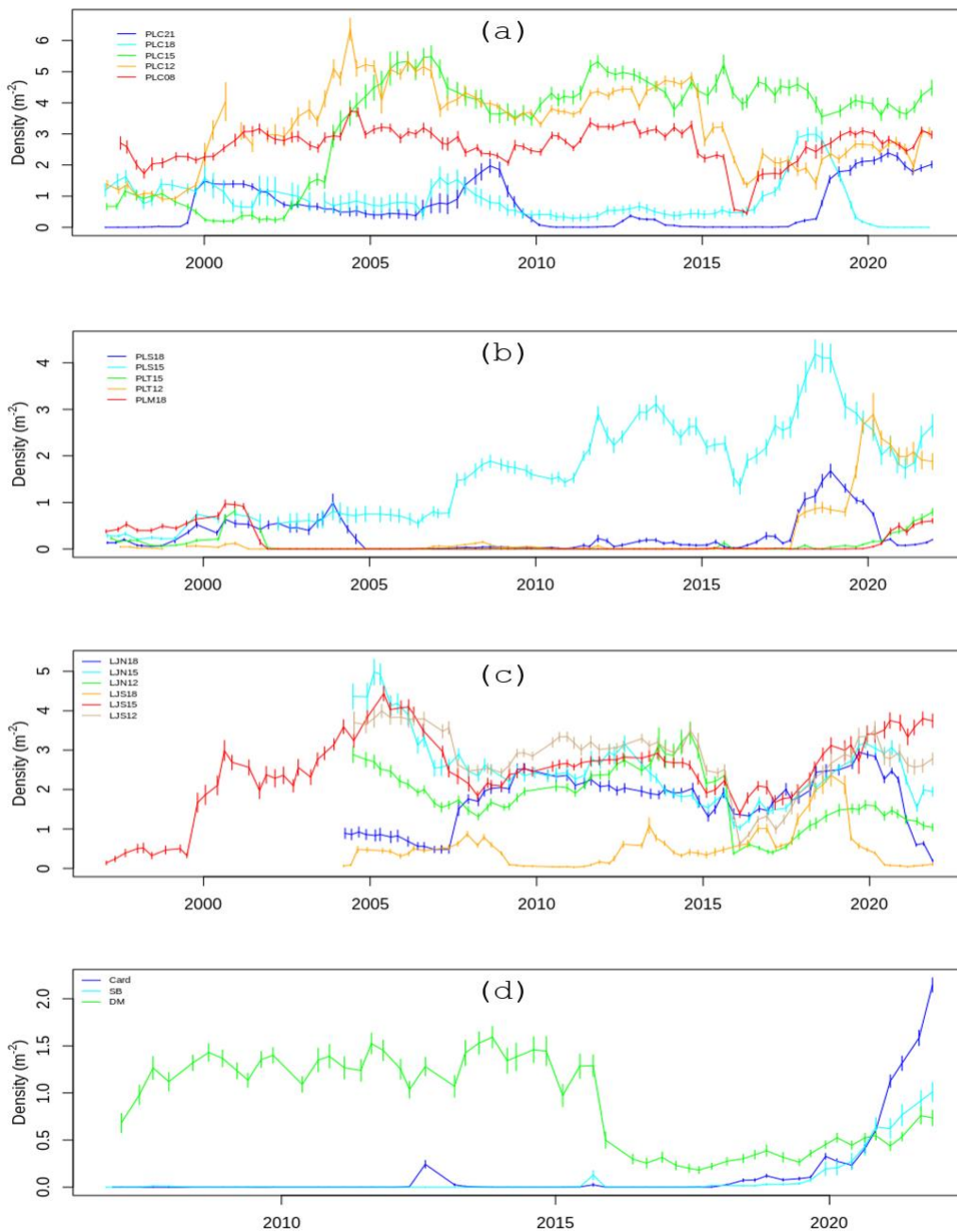


Figure 17. Mean densities of the understory kelp *Laminaria farlowii*: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

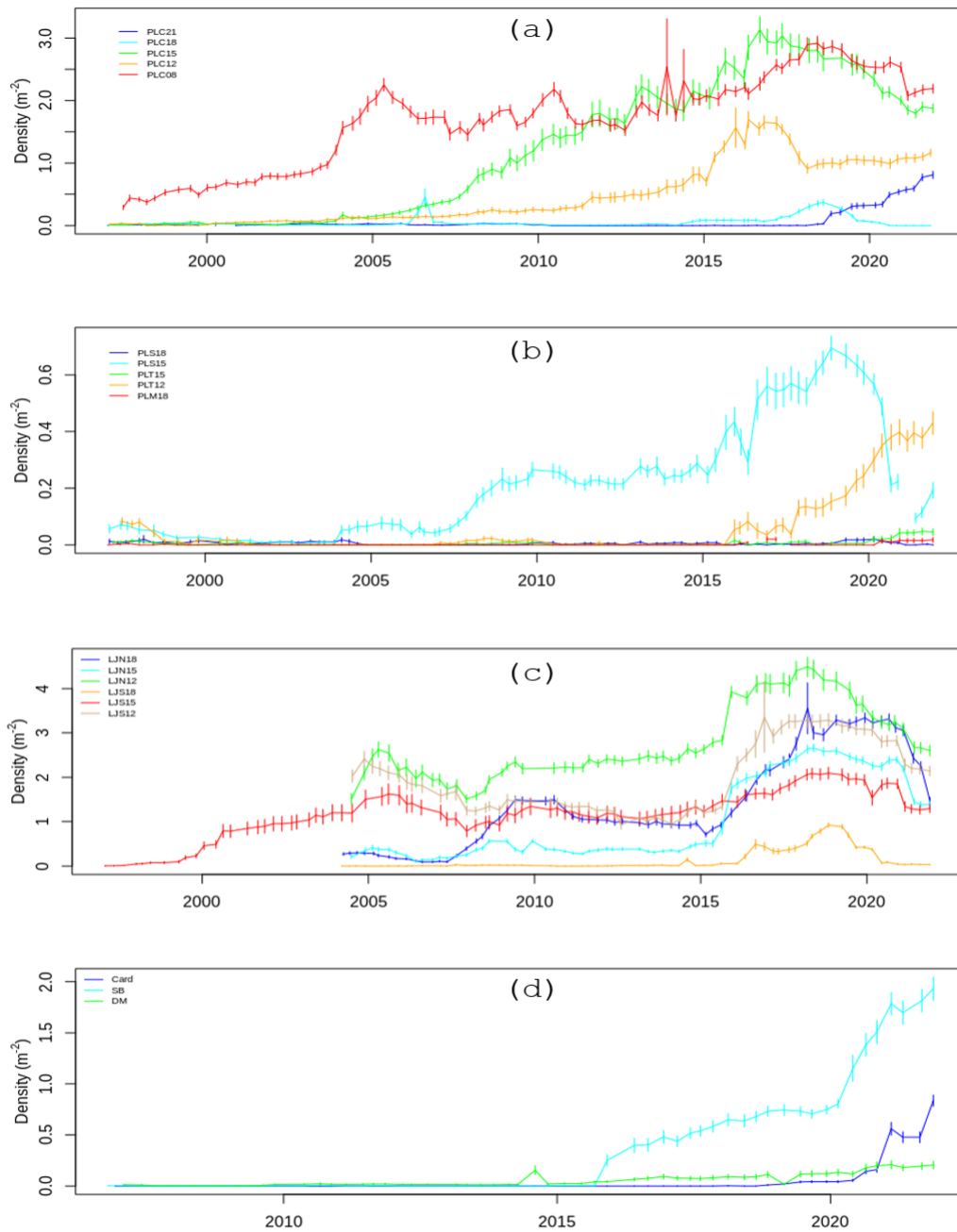


Figure 18. Mean densities of the understory kelp *Cystoseira osmundacea*: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

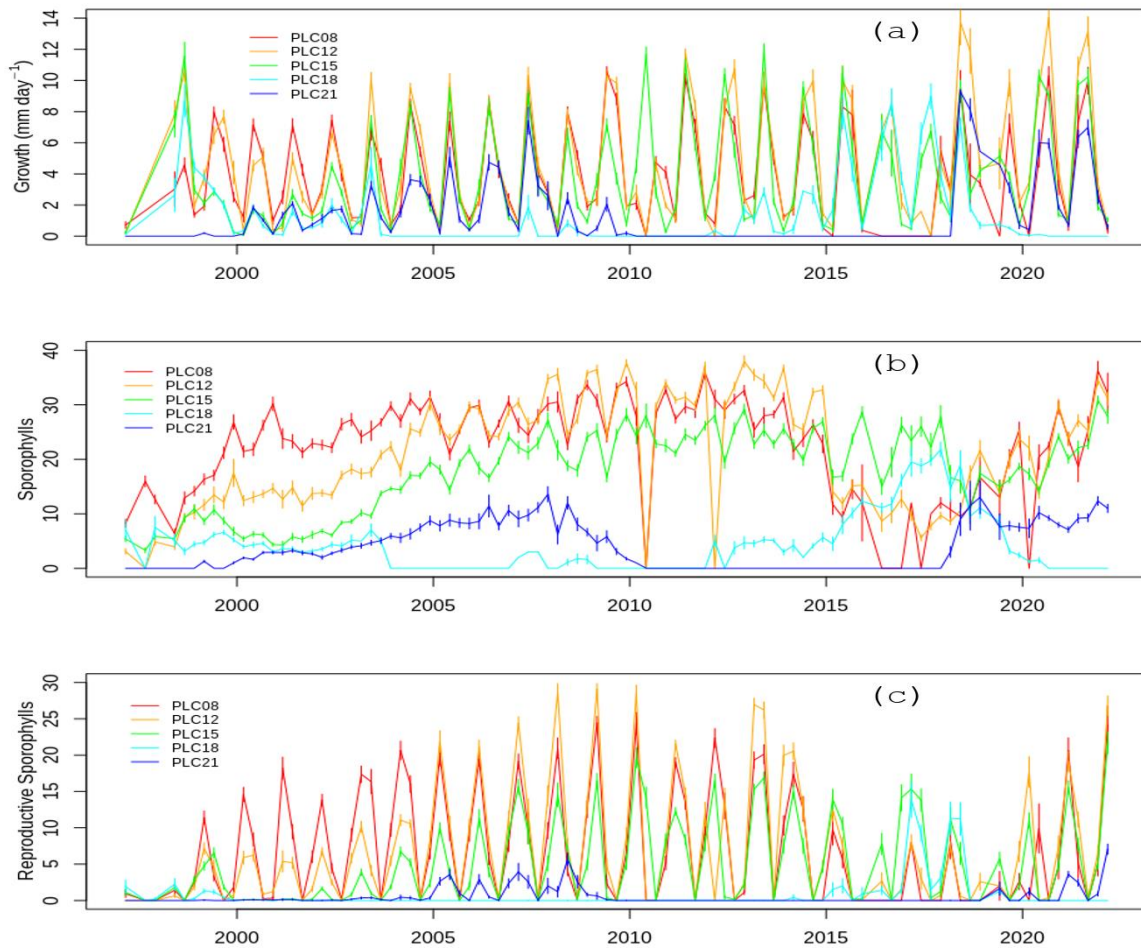


Figure 19. Growth and reproduction of the understory kelp *Pterygophora californica* at the central Pt. Loma study sites: (a) growth, (b) # sporophylls, and (c) # reproductive (sexy) sporophylls. Means are plotted and error bars indicate standard errors.

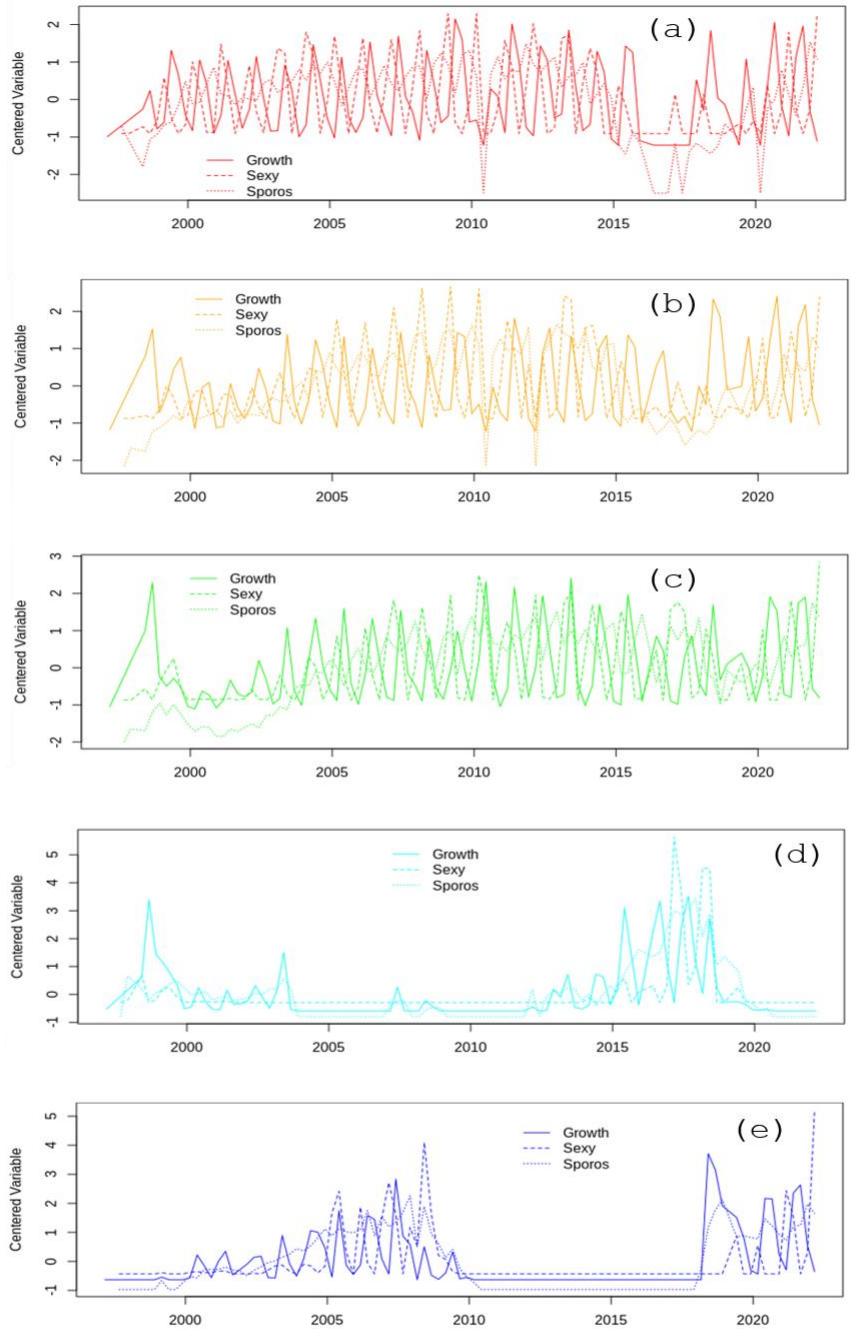


Figure 20. Centered *Pterygophora californica* growth rates, sporophyll, and # of reproductive sporophylls for (a) PLC08, (b) PLC15, (c) PLC18, and (d) PLC21 study sites. Means are plotted and error bars indicate standard errors.

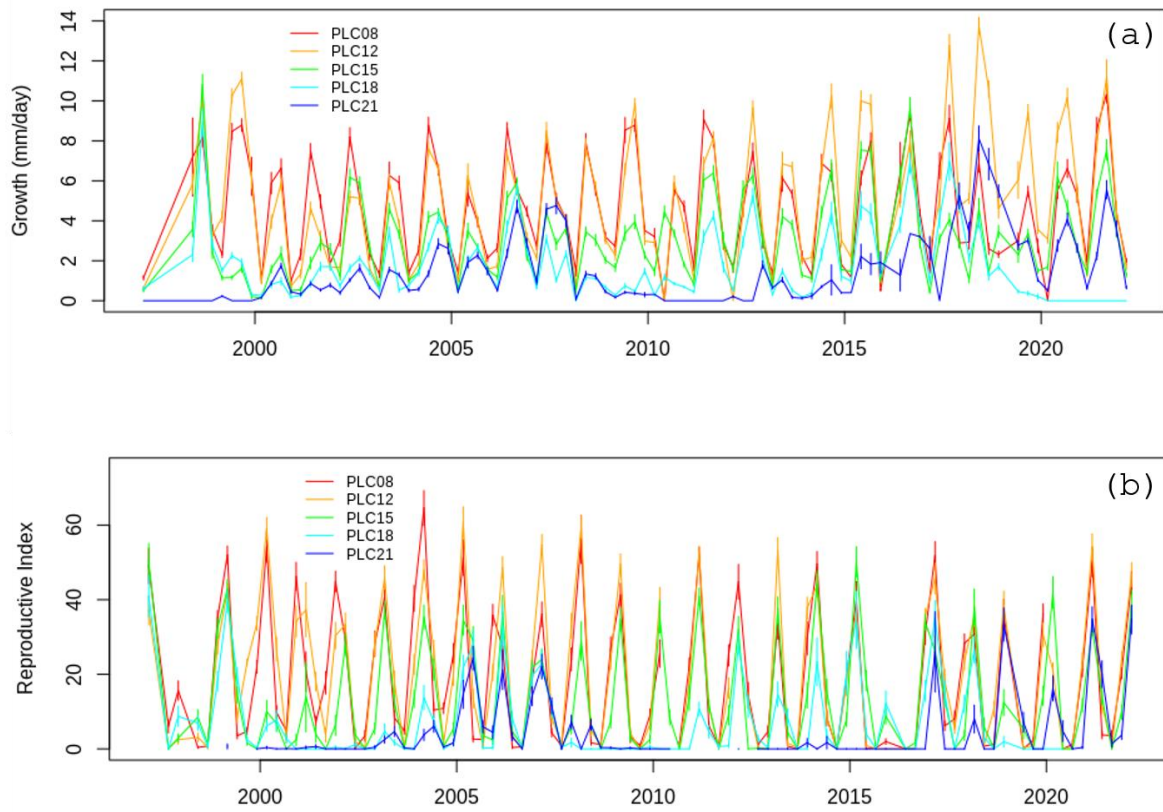


Figure 21. Growth and reproduction of the understory kelp *Laminaria farlowii* at the central Pt. Loma study sites: (a) growth, and (b) % of blade that is sori (reproductive), Means are plotted and error bars indicate standard errors.

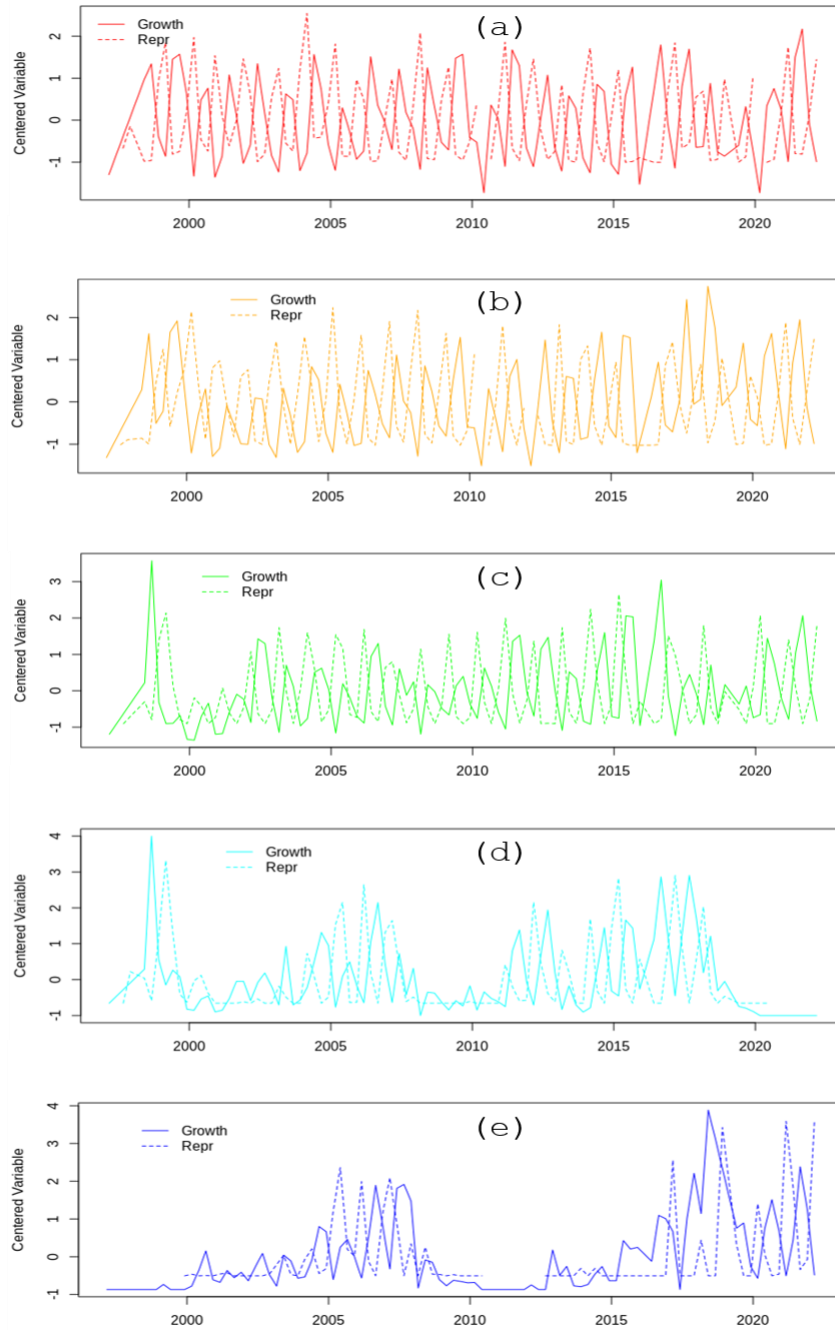


Figure 22. Centered growth and reproduction of the understory kelp *Laminaria farlowii* at the central Pt. Loma study sites. (c) standardized growth and reproduction for the PLC8 and the (d) PLC12 study sites.

Algal Community Analysis

Algal community composition among all of the study sites during the study period are shown in Figures 23 and 24 where the first two factors of the dimension-reducing factor analysis are plotted against one another. The most abundant algal species and groups were included in the analysis as well as bare space which was included as a derived ranked variable (see Methods). When plotted against one another, the first two factors graphically depict the community-wide state of algae among the study sites. Together, these factors account for ~34% of the overall variability in the dataset, and therefore provide a good representation of the algal communities over time. Factor 1 indicates a continuum of understory algal composition ranging (from positive to negative) from fleshy red and articulated coralline algae to the stipitate brown algal species, *Eisenia arborea*, and *P. californica*, the prostrate brown alga *L. farlowii*, to the post-disturbance pioneer brown alga *Desmarestia ligulata*, to bare space. This factor captures the depth gradient effect from shallow to deep (positive to negative), representing the gradient in benthic light availability. Shallower sites are typically saturated by adequate light thus facilitating algal domination, whereas deeper sites are light limited thereby reducing algal growth and reproduction, which forces a change from algal domination at shallower depths to domination by encrusting suspension feeders at depth. Factor 2 indicates the condition of *M. pyrifera*, whether sites are dominated by adults and abundant stipes (positive values) or young recruits and pre-adults (values near zero) to a virtual absence of surface canopy (negative values).

The major patterns of macroalgal community composition among the study sites are best contrasted by comparing the upper left quadrant of the plot, which indicates *M. pyrifera* domination and sparse understory and turf. The lower right quadrant represents understory and turf domination. PLC18, LJS18, and PLS18 are the only sites clearly dominated by giant kelp while most of the shallower sites are heavily dominated by understory (mainly *L. farlowii* and *C. osmundacea*) and turf algae. The lower left quadrant represents sites with reduced understory and *M. pyrifera*. The Del Mar and Cardiff study sites represent the extremes within this quadrant, characterized as poorly vegetated sites. PLT12 is sparsely covered with articulated coralline algae and *C. osmundacea*.

The forcing behind these patterns of algal cover among the sites not well understood at all of the study sites. *M. pyrifera* has failed to thrive during the cooler nutritive conditions of the last several years even after initially recovering to some extent at many of the sites where understory kelps have either remained steady or increased since the MHW. These patterns of reduced canopy cannot be attributed to sea urchin overgrazing as both locally common species crashed during the MHW and have yet to appreciably increase as recruitment has been present but limited at many of the study sites.

2020

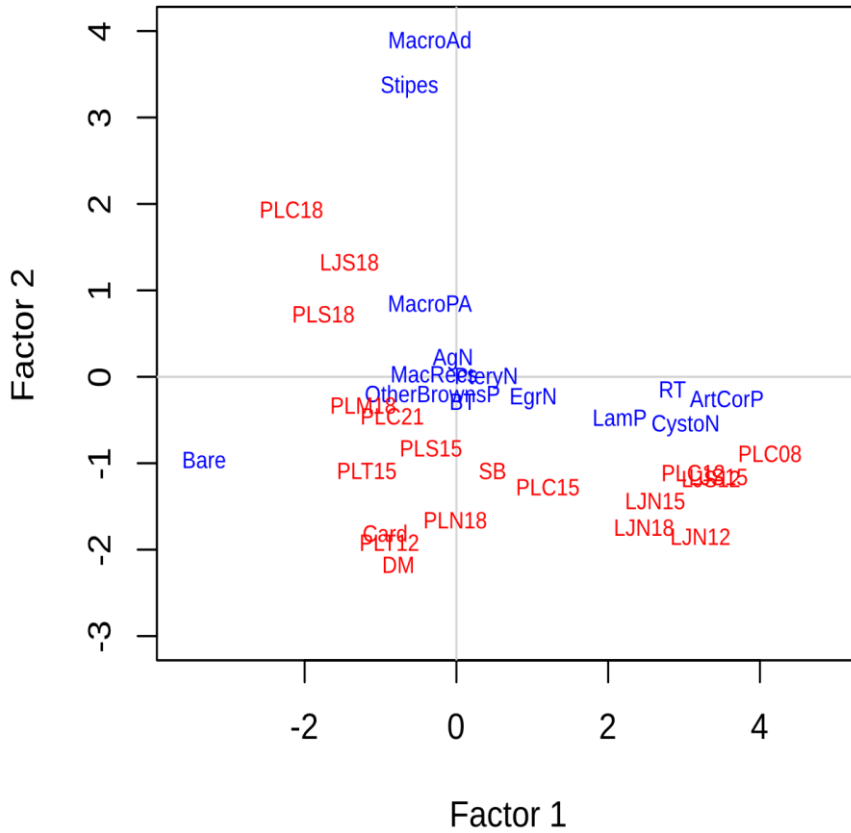


Figure 23. Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2020. Algal group definitions: Bare = derived bare space, MacRecs = *M. pyrifera* recruit stage (pre-bifurcates + bifurcates), MacroAd = *M. pyrifera* adult density, Stipes = *M. pyrifera* stipe density, MacroPA = *M. pyrifera* pre-adults (<4 stipes), PteryN = *Pteryogophora californica* density, LamP = *Laminaria farlowii* percent cover, EisN = *Eisenia arborea* density, EgrN = *Egregia menziesii* density, AgN = *Agarum fimbriatum* density, DesP = *Desmerestia ligulata* percent cover, ArtCorP = articulated coralline algae percent cover, RT = foliose red algal percent cover, BT = brown algal turf percent cover.

2021

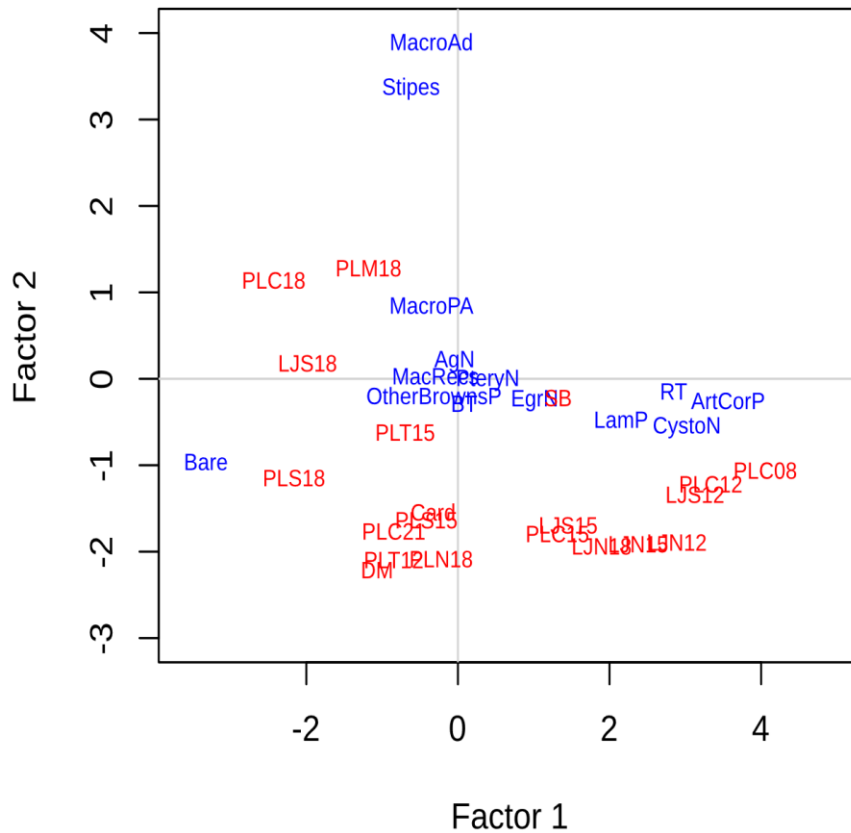


Figure 23. Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2021. See Figure 23 for description of plot.

Invasive Algal Species

Sargassum horneri is an algal species native to Japanese and Korean coastlines but has invaded southern California within the last couple of decades. *S. horneri* was first reported from Long Beach Harbor in 2006 (Miller et al., 2007) and has gradually spread along the southern California marine shelf. It was first observed in San Diego County in Mission Bay in 2008. *S. horneri* dominates some areas formerly dominated by *M. pyrifera* including areas off Santa Catalina Island and the Northern Channel Islands off Santa Barbara. *S. horneri* was first observed in the kelp forests off San Diego in early 2014. Since that time, it has spread to 13 of our study sites. Initially, it was only observed near some of the study sites, but has subsequently been consistently observed within the permanent band transects at several sites. Table 5 lists first sightings within the actual band transects, and Fig. 25 shows the relative observational frequencies among the study sites pooled over time. The greatest percent cover observed thus far has been at PLC08 (Fig. 26) in the fall of 2017 when mean percent cover exceeded 3.5%. This maximum was followed by a maximum percent cover of ~3% at LJN18 in the fall

of 2018 where it has varied in percent cover ever since. However, while *S. horneri* spread relatively quickly to many study sites by 2018, it has still not been observed at seven other sites (Cardiff, Del Mar, PLC15, PLC12, PLS15, PLM18, and PLT15). Rather, it has decreased or disappeared at many of the invaded sites, and presently persists at at very low cover at all sites with the exception of LJN18.

However, *S. horneri* clearly poses a risk to *M. pyrifera* and other algal species due to its potentially high seasonal growth rates. It is not implausible for it to take over some areas of San Diego kelp forests especially after a future major disturbance that reduces the densities and cover of native algal species. Presently, it is too sparsely distributed to be significantly affecting giant kelp with the exception of the LJN18 study site and the deeper portions of the northern La Jolla kelp forest.

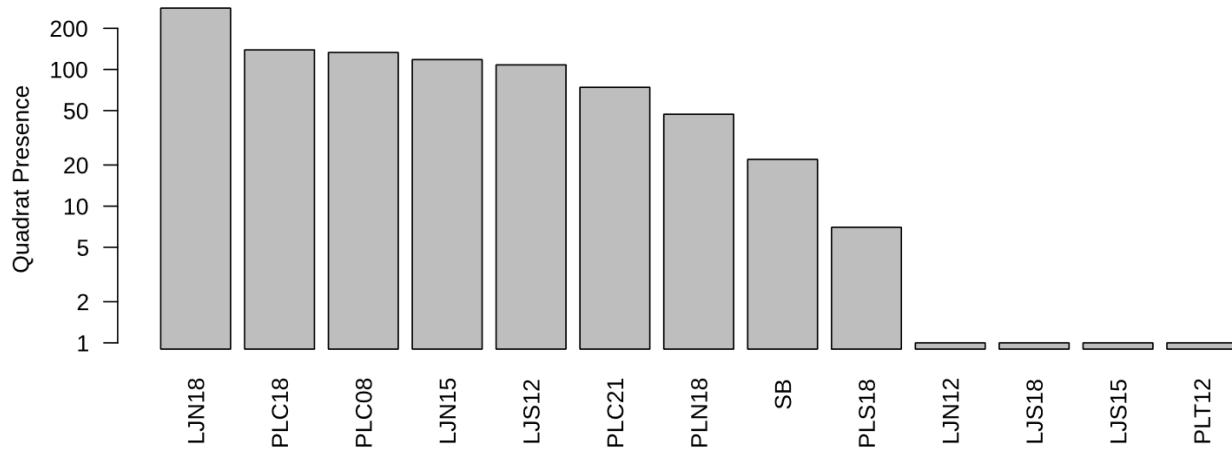


Figure 25. Presence of the invasive alga, *Sargassum horneri*, among the study sites where it has been observed within the permanent band transects. *Quadrat presence* indicates the total number of 5x2 m quadrats along the transects where it has been observed over time since first sighting at each individual site.

Study Site	Date 1 st Observed
SB	Sept. 9, 2105
PLC18	Oct. 10, 2015
PLN18	Dec. 2, 2015
LJN15	Dec. 3, 2015
LJS12	Feb. 8, 2016
PLC08	Mar. 31, 2016
LJS18	May 3, 2016
LJS15	May 3, 2016
PLT12	May 11, 2016
LJN18	May 19, 2016
PLC21	April 18, 2017
LJN12	Jun. 30, 2017
PLS18	May 30, 2018

Table 5. List of study sites where the invasive alga, *Sargassum horneri*, has been observed within the band transects and the dates it was first observed.

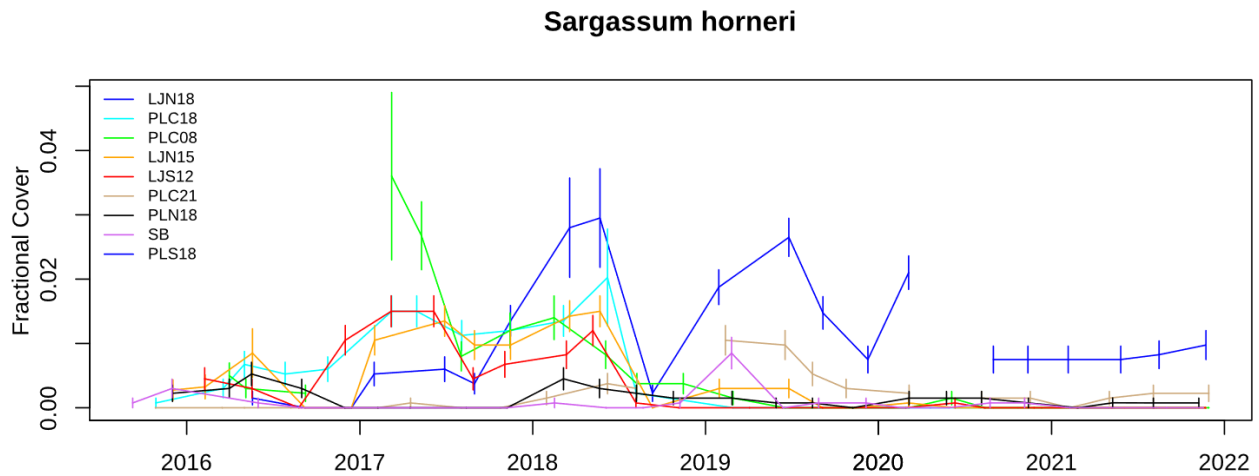


Figure 26. Fractional cover of the invasive alga *Sargassum horneri* over time beginning when it was first observed in the kelp forests off San Diego (see Table 4). Some study sites where *S. horneri* has been observed were omitted because cover values approximate zero.

Invertebrates

Many invertebrate species were negatively impacted by the 2014-2016 MHW. Sea urchins (Echinoids) and seastars (Asterooids) were most affected. Both groups play important functional roles within kelp forest communities. Sea urchins are major grazers of algae capable of overgrazing kelp forests if they become too numerous and mobile. Seastars are important benthic predators and are considered by many as keystone species whose predatory activities can control benthic community structure. Both groups suffered heavy mortality off San Diego during the warm event and remain depressed as of this writing (2022). Decimation of sea urchin populations off San Diego was a direct result of disease mortality and included the 'dark-blotch' disease. Disease epidemics commonly occur in echinoids (sea urchins - Lafferty, 2004) and asterooids ('sea star wasting disease' - Eckert et al., 2000) during periods of warm water stress.

Densities of both red (*Mesocentrotus franciscanus*) and purple (*Strongylocentrotus purpuratus*) sea urchins (RSU and PSU, respectively) either crashed in response to the consecutive warm periods or were already experiencing disease mortality. Sea urchin densities are shown in Figures 27-29 for a subset of the study sites. These sites were chosen as exemplary of the major population trajectories for red and purple sea urchins and where sea urchins have been most numerous historically. Presently, there are few sea urchins of either species at any of the study sites, even off south Pt. Loma where sea urchin overgrazing has been historically resilient (Parnell, 2015).

The two major patterns of sea urchin population trends among the sites include (1) dramatically reduced densities at sites where they have spiked in the past and (2) stability at sites where they have typically been observed at low densities. Red sea urchins at the central Pt. Loma study sites have been relatively stable but at low density. These animals are sparsely distributed in cryptic habitat and have not exhibited overgrazing during the entire time series. By contrast, red and purple sea urchin overgrazing associated with population spikes have been observed at several of the south Pt. Loma study sites. An example for red sea urchins is the dramatic spike beginning in 2012 at PLM18 when giant kelp densities crashed. The sea urchins then emerged into feeding fronts at high densities. The subsequent MHW decimated these feeding fronts mainly through disease, though population diffusion may have also contributed. Purple sea urchins are typically observed at higher densities than reds and have exhibited population spikes along some of the central Pt. Loma study sites. However, their densities at these sites have remained stable and cryptic over the last two decades and did not succumb in large numbers to the MHW event. That has not been the case in south Pt. Loma where densities have greatly varied and where urchin feeding lines have developed leading to episodic overgrazing fronts that remove young stands of giant kelp.

Sea urchin populations are typically cohort dominated with episodic periods of enhanced larval settlement and juvenile survival. Recruitment of both species was depressed during the MHW (Figs. 30-32), being absent or extremely limited at all study sites until the fall of 2017 when significant recruitment was observed once again. Patterns of recruitment then varied among sites and by species but the general pattern included increased levels of recruitment in 2017-2018 followed by a decrease in 2019-2020 and another increase in recruitment at some of the sites. However, the biggest pulse of recruitment for both species occurred in 2018 and winter of 2019. This cohort of red and purple sea urchins does not appear to have resulted in increased adult densities thus far, indicating that their post recruitment survival has been relatively low or they are remaining cryptic (likely a combination of both). Therefore it is highly likely that sea urchin overgrazing will not be problematic in the near future in most areas of the LJKF and PLKF.

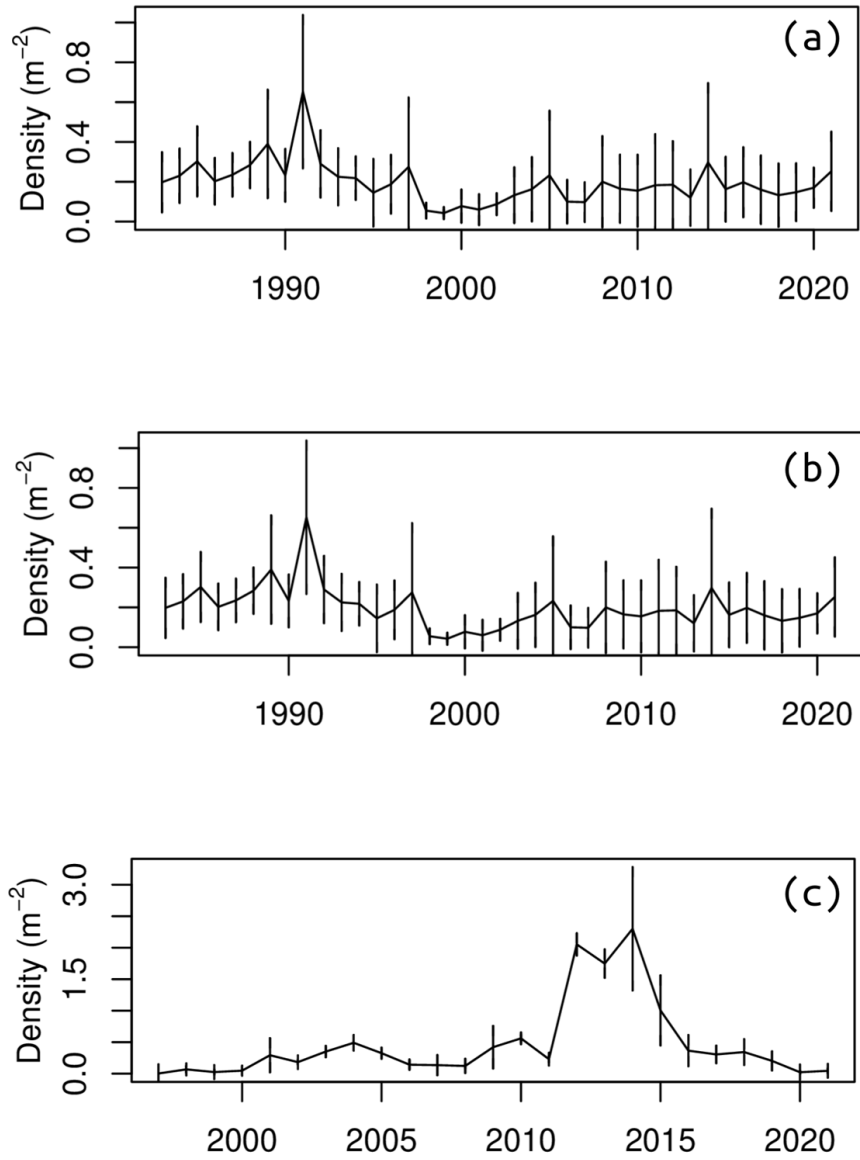


Figure 27. Time series of the red sea urchin (*Mesocentrotus franciscanus*) mean densities at the (a) PLC15, (b) PLC18, and (c) PLM18 study sites. Error bars are standard errors.

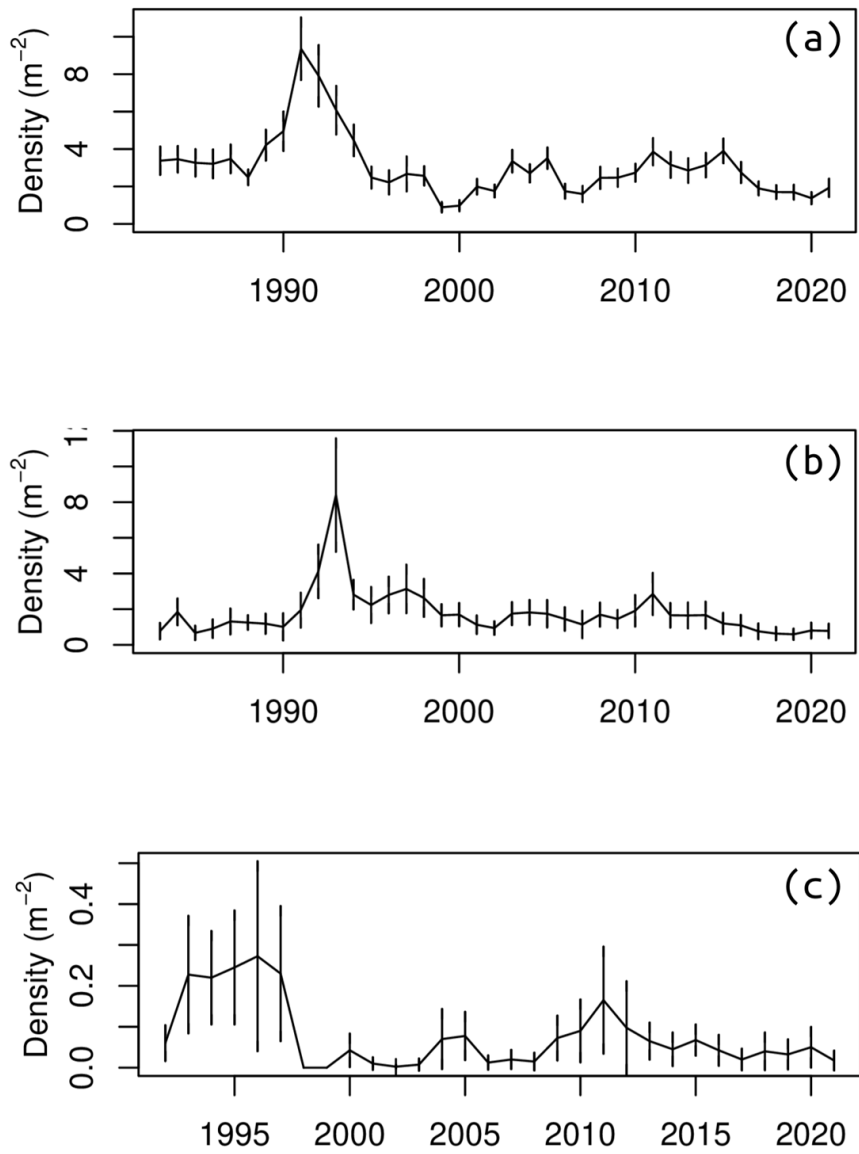


Figure 28. Time series of purple sea urchin (*Strongylocentrotus purpuratus*) mean densities at the (a) PLC15, (b) PLN18, and (c) LJS15 study sites. Error bars are standard errors.

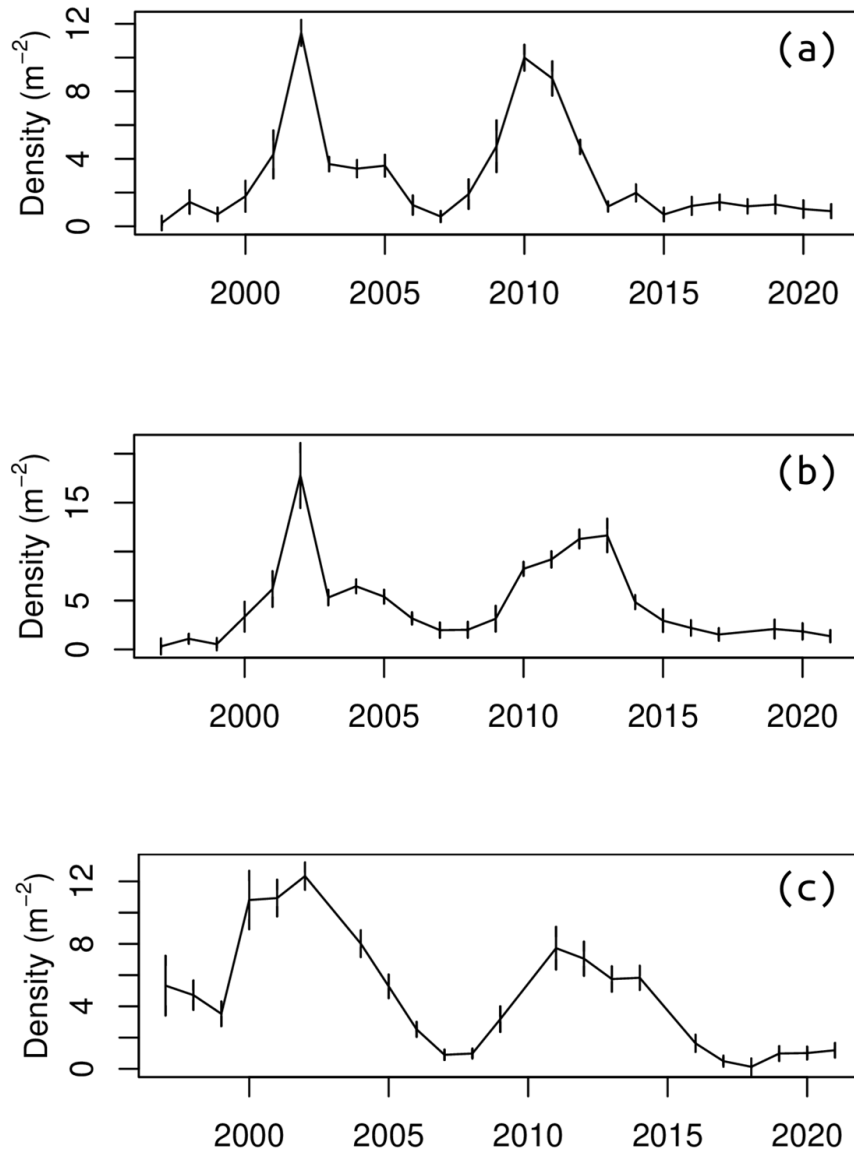


Figure 29. Time series of purple sea urchin (*Strongylocentrotus purpuratus*) mean densities at the (a) PLM18, (b) PLT15, and (c) PLT12 study sites. Error bars are standard errors.



Figure 30. Time series of red (top) and purple (bottom) sea urchin recruitment (fraction of the population considered in the first year class by size - see Methods) at the central Pt. Loma study sites.



Figure 31. Time series of red (top) and purple (bottom) sea urchin recruitment at the southern Pt. Loma study sites.



Figure 32. Time series of red (top) and purple (bottom) sea urchin recruitment at the La Jolla study sites.

Diseases and associated die-offs affected many other echinoderm species, mainly asteroids (seastars), throughout the Southern California Bight during the just prior to and during the MHW. Species that suffered the greatest mortality at our study sites included *Pisaster giganteus* (Fig. 33) and *P. brevispinus* where densities were reduced to zero for both species, even at sites where they were previously abundant. Disease induced mass mortality events of asteroids and echinoids are commonly followed by recovery at differing rates (Hewson et al., 2014). Juvenile *P. giganteus* were observed recruiting onto giant kelp fronds off Pt. Loma beginning in 2017 continuing into 2018, thus heralding their recovery. However this species is still very uncommon or absent at all of the study sites. *P. brevispinus* is virtually gone from all the south Pt. Loma study sites where they had been common in the past. Disease has also decimated *Pycnopodia helianthodes*, an important sea urchin predator (Moitza et al., 1979). This species has not been observed anywhere off Pt. Loma since 2014 even in areas where they were commonly observed. *P. helianthodes* was in decline even prior to the BLOB event.

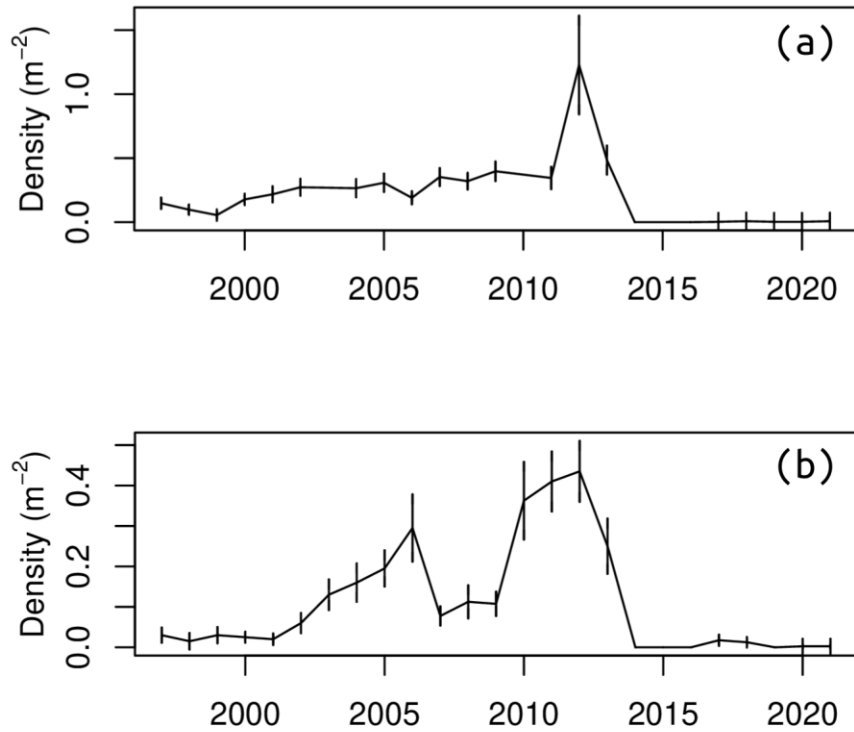


Figure 33. Time series of the seastar *Pisaster giganteus* mean density at the (a) PLT12 and (b) PLM18 study sites. Error bars are standard errors.

Abalones once supported an economically important commercial fishery throughout California until the 1980's. Their primary food in southern California is giant kelp. Therefore, when kelp populations are reduced, abalones become stressed both by the lack of food as well as diseases associated with warm water events (Vilchis et al., 2005). Historically, seven species of abalone have been common off San Diego. Two species, *Haliotis cracherodii* and *H. sorenseni*, are now on the federal endangered species list. Another species, *H. rufescens* has been in decline off southern California since the 1970's, and populations off Pt. Loma crashed in the 1980's (Tegner and Dayton, 1987). However, *H. rufescens* persisted in low numbers near PLS18 and LJS18. Those few were lost during the recent prolonged MHW. Presently, there are relatively few *H. rufescens* throughout San Diego County with the exception of a small population at the extreme western end of the southern Pt. Loma shelf where there has been an increase in kelp canopy cover since the MHW. However, densities of pink abalone (*H. corrugata*) have increased steadily at PLC8 beginning in the early 2000's (Fig. 34). *H. corrugata* has since increased in density even throughout the warm period reaching peak densities approaching 0.1 m⁻² but have since been halved by 2021 indicating this population increase may have subsided. For comparison, densities of pink abalone in the early 70's at similar depths off Catalina were >1 m⁻². (Tutschulte, 1976).

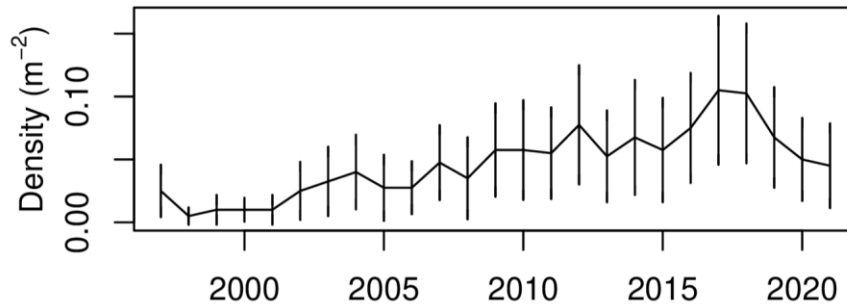


Figure 34. Time series of pink abalone (*Haliotis corrugata*) mean densities at the PLC08 study site. Error bars are standard errors.

North County Sedimentation

The grain size of sediments used for beach replenishment is an important determinant of beach stability. Finer sediments dredged from deeper waters offshore are more rapidly eroded from replenished beaches and are more likely to pose sedimentation risks to nearby kelp forest platforms off North County. The beaches from Carlsbad to Solana Beach were replenished with ~327,000 cubic meters of sand in 2012 using coarser sediments from the San Elijo Lagoon as part of a project to restore the estuary to more marine conditions. Sediments within the NCKF sites have been relatively stable since 2008 indicating that the 2012 replenishment has not been problematic for these kelp forests. Sediment horizons have varied less than 10 cm since 2008 when the sediment time series began. A 50 year replenishment project has recently (2021) been approved for the same area in which sediments will be augmented at 5 to 10 year intervals beginning as soon as 2024. The grain size composition of these sediments is not clearly defined but are anticipated to be from offshore dredging. Therefore, potential risks to north county kelp forests may be more pronounced than the 2012 based on source and replenishment volumes. The initial plan includes replenishing a 2.2 km stretch of Solana Beach with ~535,000 cubic meters of sediment in 2024.

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