Evaluation of Anthropogenic Impacts on the San Diego Coastal Kelp Forest Ecosystem - Final Project Report: 2019 to 2024

Prepared By:

Ed Parnell, PhD[1*]

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[*] Corresponding Author: edparnell@ucsd.edu
[1] Scripps Institution of Oceanography, UC San Diego
9500 Gilman Dr, Mail Code 0227, La Jolla, CA 92093-0227

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 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.

Kelp forests off southern California are affected by both natural and human disturbances. The El Niño Southern Oscillation (ENSO) is the primary climate mode that affects kelp abundance, growth, and reproduction along the west coast of the Americas. Positive ENSO's, termed El Niños, are associated with warm water, depressed concentrations of nitrate, the principal nutrient limiting giant kelp, and an altered storm environment off southern California which can produce destructive storm waves. Both phenomenon can severely stress giant kelp and accompanying species of algae. The opposite conditions occur during negative ENSO events known as La Niñas, enhancing both the growth and reproduction of kelps. Together, the two ocean climate states 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 varied degrees of recovery afterwards. Recovery rates depend on growth conditions after El Niños ebb.

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. All algae and associated animals are currently monitored at twenty permanent study sites. These surveys represent a continuation of ecological studies in the Point Loma and La Jolla kelp forests at some of the same sites established as part of earlier studies conducted in the 1970s and 1980s. These two kelp forests are the largest contiguous kelp forests off the western coast of the United States and are historically one of the most studied kelp forest systems in the world. Additional study sites have been established more recently in both Point Loma and La Jolla, and in kelp forests off northern San Diego County. The main components of the current kelp forest monitoring program include surveys of (1) algal density, growth reproduction, and recruitment, (2) benthic invertebrates, (3) sea urchin demography, (4) ocean temperature, (5) fish and invertebrate censuses at 8 additional reef sites, and (6) benthic light levels.

The kelp forests throughout much of southern California including San Diego County were decimated by a marine heat wave that began in 2014 and persisted through the spring of 2016 due to the combination of two independent but consecutive ocean climatic phenomena. 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 the ENSO which is 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) of 2014-15 which was the longest and warmest heat event ever observed in the 115 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 2017-2018 brought cool nutrient-laden waters up onto the inner continental shelf and the kelp forests off southern California but was briefly interrupted by a mild El Niño from the fall of 2018 to the summer of 2019. Conditions during the present reporting period (2019-2024) returned to favorable conditions for giant kelp recovery due to persistent La Niña conditions that persisted from 2021 to early 2023. Most recently, a strong El Niño developed beginning in the fall of 2023 and is expected to persist through at least spring of 2024 after which La Niña conditions are predicted to return by summer.

The MHW of 2014-2015 decimated giant kelp (*M. pyrifera)* and had a negative effect on many other species of macroalgae off San Diego. Densities of adult *M. pyrifera* were reduced >90% across our 20 study sites (Fig. 1). 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 2015-16. Rates of giant kelp recovery between 2017 and 2019 were variable among the study sites and have been depressed since that time. Giant kelp recruitment occurred at many of the sites both after the combined MHW of 2014-16 and the mild El Niño of 2019-2020 but both sets of recruitment cohorts have failed to yield dominant healthy stands of giant kelp. Presently, giant kelp off San Diego is at its lowest historical density (Fig. 1) despite supportive ocean climate conditions over the last three years. The present patchy condition of giant kelp off San Diego can be categorized into four different states. The first includes many of the shallower sites where understory algae that grow close to the bottom have gained a foothold since the MHW. The presence of these kelps can prevent giant kelp from recruiting via competition for space. Category two includes deeper areas of the kelp forest (>16 m) which been affected by low light levels at the sea bottom due to recent extensive phytoplankton blooms. Giant kelp requires adequate light to germinate and produce young plants. Light levels were reduced from 2020 through 2022 and only recently have supported some giant kelp recruitment at these sites. The third category includes sites at mostly intermediate depths where there has been alternation between bouts of moderate giant kelp recruitment and recovery followed by collapse that may be at least partly due to the unprecedented surface warming that has occurred over the last several summers. The fourth category includes sites off North La Jolla and North County, except for Solana Beach, where most algae is now absent, and the areas are becoming dominated by suspension feeding invertebrates including bryozoans and suspension feeders that have negative effects on kelp recruitment. The conditions at these sites will likely continue indefinitely without a large disturbance.

One of the factors that may account for the presently patchy and degraded condition of giant kelp stands off San Diego is the recent extreme (relative to historical records) surface warming during the last four summers. This phenomenon is quite recent occurring only within the last decade. The warming is limited to the upper 3-5 meters of the ocean's surface, and affects much of the southern California coast. Sea surface temperatures have exceeded 28°C during this period, exceeding the previous temperature maximum recorded at the SIO Pier by ~3°C . Summer surface temperature maxima in this record are typically ~23°C. This surface warming has degraded giant kelp canopy tissue which mostly sloughs off and drifts onto nearby beaches. During this period, cooler temperatures have persisted closer to the bottom due to the La Niña conditions, and most 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. This was generally not the case for the post 2018-2019 recruitment.

Diseases in many invertebrates, including sea urchins (echinoids) and predatory seastars (asteroids), are common during MHWs. 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 persisted through 2017. Sea urchins are primary grazers of most 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. Overgrazed areas, termed urchin barrens, can persist in some areas for decades. The echinoderm epidemic associated with the MHW resulted in the 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 with later episodes occurring after the 2018-19 El Niño. However, there has been no increase in sea urchin densities or evidence of overgrazing despite these pulses of recruitment. This indicates that these cohorts either mostly failed or they remain cryptic and are not actively grazing live plants. These new cohorts of sea urchins may eventually overgraze some areas off San Diego if they emerge from cryptic nursery habitat in high densities 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 appear to contribute to a large and resilient sea urchin barren. However, giant kelp recovery has been the strongest within this formerly resilient sea urchin barren, an apparent reversal of the historcal spatial pattern of *M. pyrifera* canopy cover. Sea urchin over grazing does not appear to be contributing to the current degraded state of giant kelp off San Diego.

Some invertebrates including predators of sea urchins also collapsed due to disease associated with the 2014-16 MHW. These species include the seastars *Pisaster giganteus* and *Patiria miniata*, which have still not shown any sign of recovery off San Diego. Densities of both species has remained historically low and it is presently unknown whether they will recover to their former densities. Abalone, an important herbivore 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*) which exhibited some recovery at the two shallowest study sites off central Pt. Loma.

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 distance gradients 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.

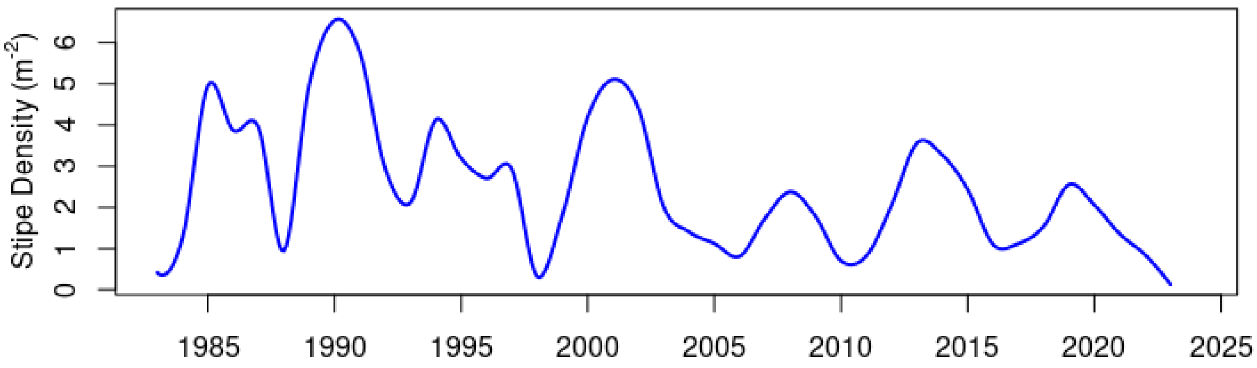

Figure 1. *Mean giant kelp (Macrocystis pyrifera) stipe densities pooled across all sites over time. Stipe density is a useful proxy for kelp biomass.*

INTRODUCTION

Kelp forests are vulnerable to human disturbance mainly due to their proximity to urbanized coasts thereby 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). Historic 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 is common in those areas.

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. 2) 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 wave energy which can cause 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. 3). Concentrations of nitrate, the main limiting nutrient for kelp growth in southern California switched from being supportive for kelp growth most years prior to the regime shift, with the exception of the most intense El Niños, to being marginal or inadequate most of the time afterward (Parnell et al., 2010). The ecology of giant kelp forests off San Diego has changed fundamentally over the last 50 years due to the increased frequency of natural disturbances resulting in a demographic shift towards younger and smaller *Macrocystis pyrifera* individuals (Parnell et al., 2010) as well as an overall decreased density and post disturbance resilience (see Fig. 1).

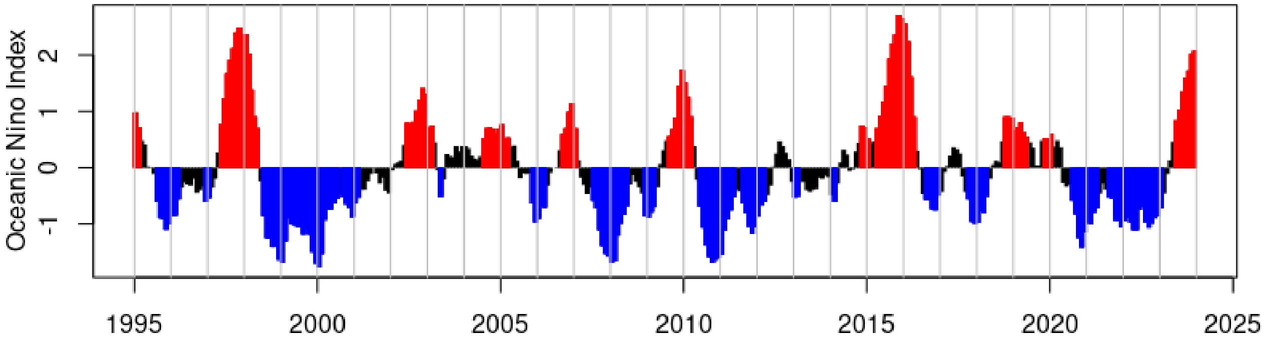

Figure 2. *Barplot of the Oceanic Niño Index (ONI) since 1995. Red bars indicate El Niño conditions, blue bars indicate La Niña conditions, and black bars indicate ENSO neutral conditions (data from NOAA, 2024). The ONI index is based on equatorial sea surface temperatures in the Eastern Pacific.*

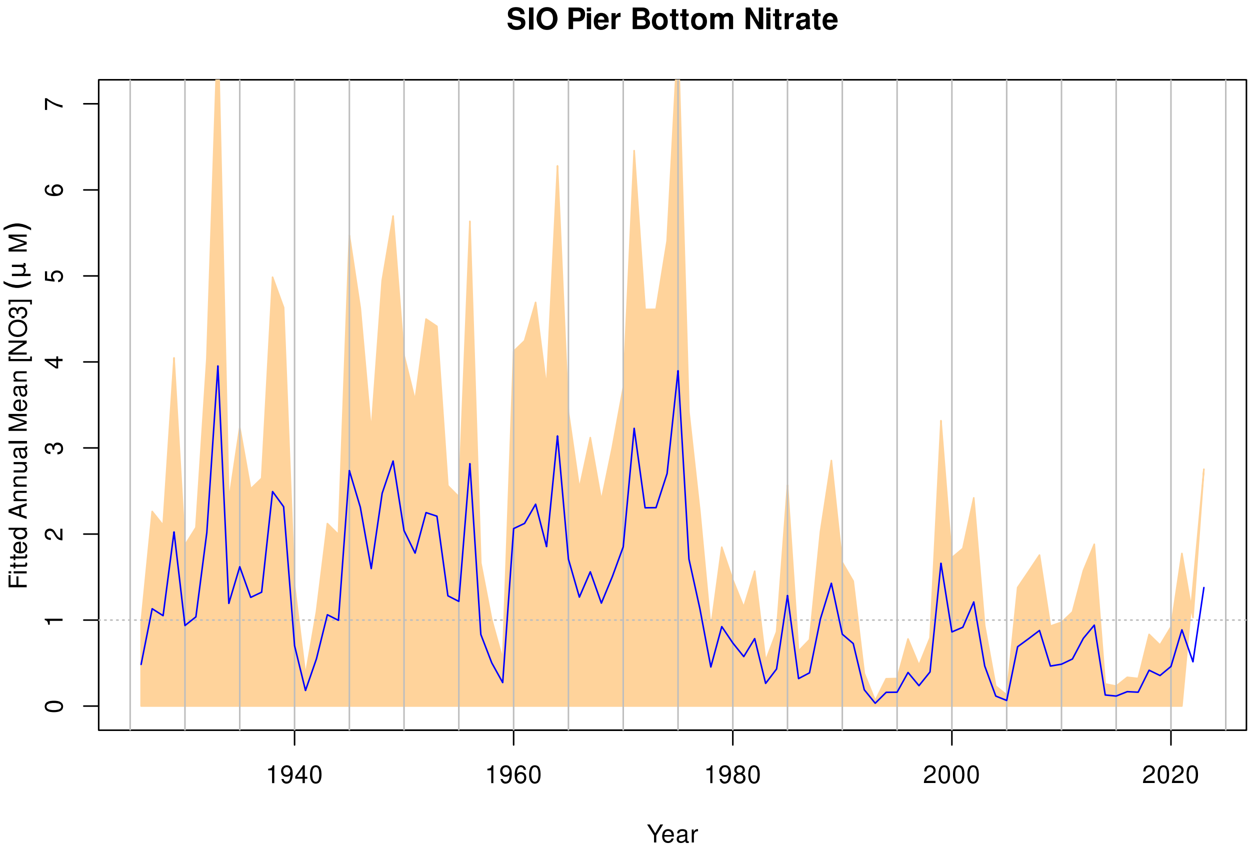

Figure 3. *Time series of annual mean nitrate concentrations estimated from daily temperature and salinity sampled at the base of the Scripps Institution of Oceanography Pier (see Parnell et al., 2010 for details). Dotted gray line indicates the minimum nitrate threshold for the growth and reproduction 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 that were previously dominated by *M. pyrifera*. Presently, 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. 4). 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 induced by high temperatures, inadequate nutrient levels, overgrazing by invertebrates, and 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 m^2) 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.

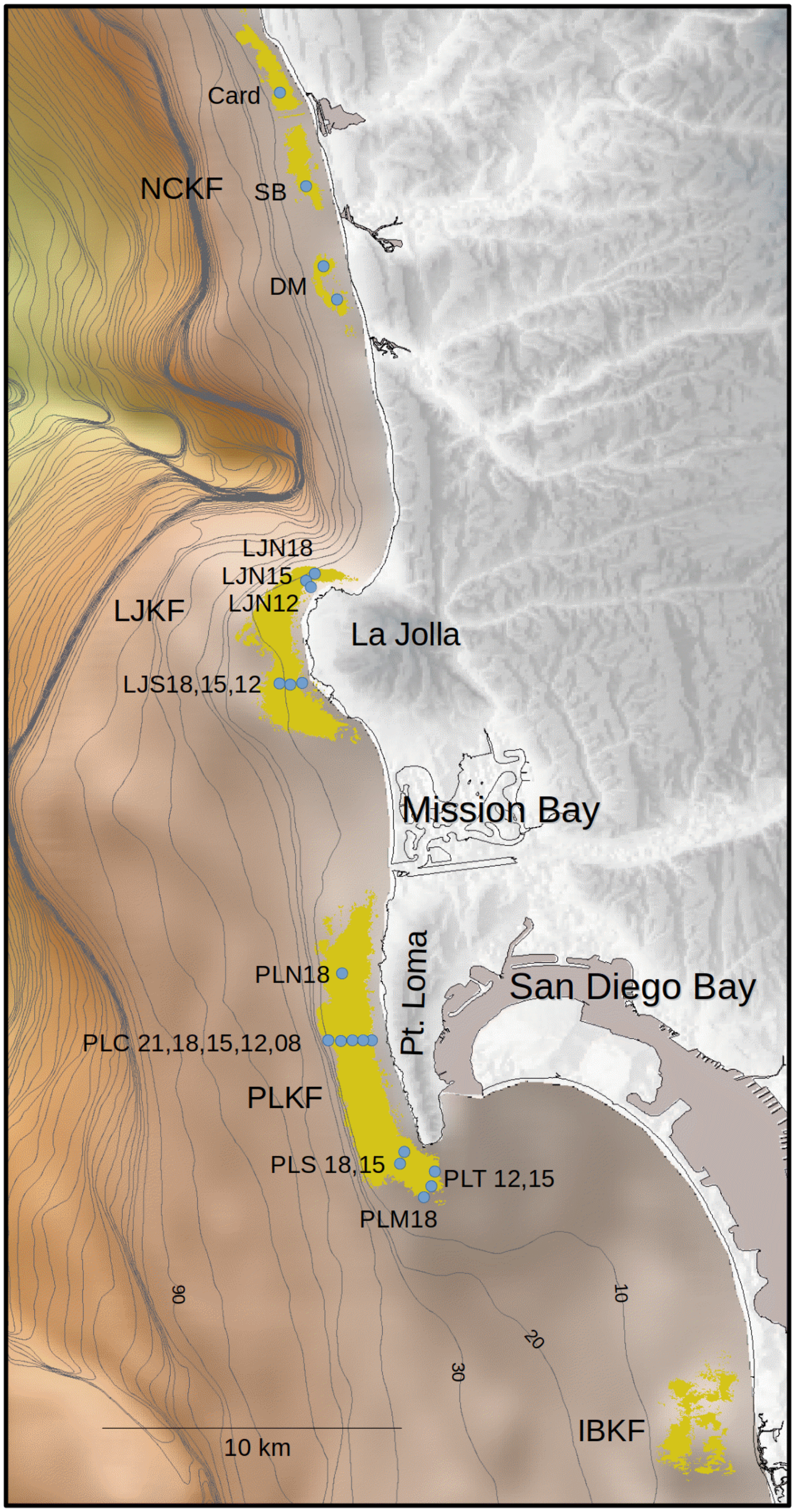

Figure 4. *Map of the San Diego inner shelf showing locations of the Point Loma, La Jolla, North County, and Imperial Beach kelp forests (indicated by PLKF, LJKF, NCKF, and IBKF, respectively). Permanent study site locations are indicated by blue circles and corresponding study site names. Depth contour 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 $10m^2$ 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 m^2 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 haphzardly placed 1 m^2 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 been historically episodic. 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 st*ate.

Finfishes

Fish surveys were initiated in the fall of 2019 and continue semi-annually (fall/spring) at four sites within the LJKF and four sites within the PLKF (Figs. 5 and 6, respectively). One of the sites off La Jolla (‘CGSB’) was discontinued in 2021 and was replaced by a site having a reef more similar to the other sites but was previously unknown (‘14G’). 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. 5). 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 as best as possible 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 torch.

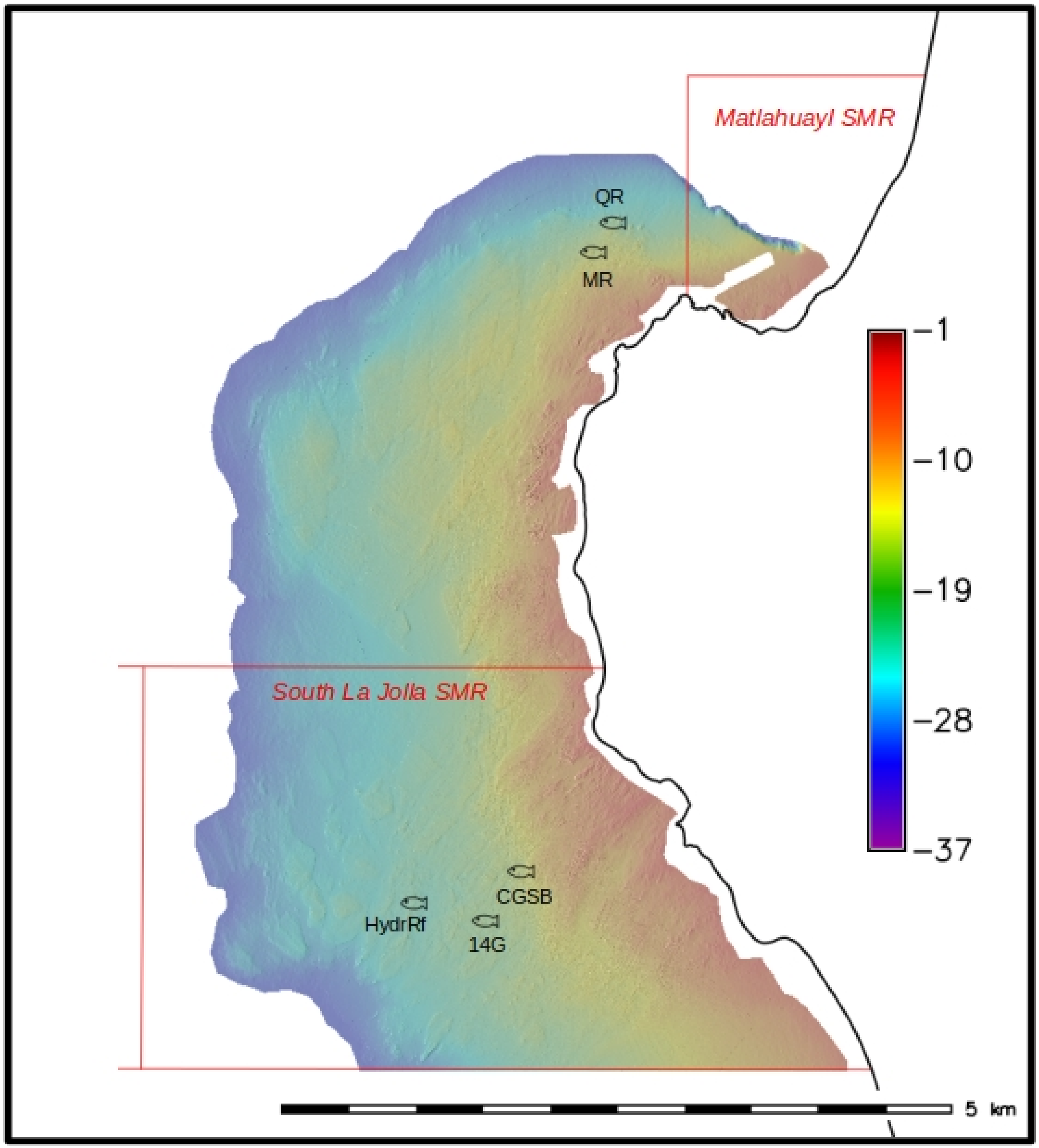

Figure 5. *Locations of fish survey study sites within the La Jolla kelp forest. Color legend indicates depth in meters. Note: surveys at 'CGSB' were discontinued in 2021 (see text).*

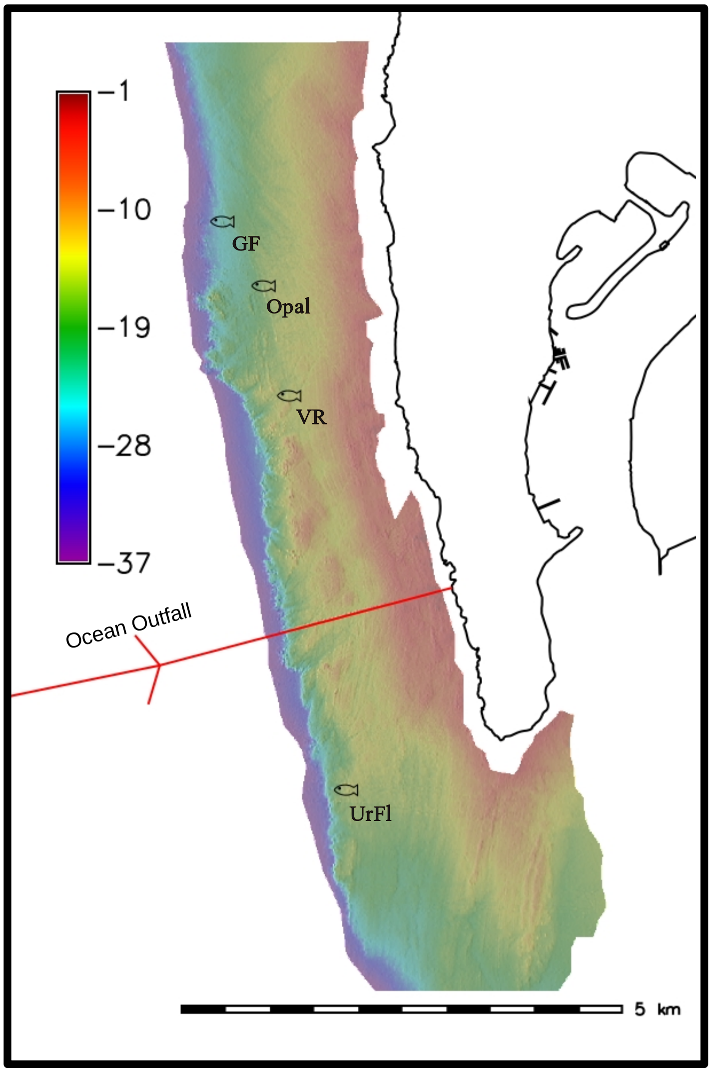

Figure 6. *Locations of fish survey study sites within the Pt. Loma kelp forest. Color legend indicates depth in meters. Note: 'UrFL' was replaced by 'VR' in 2020 (see text).*

Site	Kelp Forest	Depth (m)	MPA	MPA Pairings	Species Richness
QR	La Jolla	21	No	A	27
HydRf	La Jolla	21	Matlahuayl SMR	A	39
MR	La Jolla	15	No	B	30
14G	La Jolla	17	Matlahuayl SMR	B	38
VR	Pt. Loma	15	No	A	33
Opal	Pt. Loma	15	No	A	37
UrFl	Pt. Loma	16	No	B	
GF	Pt. Loma	21	No	B	33

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

Bottom Light Levels

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 $m^{-2}d^{-1}$ (Deysher and Dean, 1984), and ~0.7 mol of photons $m^{-2}d^{-1}$ for early sporophyte growth (Dean and Jacobsen, 1984). As light becomes more limiting with increasing depth, the recovery of giant kelp from disturbances such as a MHW, is increasingly limited due to the abbreviated periods that bottom illumination is adequate for gametogenesis and the growth of the early sporophytes.

Bottom PAR is 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. 2) 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 magnitude of ENSO events at the equator and temperatures within the SCB can be somewhat decoupled.

The bottom temperature record along the central Pt. Loma study sites (Fig. 7) extends back to 1983 when the strong El Niño of 1982/83 was at its peak. Since then, the largest temperature signals in the time series include the 1997/98 El Niño and the extended warm period of 2014-2016 associated with a large scale anomalous NE Pacific warming event (DiLorenzo and Mantua, 2016) now referred to as the marine heat wave (MHW) of 2015. This was immediately followed by a strong El Niño in 2015/2016 (Figs. 2, 7, and 8). The ONI (Fig. 2) and the Pt. Loma bottom temperature time series (Fig. 7) are highly concordant for the largest ocean climate events including the onset of the coupled MHW/El Niño warm period. A cool period occurred between the fall 2018 and the summer of 2019 followed by slight warming. Most recently conditions have been conducive for kelp growth due to an extended La Niña between 2020 and 2023. However, even though bottom temperatures were cool during this period, there have been increasing episodes of near surface warming during summer when temperatures have exceeded historical levels by as much as 3°C. Surface temperatures 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. 8) and included the warmest temperatures ever observed in the time series. This surface warm event caused significant deterioration of the giant kelp surface canopy which virtually disappeared that 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 has continued to occur with similar negative effects on the kelp surface canopy during the summers of 2020 to 2023 (Fig. 9, 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 9 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 2015/16 El Niños. These include the 2005/06, 2009/10, 2018/2019 events when most of the giant kelp canopy disappeared at the surface but plant tissue was still healthy below the thermocline where nutrients were more abundant. Because bottom temperature decreases 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 shallowest central Pt. Loma sites, leading to recruitment and growth at many of the study sites. Warming occurred during the fall and winter of 2018/19 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 began to ebb during the late fall of 2022 when ENSO neutral conditions were observed along the equator. El Niño conditions began in the Eastern Pacific tropics in April of 2023 and these conditions persist at present. This latest El Niño has been classified as strong by NOAA and its warming signature in southern California was evident by November of 2023 and is predicted to persist through the spring of 2024 which will likely lead to further loss of giant kelp biomass off San Diego. This is highly likely because giant kelp adult and stipe densities were near or at historic lows for all of the study sites prior to the latest El Niño.

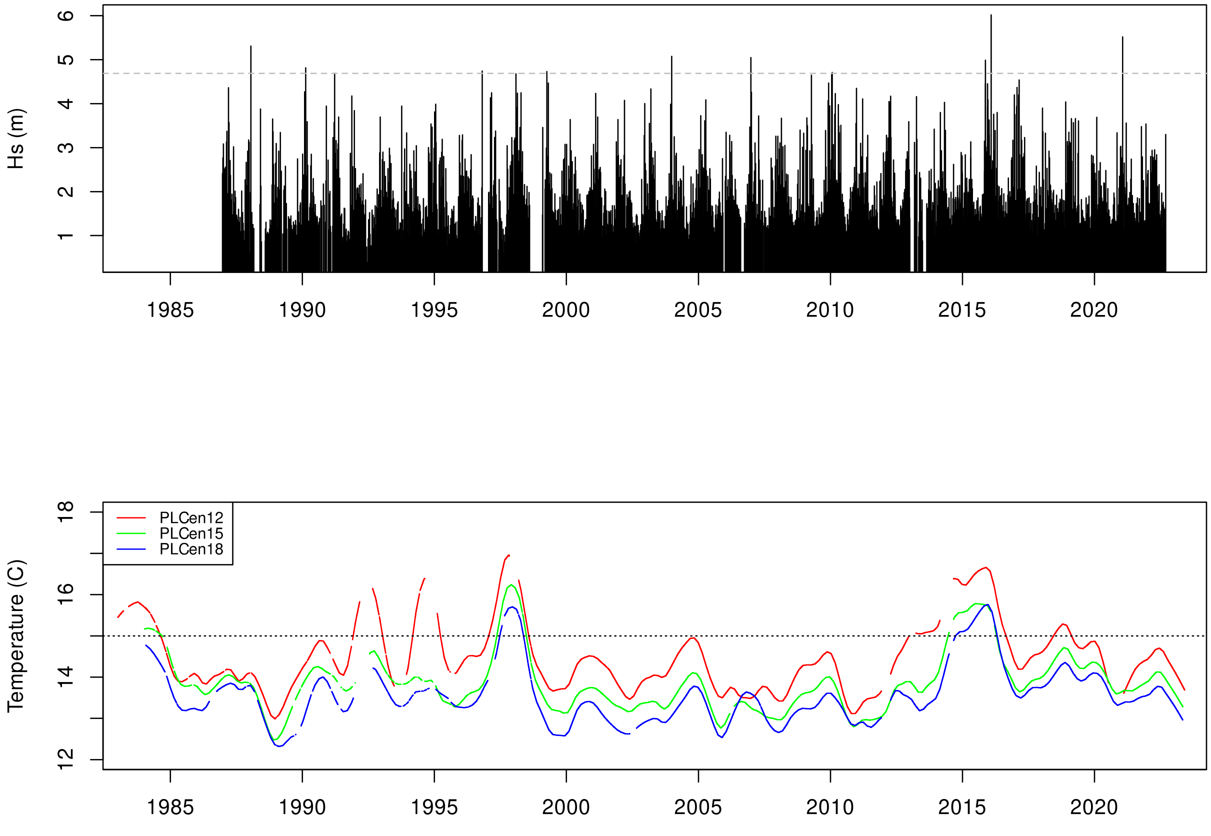

Figure 7. *Significant wave height (Hs) offshore of San Diego (top panel), and ocean bottom temperature trends along the central Pt. Loma study sites. Horizontal gray line indicates the temperature above which nitrate concentrations are typically limiting for giant kelp growth.*

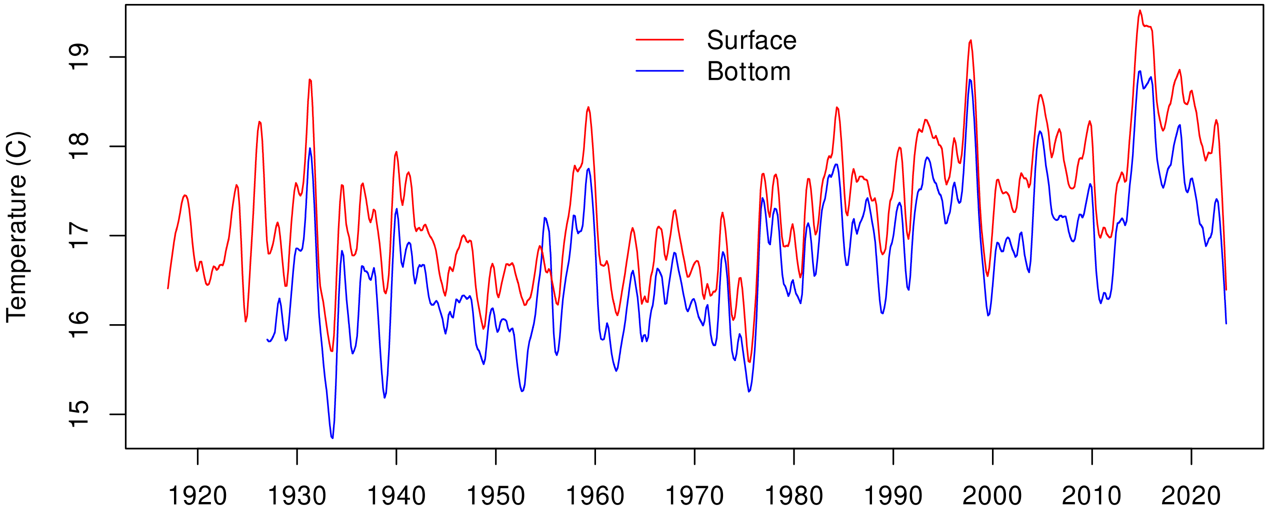

Fig. 8. *Trend of surface and bottom (depth=8m) temperatures at the Scripps Institution of Oceanography Pier. Data inclusive through Fall 2021.*

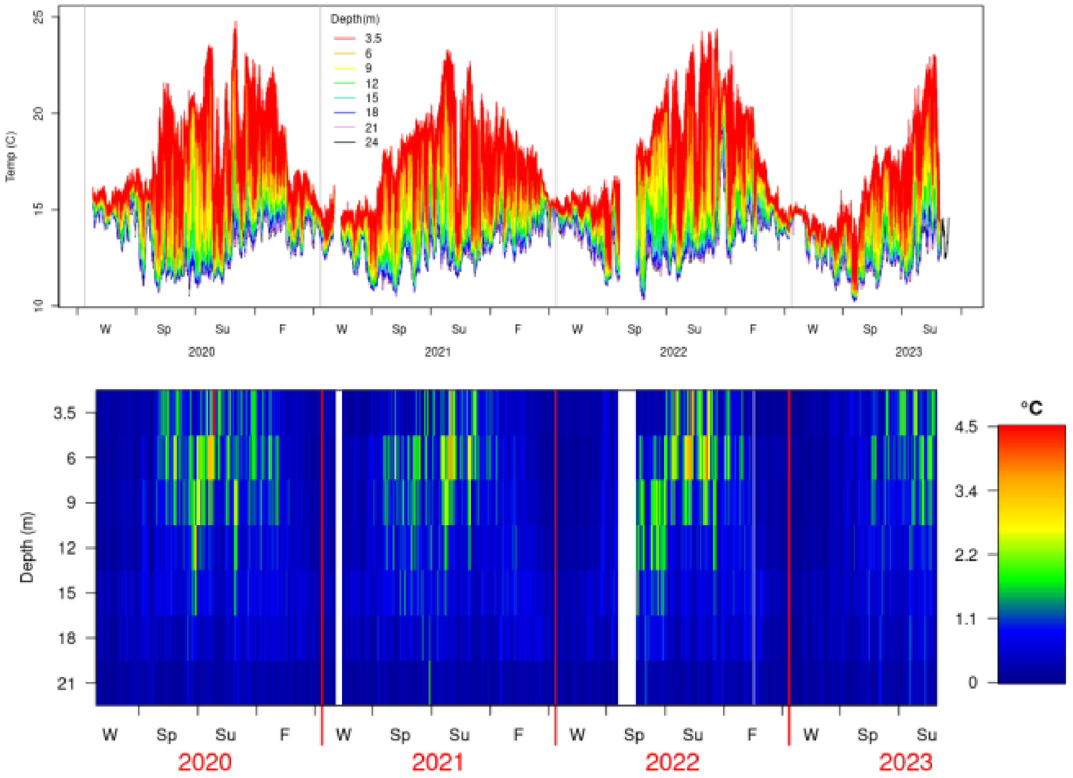

Figure 9. *Time series of temperature profiles off south La Jolla (top panel). Bottom panel shows near-surface temperature stratification (temperature difference among thermistors by depth) during spring and summer of 2020 and 2021.*

Light

Integrated daily PAR values for the three cross-shore study sites offshore of central Pt. Loma are shown in Fig. 10. Daily PAR levels were typically saturating for giant kelp growth and reproduction at the 9m site except durring periods of intense microalgal (phytoplankton) blooms, such as the intense red tide event of spring 2020 when benthic light levels remained near zero for more than a month. This bloom affected the entire coastline of southern California. In contrast, light at the deeper end of the kelp forest at 24 m from 2020 to 2022 was below the gametogenesis and growth thresholds for giant kelp most of the time except for brief periods of increased illumination. Limited benthic light levels at depths >16 m was likely the reason for limited recovery of giant kelp and Pelagophycus porra (elk kelp) after the extreme MHW of 2014/15. Benthic light levels at this deeper and all other light meter sites increased for extended periods of time in 2023. Daily PAR values at the 24 m site were saturating for giant kelp growth for much of the summer of 2023.

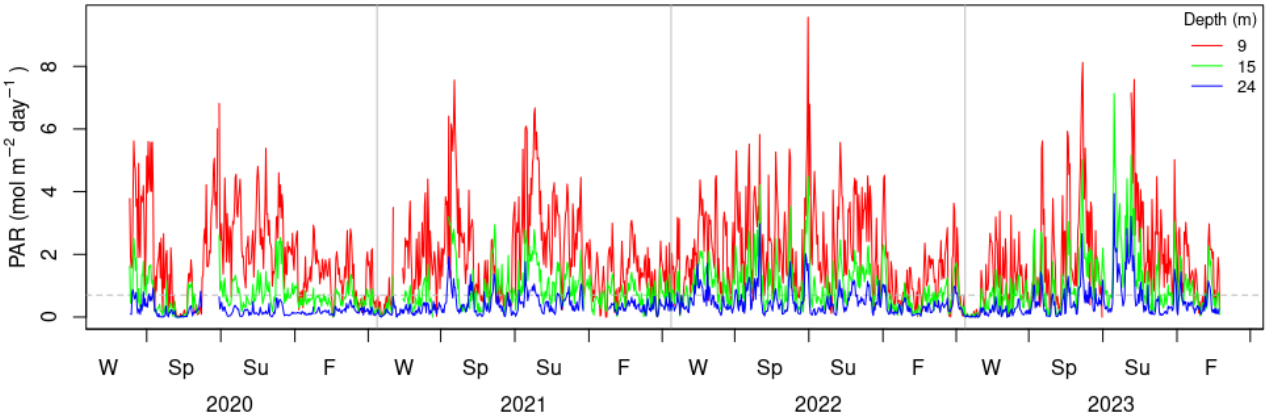

Fig. 10. *Daily PAR illuminating the bottom along the central Pt. Loma algal study sites. Horizontal dashed line indicates PAR threshold values for juvenile giant kelp growth (Dean and Jacobsen, 1984).*

Giant Kelp Status and Reproduction

The primary pattern of *M. pyrifera* abundance since the 1980's includes rapid declines associated with El Niños and storms (Fig. 11) followed by step increases in plant and stipe density chiefly due to discrete pulses of recruitment after major disturbances. This pattern has been historically reported from aerial photographs and in situ study sites dating back to the 1940s and results from varying levels of recovery. Post-disturbance recovery can also fail due to a lack of reproductive capacity or if a cohort of recruits does not survive to reproductive adulthood or succumbs soon afterward. There are many possible reasons that affect rates of giant kelp recovery that include (1) the magnitude of disturbance leading to kelp mortality, (2) oceanographic conditions and their seasonal timing during the recovery phase, (3) turbidity due to phytoplankton blooms or sediment plumes, (4) space competition with early successional species including *Desmerestia ligulata*, (5) space competition with long-lived understory species, (6) active herbivory, and (7) fouling. Another important factor is the reproductive output of extant adults and their spatial configuration relative to disturbed areas. Presently, there are no nearby sources of giant kelp propagules to support recruitment off northern La Jolla and much of North County.

Adult densities and cohort sizes of *M. pyrifera* off San Diego have decreased since observations began at all long term study sites in the 1980s (Fig. 11 – PLN18, PLC18, PLC15, PLC12, and PLS18) Recent cohorts have become obscured or non-existent despite favorable oceanographic conditions that persisted from 2020 to 2023. The response of giant kelp to disturbance since the 2014/15 MHW appears muted with varying degrees of post-disturbance recovery, resulting in only minor pulses of adult cohort development (Figs. 11-15). Presently, densities of both adults and stipes are at historic lows (Figs. 1, 11, and Table 4) and recruitment has been minimal or non-existent since 2020 (Figs. 12 and 13). The only exceptions are the PLS18 and PLM18 stations in south Pt. Loma. Other southern Pt. Loma stations also experienced some recruitment but only at historically low levels. The reasons for poor kelp performance varied among sites. The most obvious cause was competition for space with understory species at the shallower sites (<15 m) where light is rarely limiting for these species to grow thus supporting exclusion of *M. pyrifera* recruitment. Deeper sites have likely failed to recover due to low light levels caused by enhanced phytoplankton blooms (Fig. 10). Overgrazing by sea urchins has not been problematic due to their low densities off San Diego since the MHW during which disease decimated their populations.

The 2014-2016 MHW caused massive mortality of giant kelp off San Diego County mainly through a combination of nutrient and temperature stress in addition to storm waves (Fig. 7). Giant kelp surface canopy was nearly entirely lost off most of San Diego, Orange, and Los Angeles counties by 2016. Densities of adult *M. pyrifera* plants (Fig. 11) and stipes (Fig. 14) 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. 12 and 13). Some of the study site cohorts observed in 2016 partially matured into pre-adults and adults at a subset of the sites but all have since died.

Generally, the status of giant kelp after the last major disturbance can be categorized among the study sites as: (1) recovery to giant kelp dominance, (2) cohort currently in development, (3) recovery followed by collapse, (4) partial recovery followed by collapse, (5) no recovery, and (6) not kelp dominated prior to the latest disturbance nor afterward. These six states are tabulated in Table 4 with regard to the combined warm event of 2019 and the extended period of decreased bottom light of 2020.

Category	**Kelp State**	**# of Study Sites**	**Study Sites**
1	Recovery to dominance	0	
2	Cohort in development after collapse	1	PLS18
3	Recovery followed by collapse	2	PLM18, PLC21
4	Partial recovery followed by collapse	10	CARD, SB, PLT15, PLS15, PLC18, PLC08, LJS18, LJS15, LJS12, LJN15
5	Kelp abundant prior to disturbance but no recovery	2	PLT12, PLN18
6	Kelp not abundant prior to disturbance	5	PLC15, PLC12, LJN18, LJN12, DM

Table 4. *Recovery states of M. pyrifera after the combined disturbances of the 2018/19 warm event and the 2020 phytoplankton bloom which limited light levels to near zero throughout the water column.*

Giant kelp stands are presently in a collapsed state where it is absent or nearly so at all but 3 of the 20 sites (PLC08, PLS18, and PLS15). There has essentially been no giant kelp recovery at LJN18 where giant kelp was abundant prior to the MHW and at Del Mar where giant kelp is now completely absent and was sparse 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 LJN18. 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, *Desmerestia ligulata*, dominated the

PLT15 and PLM18 study sites until 2019, thus delaying giant kelp recovery via competitive exclusion.

The present poor condition of *M. pyrifera* at most of the study sites is best exemplified in Table 5 which lists the quantiles of stipe sums at each of the sites for the latest sampling bout (Fall, 2023). The site that is currently in the best condition relative to historical data is PLC08 where the quantile for the present stand is ~0.46 representing only 15% of its all time maximum. The next greatest quantiles were observed at PLS18 and PLS15 where stipes counts are <10% of their historical maxima. Presently there are no stipes at half of the study sites which is unprecedented. Table 4 highlights the extremely poor condition 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* shifts 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 presently developing El Niño that will likely peak in spring of 2024 will likely further decimate giant kelp. However, this could be buffered by powerful winter storm waves effectively eliminating or significantly reducing understory species followed immediately by the onset of supportive growth conditions such as a La Niña which is now predicted for late summer (NOAA).

Site	**Stipes All Time Maximum**	**Date of Maximum**	**Stipes Fall 2023**	**Stipes Quantile 2023**	**Ratio Max/ Fall 2023**
PLC08	2454	2018-08-09	363	0.46	0.15
PLS18	2483	1994-06-06	256	0.45	0.10
PLS15	2110	1994-08-25	123	0.27	0.06
LJS15	3341	1994-08-23	49	0.35	0.01
LJS18	2114	2009-08-14	41	0.05	0.02
PLT15	770	1999-10-20	34	0.61	0.04
PLM18	926	2008-12-17	24	0.53	0.03
LJS12	1013	2018-08-07	14	0.04	0.01
PLC18	3336	1990-10-19	9	0.05	0.00
PLC21	3274	2013-05-02	4	0.25	0.00
DM	519	2010-09-03	0	0.48	0.00
PLT12	1952	2008-08-19	0	0.44	0.00
LJN12	607	2014-02-11	0	0.28	0.00
LJN18	2093	2010-08-04	0	0.24	0.00
Card	3341	2014-02-13	0	0.19	0.00
LJN15	2161	2013-11-13	0	0.14	0.00
PLC12	2665	1985-04-11	0	0.13	0.00
SB	2933	2011-11-10	0	0.13	0.00
PLN18	3083	2013-08-15	0	0.10	0.00
PLC15	3819	1989-06-29	0	0.01	0.00

***Table 5.** Quantiles of giant kelp (M. pyrifera) stipe sums observed during the latest sampling bout (Fall, 2023) for all study sites. Date indicates the day that each site maximum was observed. Rows are ordered by decreasing numbers of stipes for Fall, 2023.*

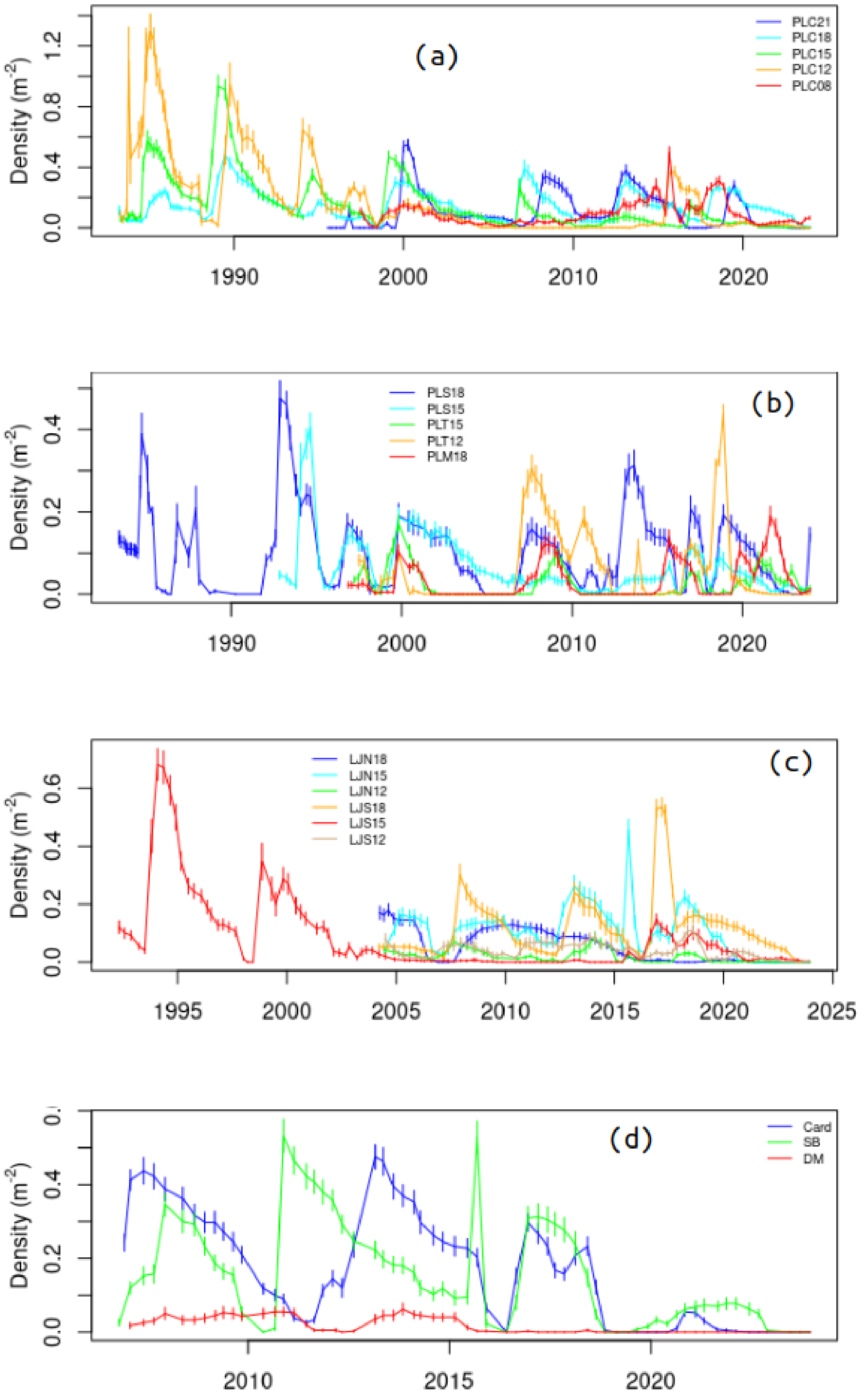

Figure 11. *Mean densities of adult Macrocystis pyrifera among study site groups: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County. Error bars indicate standard errors.*

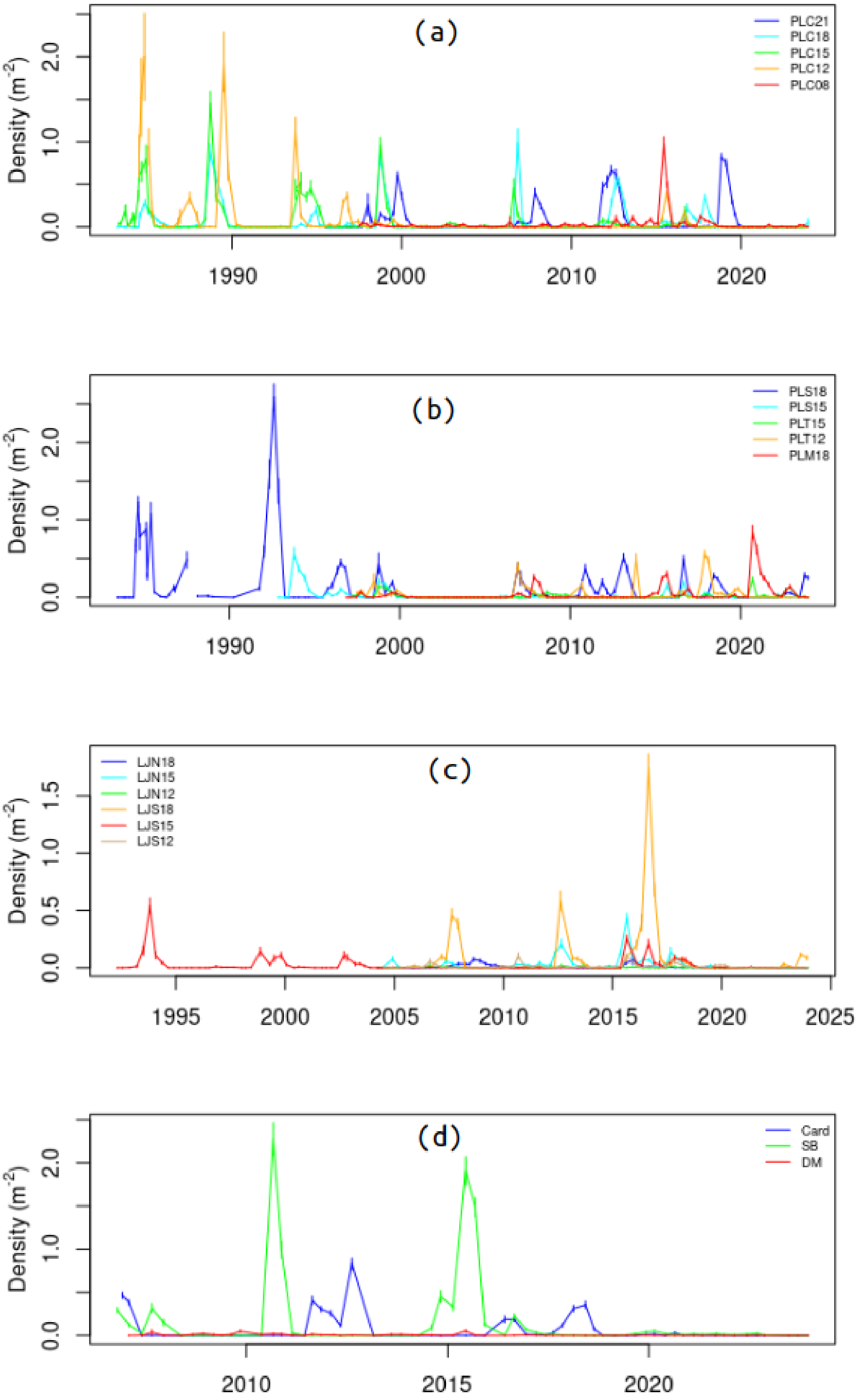

Figure 12. *Mean densities of Macrocystis pyrifera pre-adults (<4 stipes): (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.*

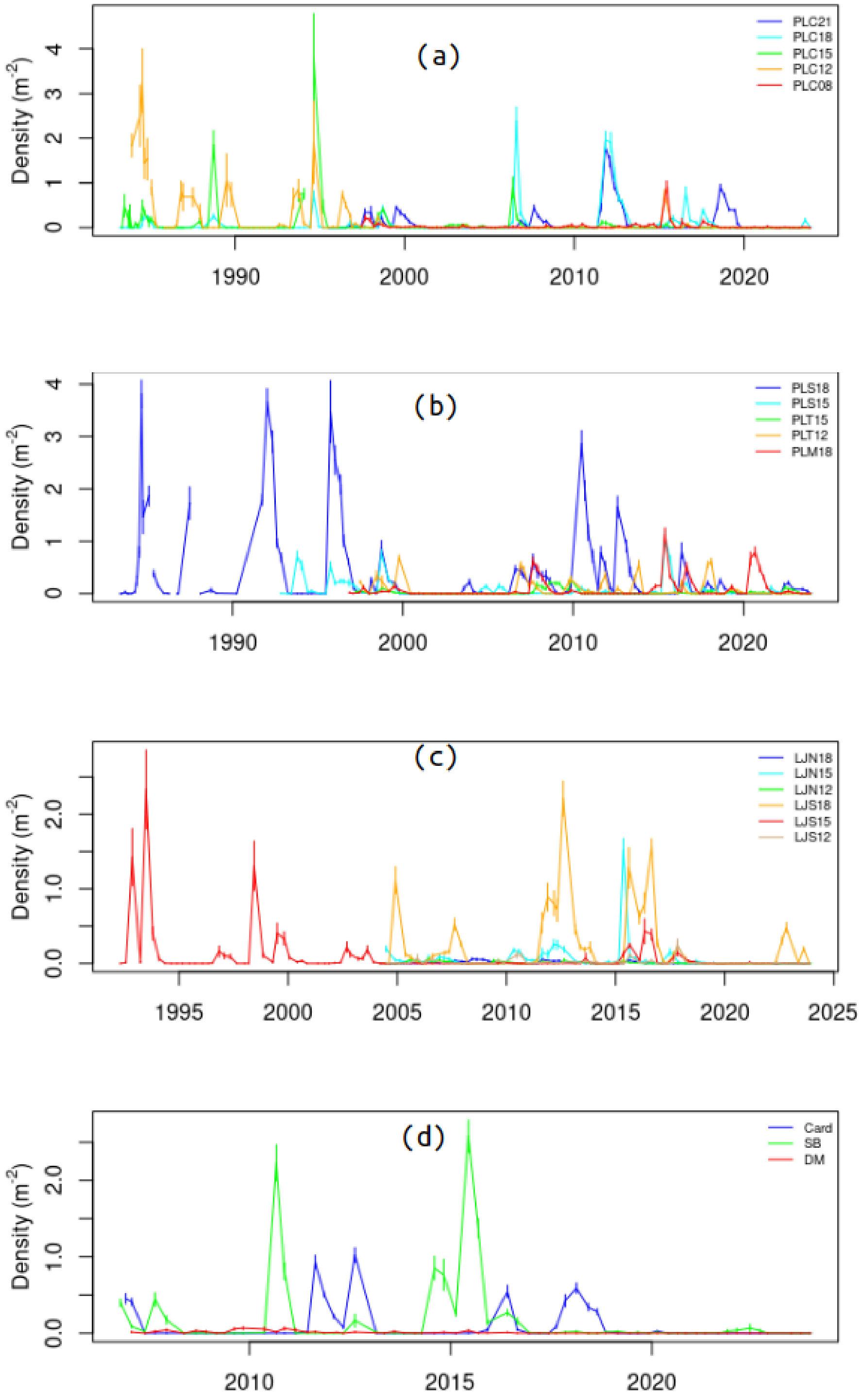

Figure 13. *Mean densities of Macrocystis pyrifera bifurcates: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors*

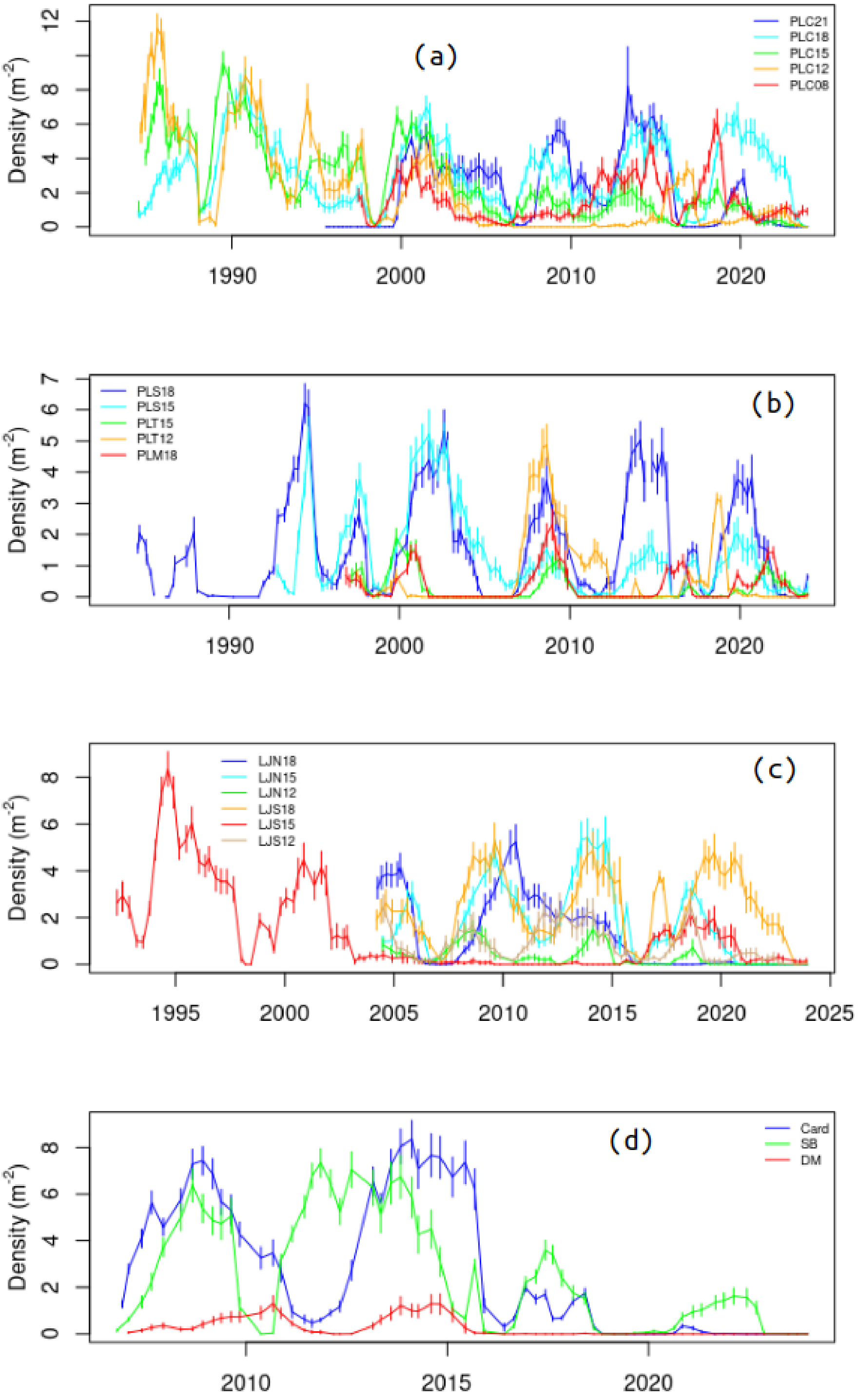

Figure 14. *Mean densities of Macrocystis pyrifera stipes: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.*

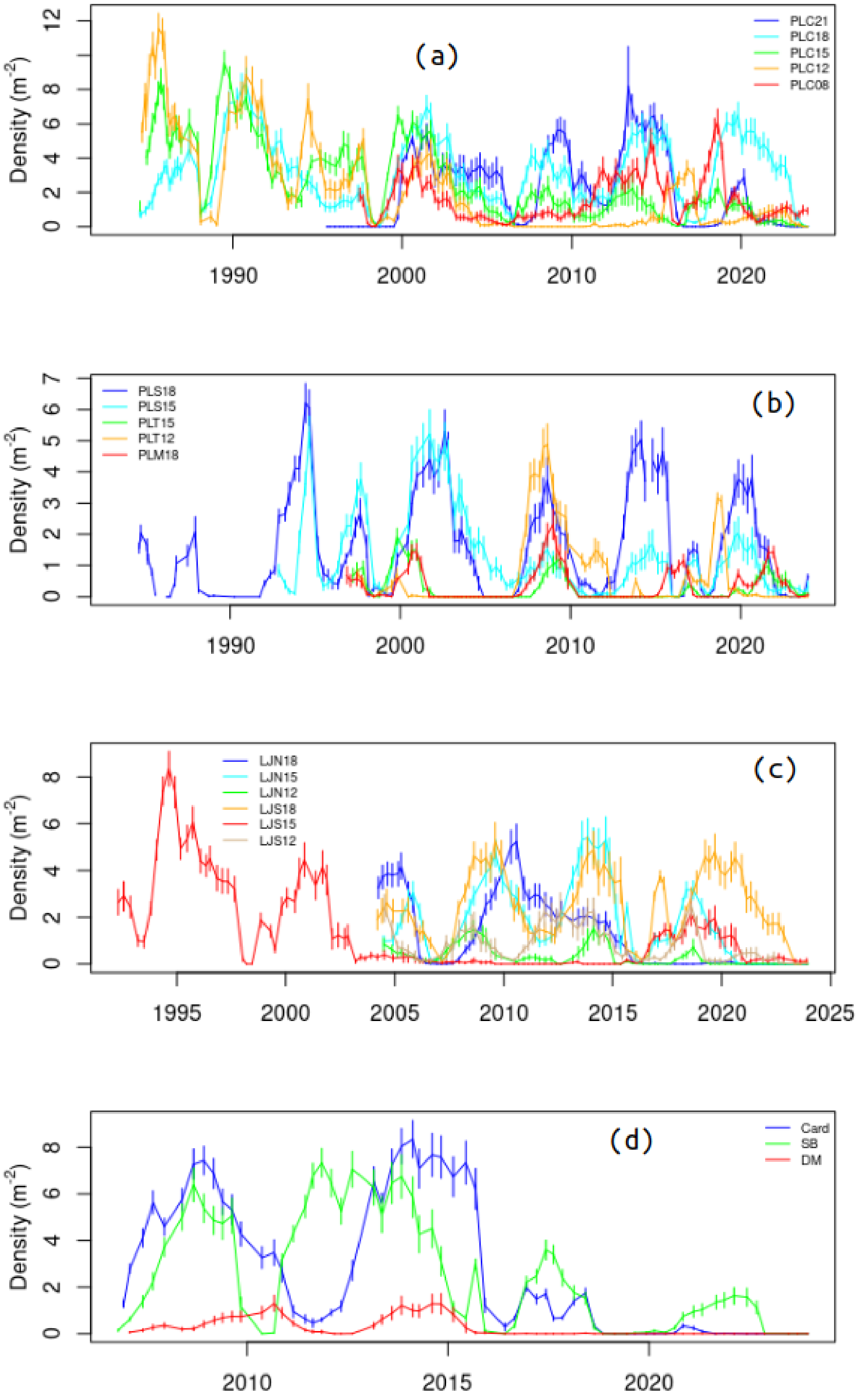

Figure 15. *Mean densities of Macrocystis pyrifera (a) adults, (b) pre-adults, (c) pre-bifurcates, and (d) stipes along the 18 m sites off La Jolla and Pt. Loma. Error bars indicate standard errors.*

The reproductive condition of giant kelp along the central Pt. Loma study sites was greatly diminished through the MHW. This diminution of reproductive capacity persisted at three of the five central Pt. Loma sites (PLC21, PLC18, and PLC 08 - Fig. 16). Reproductive capacity has since recovered at PLC12 and PLC15. Reproductive capacity at the remaining sites has been at historically low levels dating back to before the 1997/98 El Niño. Sporophyll volumes were greatly reduced by the end of the 2015/16 El Niño and sporophylls were not reproductive at the PLC08 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. 16d). Figure 16d indicates that the reproductive output of individual plants relative to their biomass (as estimated by stipe density) has not returned to historical levels and has also likely contributed to the diminished recruitment at these sites. The only study site where reproductive capacity has recovered somewhat is the central Pt. Loma 15 m site (PLC15) where densities of *M. pyrifera* are still low relative to the historical record. Reproductive capacity as a function of stipes (i.e., biomass) has remained diminished during this study period indicating continued reduced reproductive potential that will likely contribute to delayed giant kelp recovery into the future.

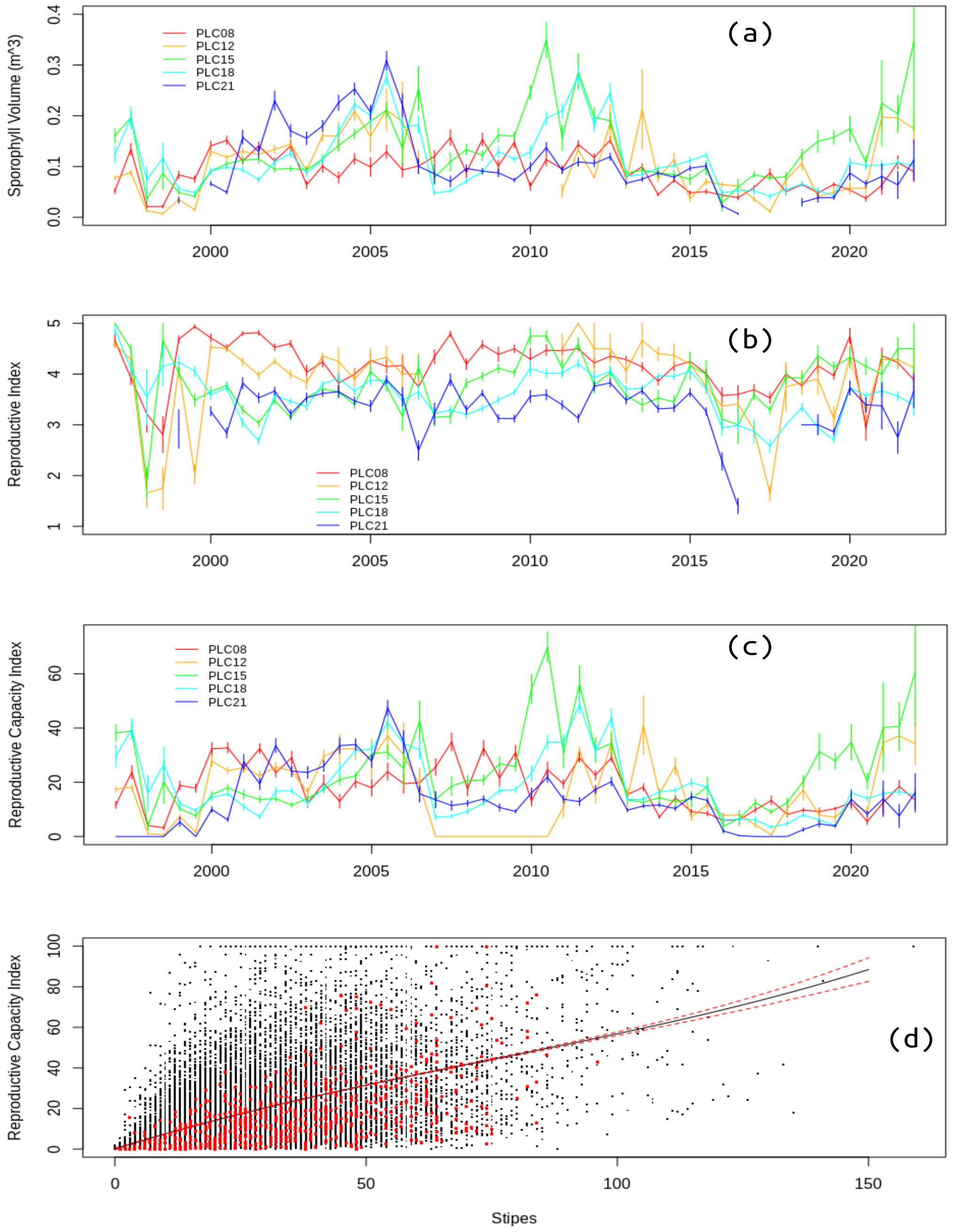

Figure 16. *Reproductive states of Macrocystis pyrifera at the central Pt. Loma study sites: (a) sporophyll volume, (b) reproductive index (see Table 2), (c) reproductive capacity (derived index of relative among-site reproductive potential - see Methods). Means are plotted and error bars indicate standard 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 Niños and MHWs. 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. *Cystoseira osmundacea* is a low growing fucoid alga in southern California that ranges from the intertidal to shallow subtidal depths and ranges from Oregon to Baja California (Schiel, 1985). Its growth and reproduction is highly seasonal with growth occurring during the spring while reproduction occurs during summer when it can extend to the surface and form a seasonal canopy in shallow depths off central California. Its growth is stunted at deeper depths (>8 m) which includes all sites in this study. It is also known to be able to survive violent storms and thus gains a competitive advantage over giant kelp during such periods.

Pterygophora californica Laminaria farlowii, and *Cystoseira osmundacea* were all profoundly affected by the 2014/15 MHW. Together along with turf species, these species have replaced giant kelp at several sites <18 m deep. Prior to the MHW, *P. californica* stands were relatively dense at the central Pt. Loma and southern La Jolla study sites but then decreased dramatically at all sites by 2016 (Fig. 17). A strong cohort of recruitment was observed at most of these sites shortly afterward leading to a rapid regrowth of young plants. These plants have since been growing and have exhibited self thinning with slow rates of decreasing density. Presently, the greatest densities are located at PLC15, PLT12, LJS15, and are increasing at CARD. Moderate densities exist at the remaining sites except for where it is nearly absent including both North County sites, all north La Jolla sites and PLS18.

Laminaria farlowii abundances also decreased at most sites as a result of the MHW and quickly rebounded within a few years afterward (Fig. 18). Abundances returned to pre-MHW levels within two to three years and still persist at these levels at all of the central Pt. Loma sites except for PLC18. Densities were low at all south Pt. Loma sites prior to the MHW except PLS15 where its abundance has increased and remained high though it is slightly decreasing at present. Abundances at PLT12, PLT15, PLM18 were low prior to the MHW but have since increased. Abundances have been increasing at all North County sites during this study period.

The growth morphology of *Cystoseira osmundacea* is nearly turf-like off southern California including at our study sites where it grows close to the bottom and only extends up to a meter off the bottom when it is reproductive during summer. The MHW had no negative effects on this species (Fig. 19) as neither the warm water nor high wave events associated with the MHW appeared to affect its density. In fact, densities of *C. osmundacea* have increased since the MHW at most sites and continue to do so with the exception of PLC18, and the southern Pt. Loma sites except for PLT12. Increasing densities have been observed at the North County sites where it had been mainly absent prior to the MHW.

The primary 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 these 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 disturbance.

The complex trajectories of understory species during and after the 2014/15 MHW 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. 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 MHW penetrated to the bottom for an extended period of time (Fig. 7). 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 increased cover of understory and turf species continues at present and is responsible for outcompeting giant kelp at PLN18, PLC15, PLC12, PLC08, LJS15, LJS12, LJN18, LJN15, LJN12, PLS15, PLT15, and PLT12.

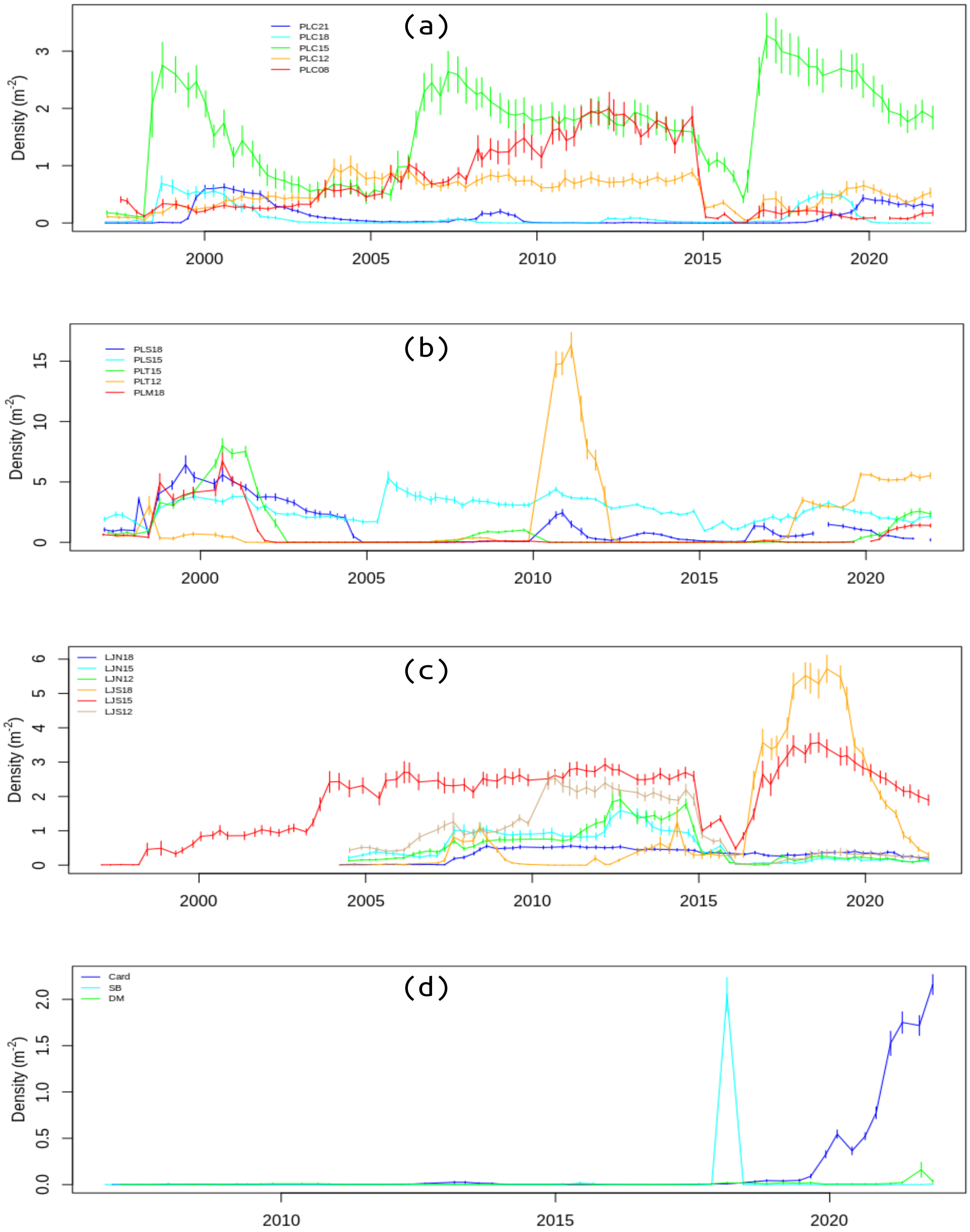

Figure 17. *Mean densities of the understory kelp Pterygophora californica: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.*

The growth and reproductive condition of tagged *P. californica* (Figs. 20 and 21) and *L. farlowii* (Figs. 22 and 23) at the central Pt. Loma study sites decreased dramatically during the MHW 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.

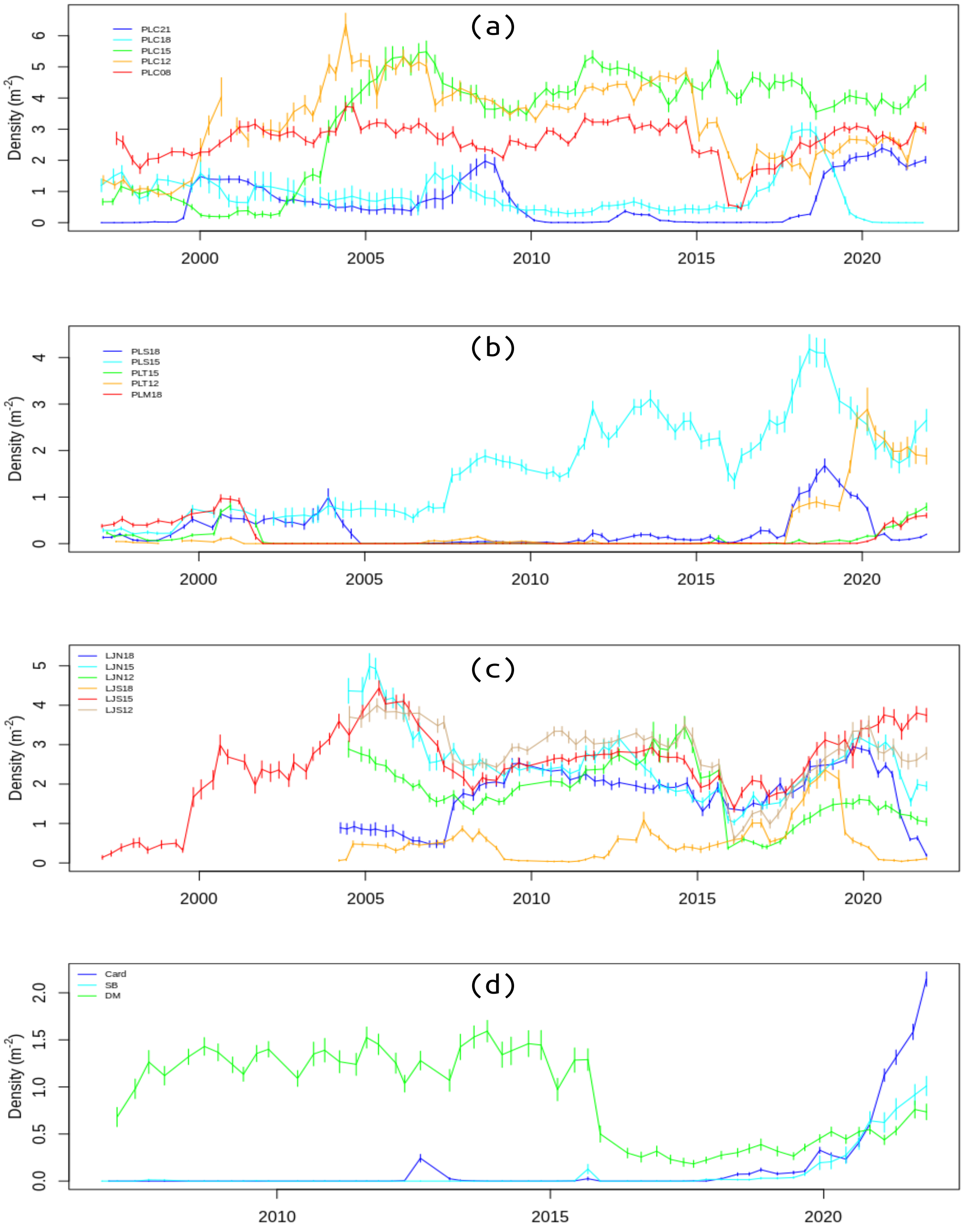

Figure 18. *Mean densities of the understory kelp Laminaria farlowii: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.*

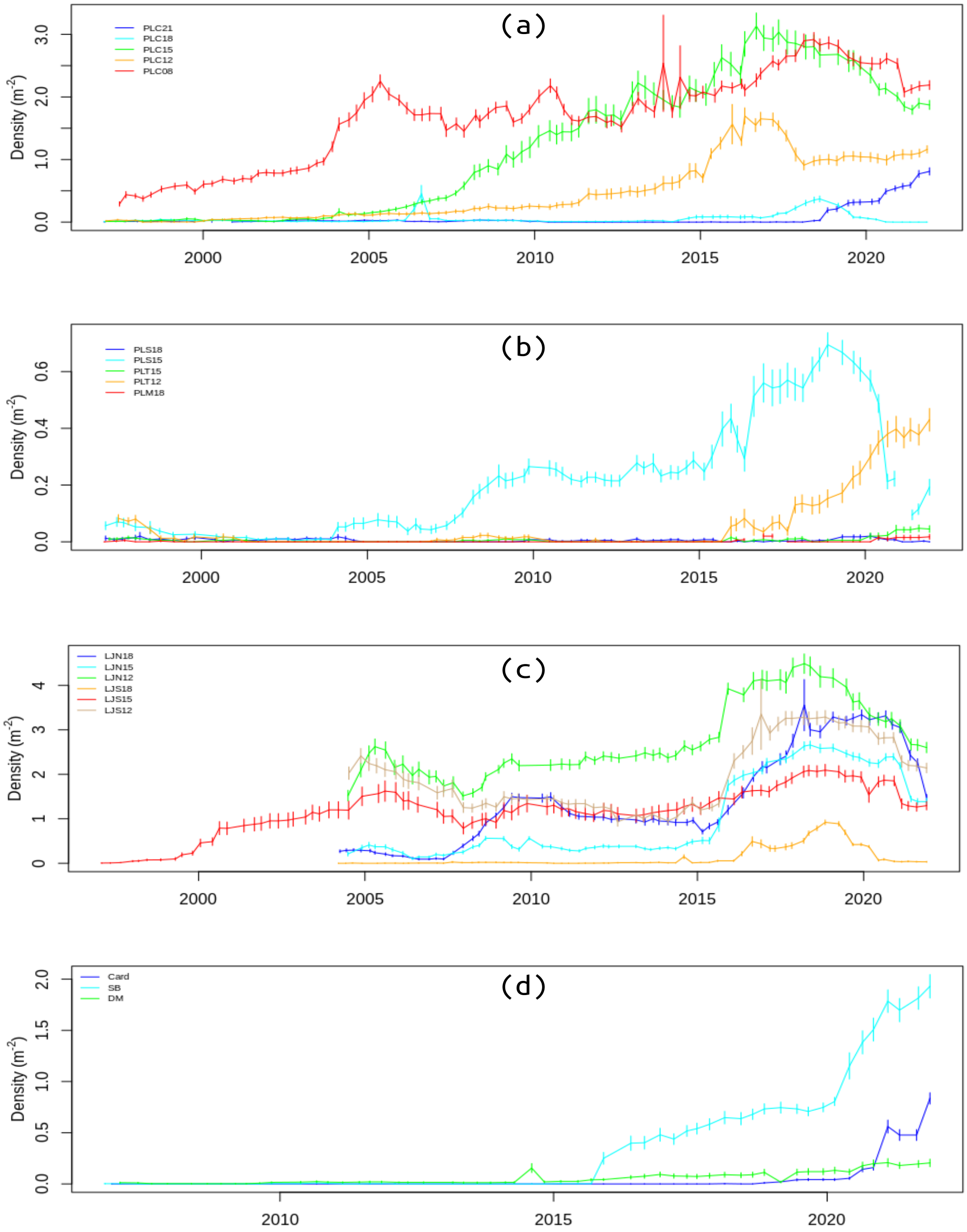

Figure 19. *Mean densities of the understory kelp Cystoseira osmundacea: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.*

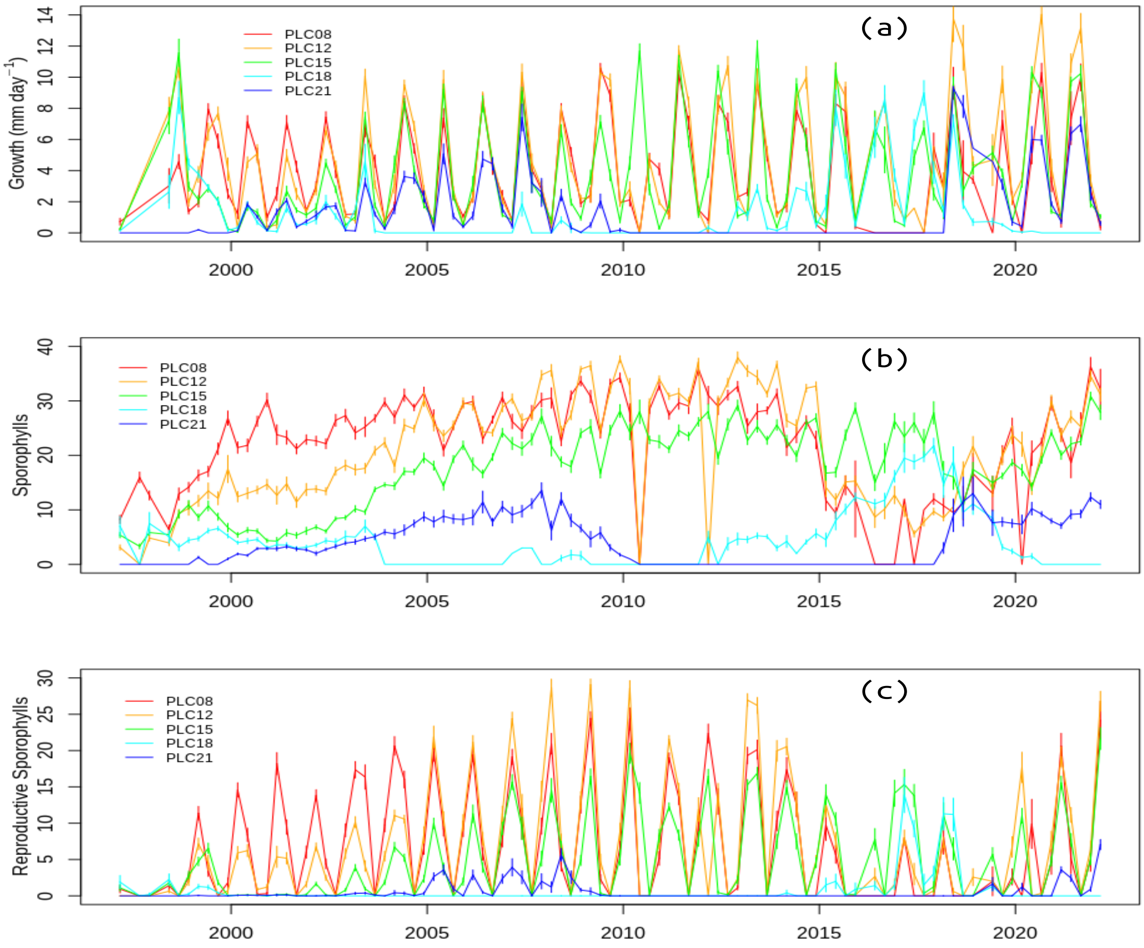

Figure 20. *Growth and reproduction of the understory kelp Pterygophora californica at the central Pt. Loma study sites: (a) growth, (b) # sporophylls, and (c) # reproductive (sexy) sporophylls. Means are plotted and error bars indicate standard errors.*

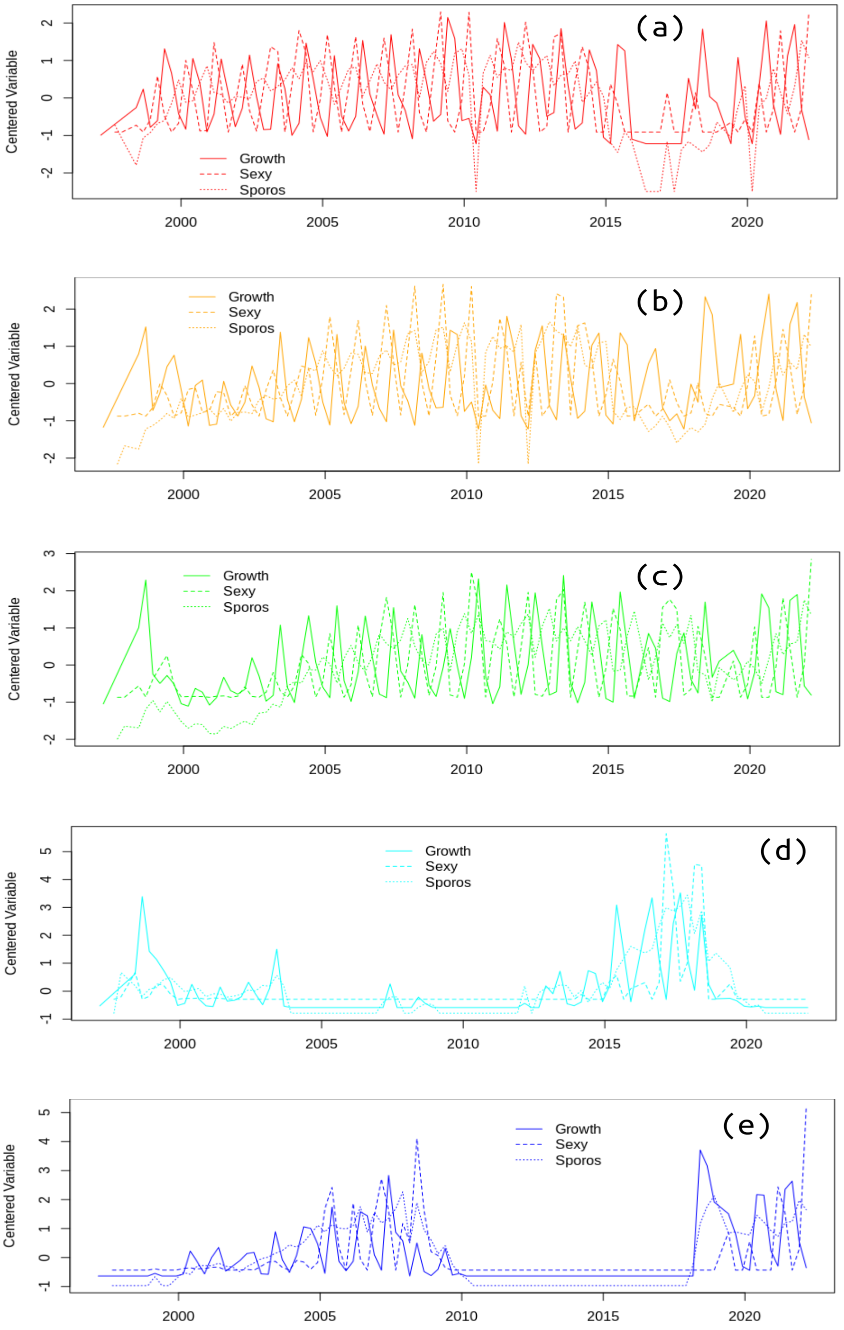

Figure 21. *Centered Pterygophora californica growth rates, sporophyll, and # of reproductive sporophylls for (a) PLC08, (b) PLC15, (c) PLC18, and (d) PLC21 study sites. Means are plotted and error bars indicate standard errors.*

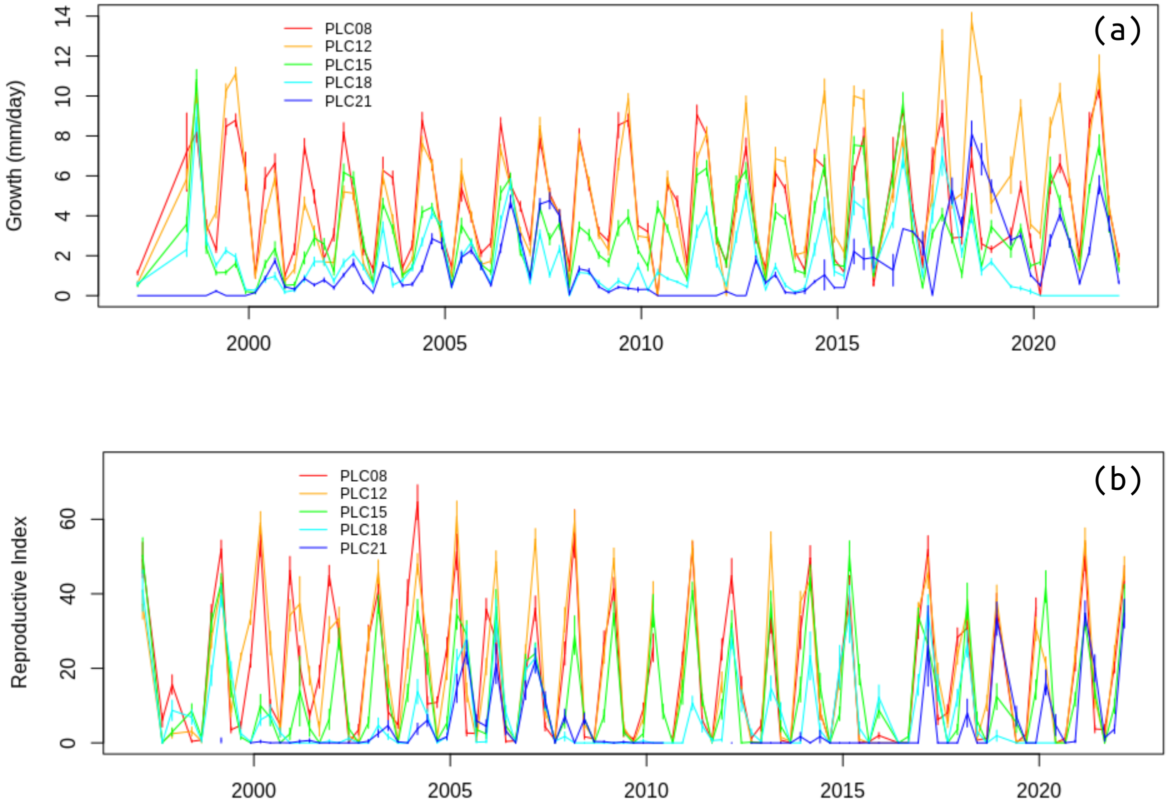

Figure 22. *Growth and reproduction of the understory kelp Laminaria farlowii at the central Pt. Loma study sites: (a) growth, and (b) % of blade that is sorus (reproductive), Means are plotted and error bars indicate standard errors.*

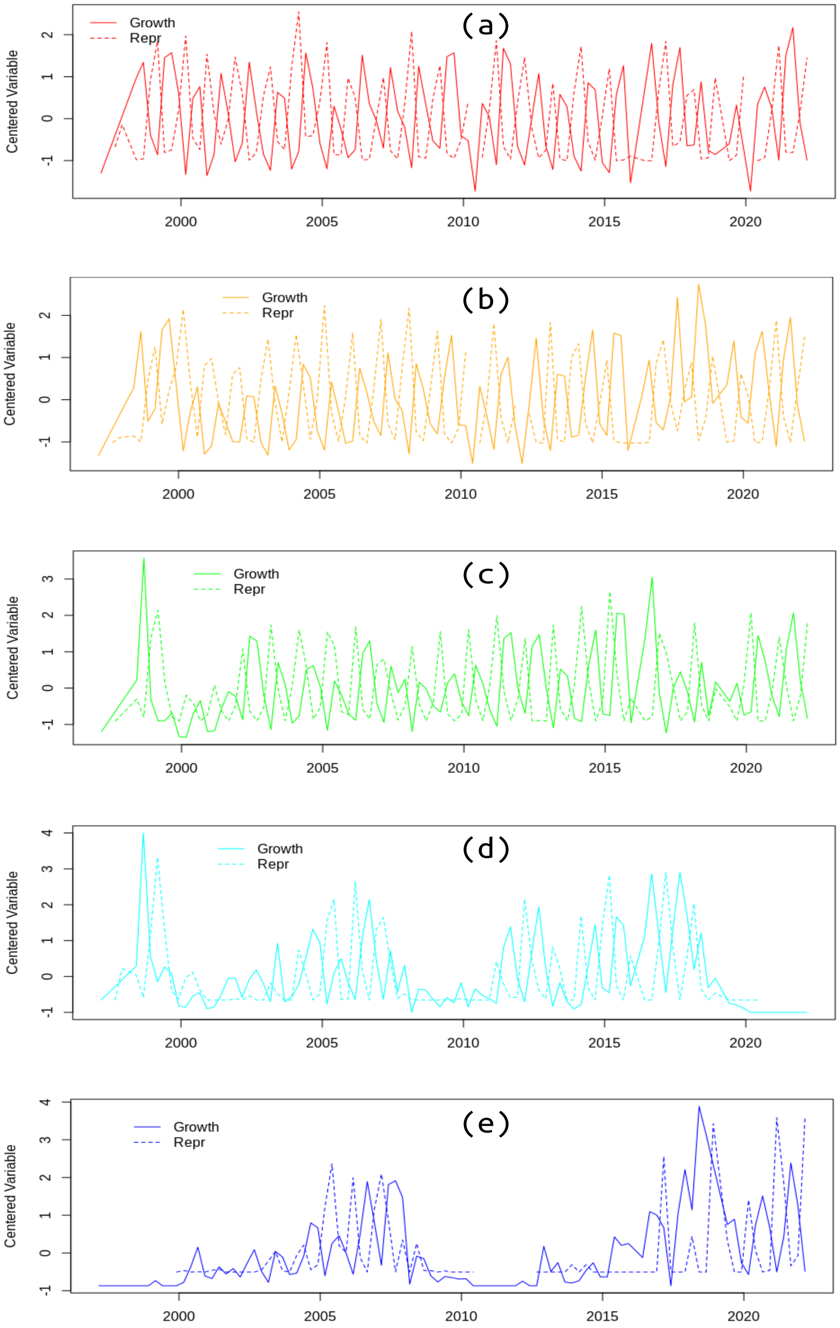

Figure 23. *Centered growth and reproduction of the understory kelp Laminaria farlowii at the central Pt. Loma study sites. (c) standardized growth and reproduction for the PLC8 and the (d) PLC12 study sites.*

Algal Community Analysis

Algal community composition among all of the study sites during the study period are shown in Figures 24-28. These figures were produced using factor analysis to reduce the number of dimensions represented each algal species being tracked over time. All of the algal species and/or groups each represent a single dimension, and factor analysis reduces the number of dimensions to graphically visualize algal community states among sites by year. 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). Here, the first two factors, which account for the greatest amount of variability in the analysis, are plotted against one another. Factor 1 indicates a continuum (from positive to negative) of understory algal composition ranging from fleshy red and articulated coralline algae to the stipitate species, *Eisenia arborea*, and *P. californica*, the prostrate brown alga *L. farlowii*, to the post-disturbance pioneer brown alga *Desmerestia 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).

A holistic view of macroalgal community composition among the study sites is best envisioned by contrasting the upper left and lower right quadrants of Figs. 24-28. The upper left quadrant indicates *M. pyrifera* domination and sparse understory and turf. The lower right quadrant represents understory and turf domination. A mature giant kelp forested area with heavy canopy will occupy the upper left quadrant whereas an area with patchy or non-existent giant kelp canopy with turf algae will occupy the lower right quadrant. The middle section of each plot represents a mixed stand of *M. pyrifera* with stipitate and laminate kelps and moderate coverage of turf algae. The progression of sites having giant kelp in 2019 after the the first wave of post-MHW recruitment to the diminution of giant kelp at most sites by 2023 is evident in the plots as is the variability among the sites which mirrors the evolving sparse and patchy nature of giant kelp forest condition off San Diego County during this study period.

The algal states of sites PLC18, PLC21, PLN18, PLS18, and LJS18 represented the best condition for giant kelp forests during the study period and generally after the MHW with moderate to moderately high densities of giant kelp over shading understory in 2019 during the first year of this reporting period. Subsequent years showed a progression of *M. pyrifera* loss with one ephemeral episode of growth at PLM18 in 2021. Even this stand began to disappear by the following year. The most consistent site with regard to giant kelp was PLC08 where it is sparse by historical standards (Table 5).

The forcing behind these patterns of algal cover among the sites is not well understood at all 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 common local species crashed during the MHW and have yet to increase, though some recruitment has recently been observed. But these animals are still small and in low enough density to not yet present a risk of over grazing. The two deeper sites off northern La Jolla are devoid of all giant kelp and look highly disturbed for unknown reasons. Del Mar is also presently highly disturbed with very little macroalgae. These sites are essentially ‘urchin-less barrens’ and have become dominated by suspension feeding invertebrates including bryozoans and gorgonians.

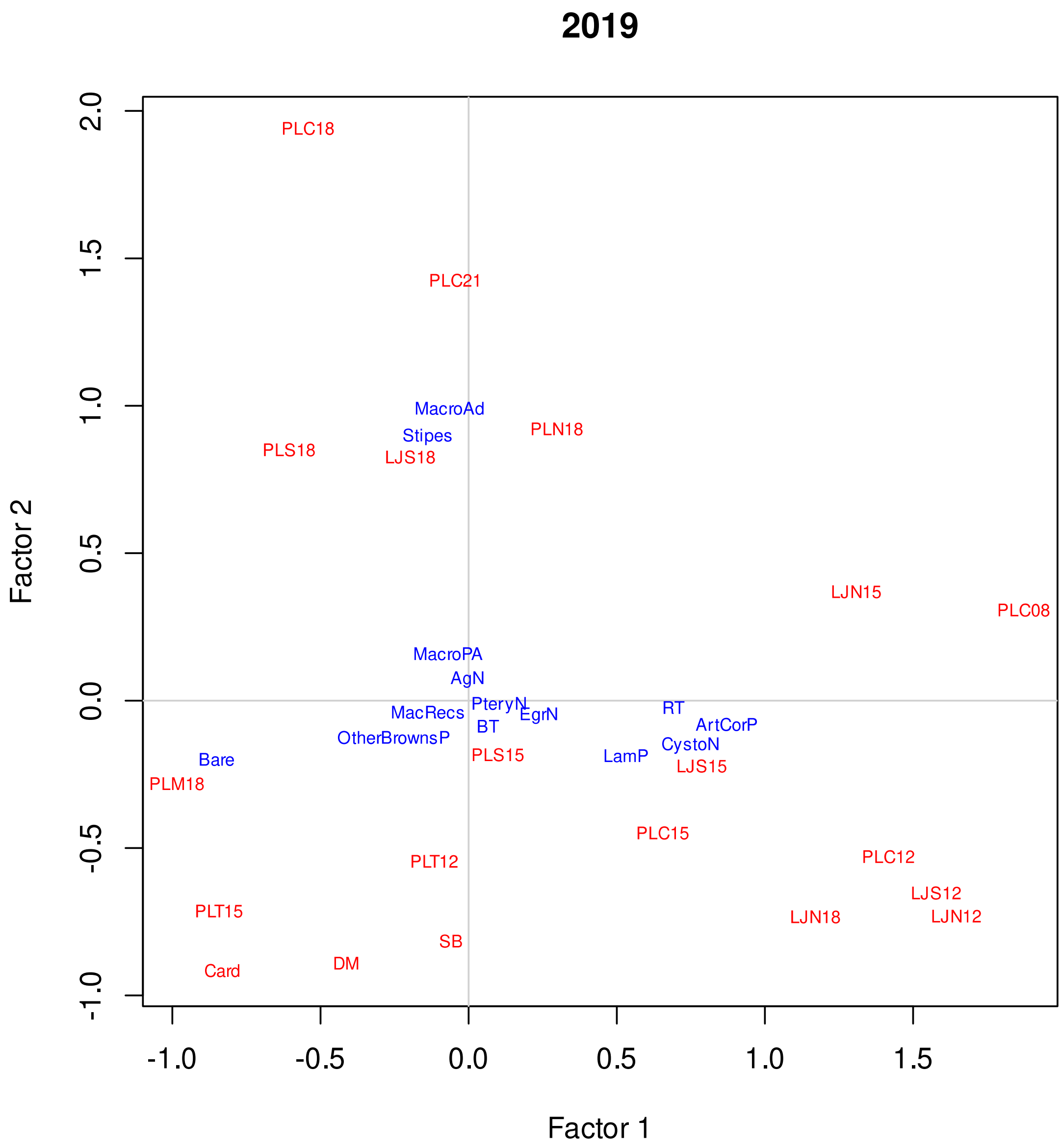

Figure 24. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2019. Algal group definitions: Bare = derived bare space, MacRecs = M. pyrifera recruit stage (pre-bifurcates + bifurcates), MacroAd = M. pyrifera adult density, Stipes = M. 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.*

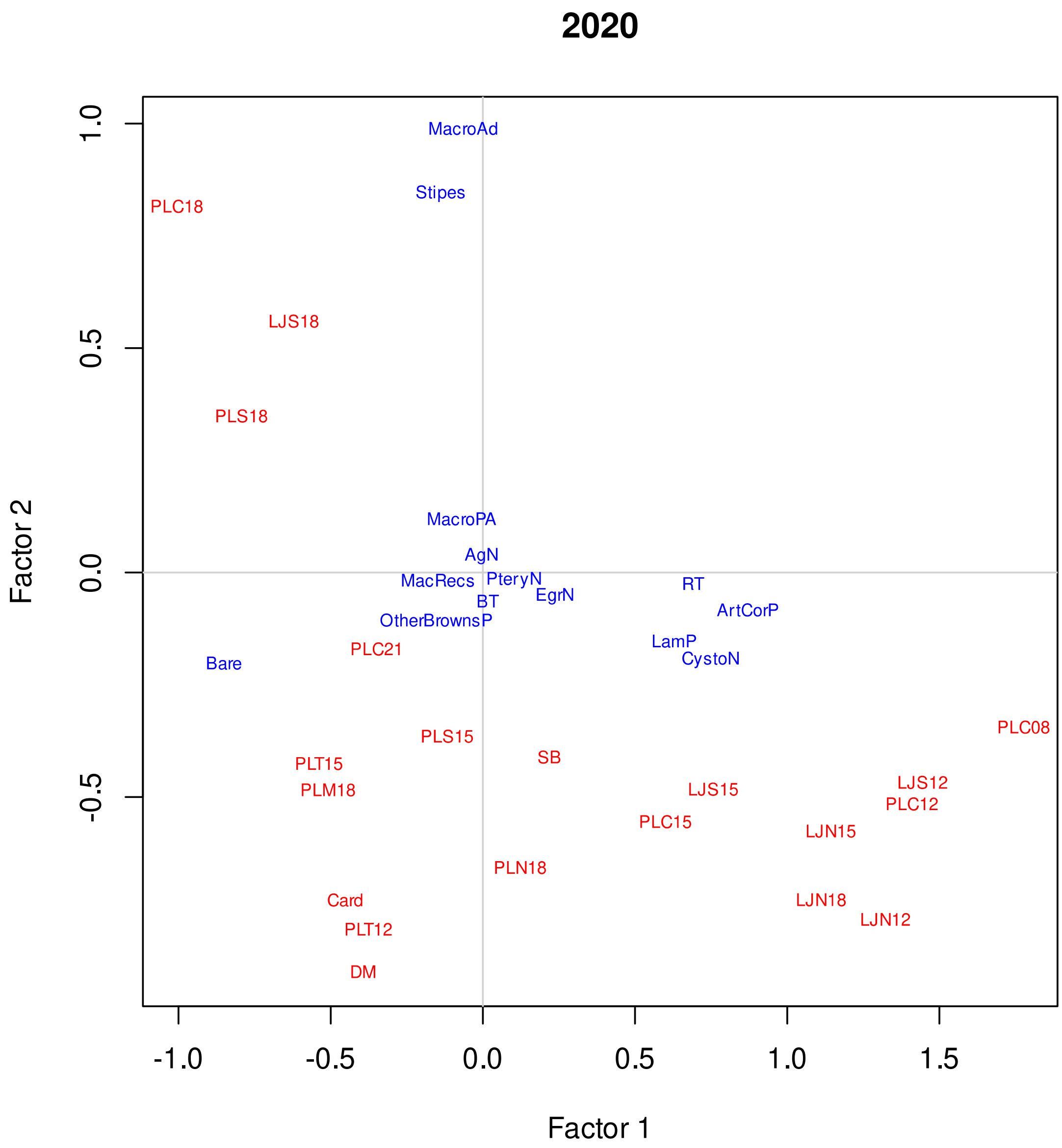

Figure 25. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2020. See Figure 24 for description of plot.*

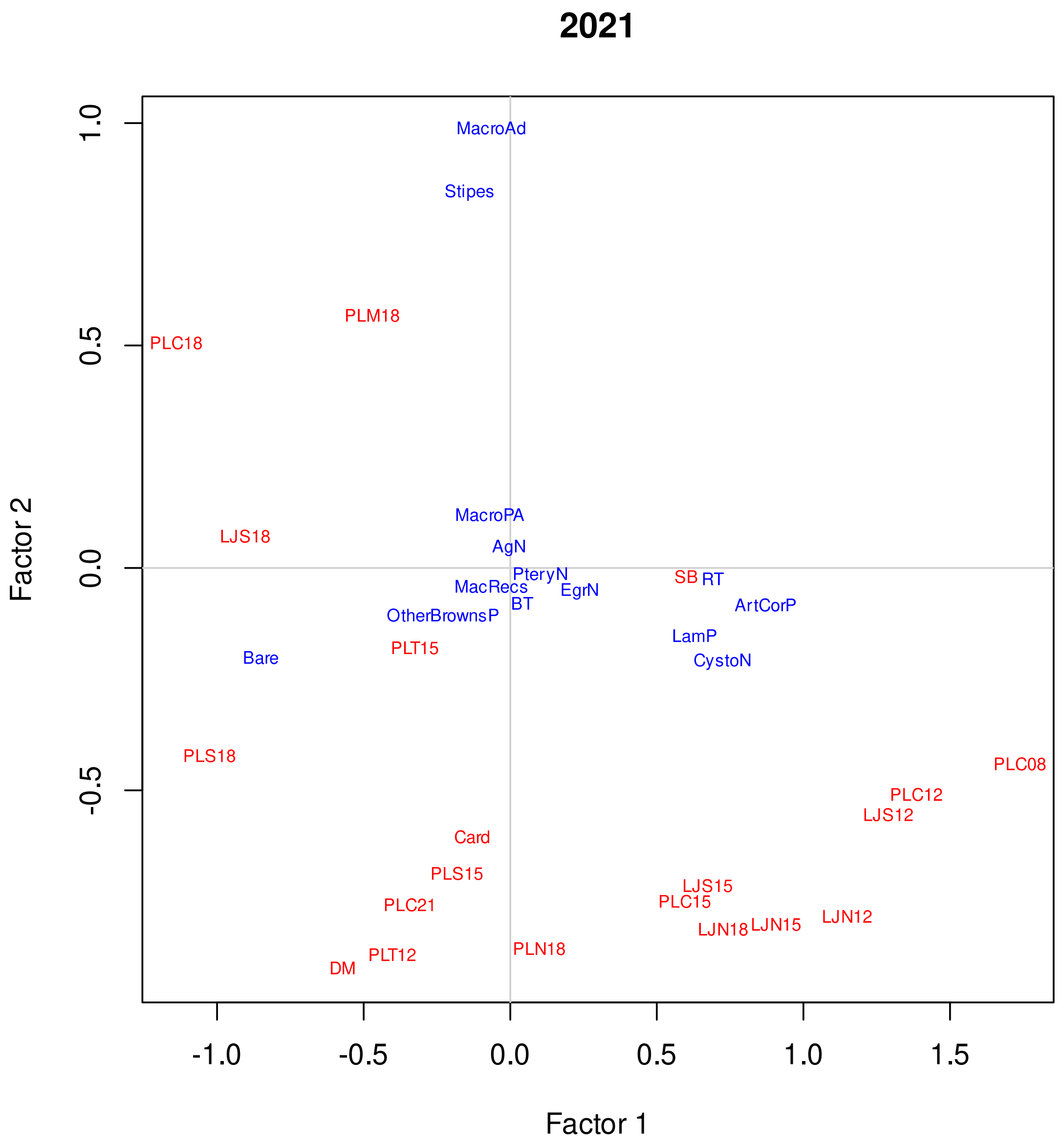

Figure 26. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2021. See Figure 24 for description of plot.*

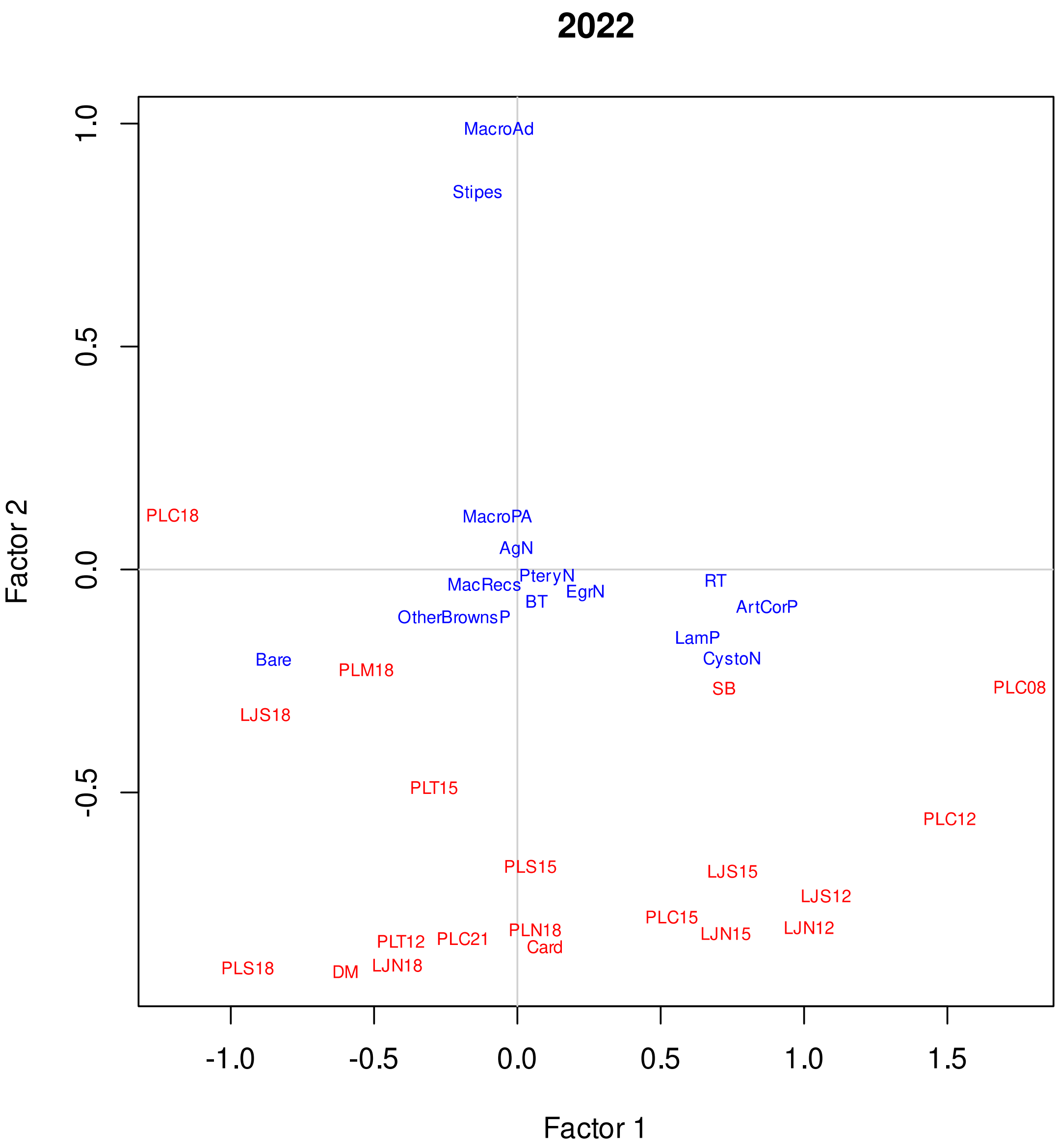

Figure 27. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2022. See Figure 24 for description of plot.*

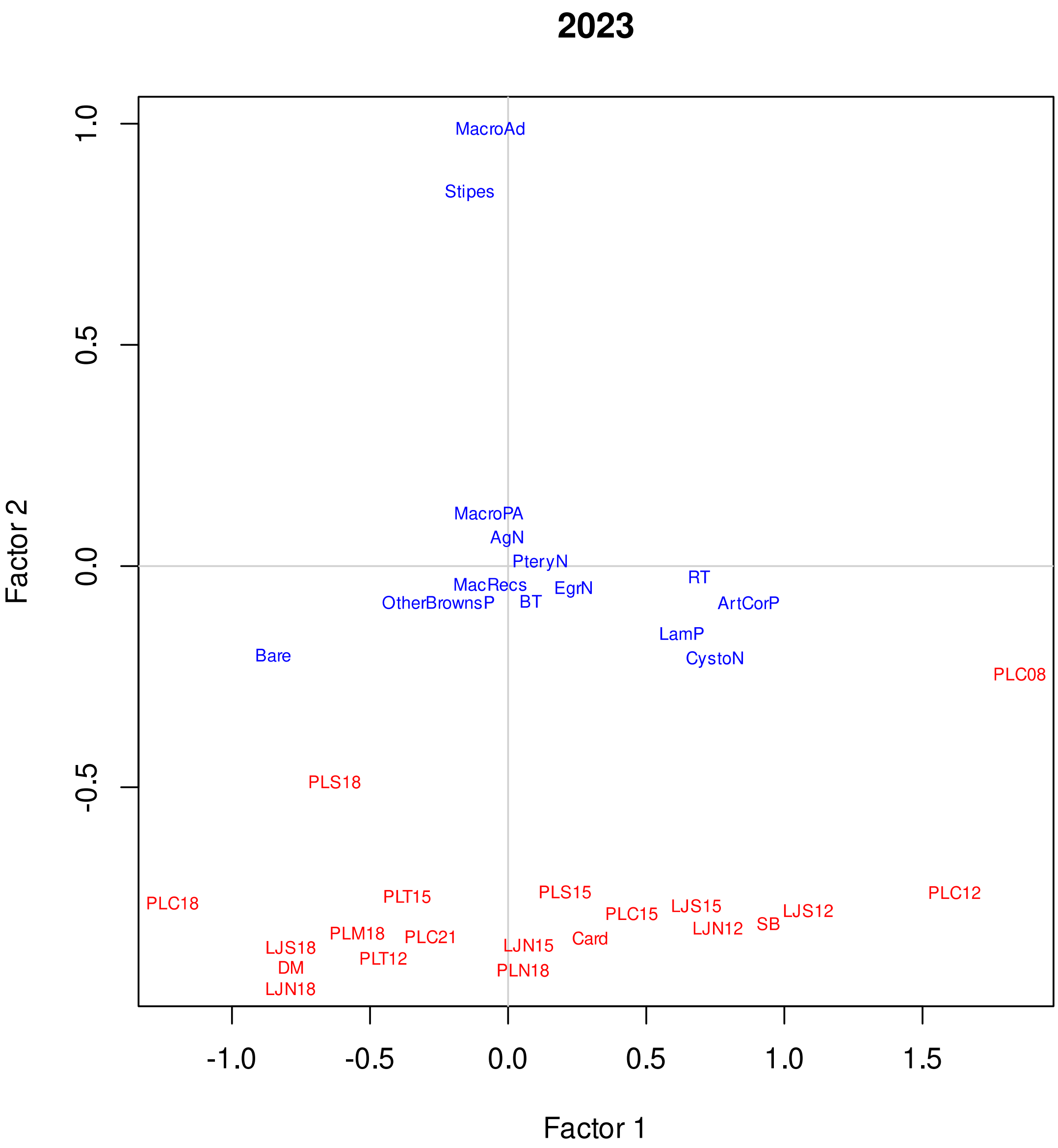

Figure 28. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2023. See Figure 24 for description of plot.*

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 coastal 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 observed along the permanent band transects at several sites. Table 6 lists first sightings within the actual band transects, and the relative frequencies among the study sites pooled over time are shown in Figure 29. The greatest percent cover observed thus far has been at PLC08 (Fig. 30) 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 still has 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 and disappearing from several others.

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 and in low densities to be significantly affecting giant kelp.

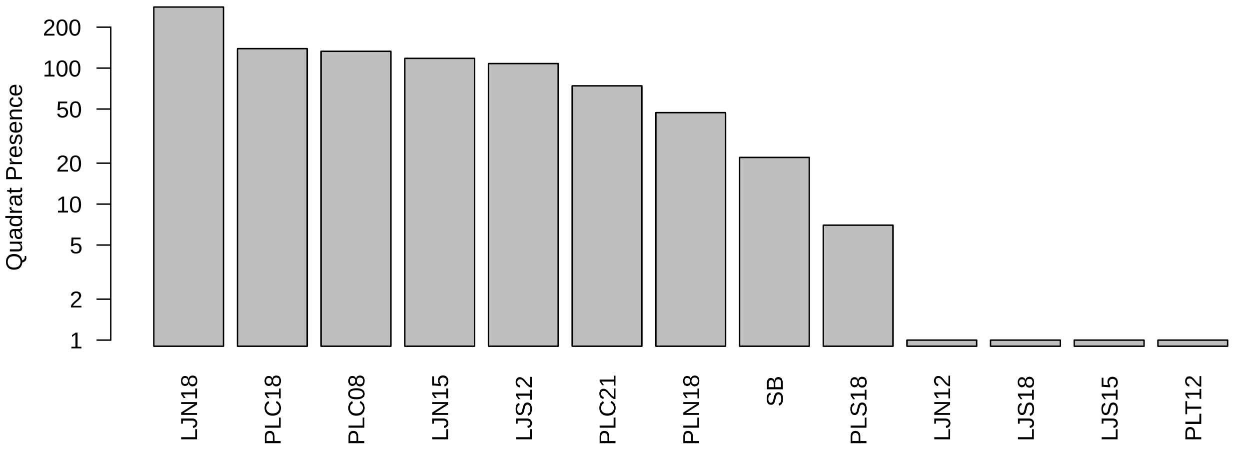

Figure 29. *Presence of the invasive alga, Sargassum horneri, among the study sites where it has been observed within the permanent band transects. Quadrant presence indicates the total number of 5x2 m quadrats along the transects where it has been observed over time since first sighting at each individual site.*

Study Site	Date 1st 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 6. *List of study sites where the invasive alga, Sargassum horneri, has been observed within the band transects and the dates it was first observed.*

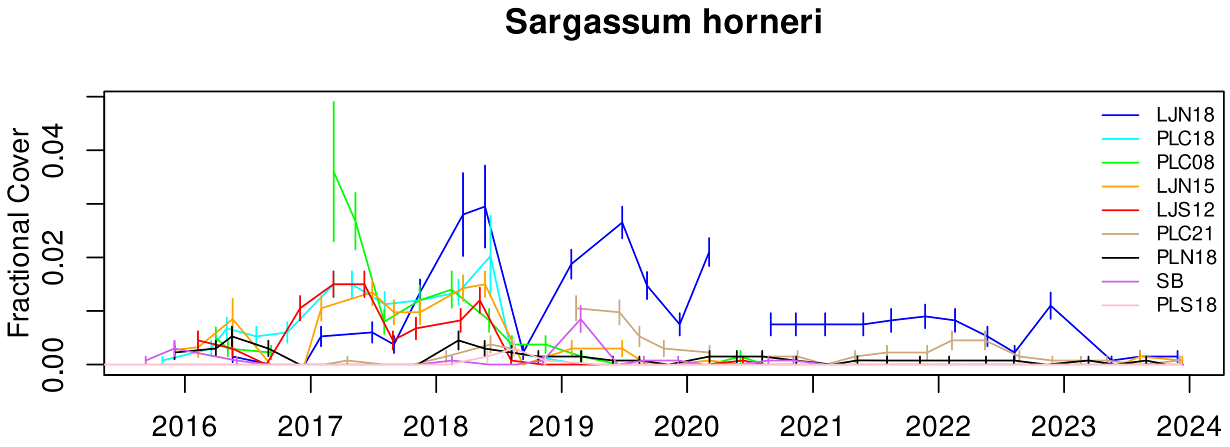

Figure 30. *Fractional cover of the invasive alga Sargassum horneri over time beginning when it was first observed in the kelp forests off San Diego (see Table 5). Some study sites where S. horneri has been observed were omitted because cover values approximate zero.*

Invertebrates

Many invertebrate species were negatively impacted by the 2014-2016 MHW. Sea urchins (Echinoids) and seastars (Asteroids) 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 asteroids ('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. Time series of sea urchin densities for a subset of the study sites that represent the general population trajectories for these species and where sea urchins have been most numerous historically are shown in Figures 31 and 32 . Presently, there are few sea urchins of either species at any of the study sites, especially 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. The only exception to this is a the recent modest increase in red sea urchin density at PLN18 in northern Pt. Loma. 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 populations continue to remain 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. 33-35), 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 which has persisted to the present. The larges post-MHW pulse of recruitment for both species occurred in 2018 and winter of 2019. This cohort of red and purple sea urchins did not appear to have led to increased adult densities, indicating that their post recruitment survival was been relatively low or they remain cryptic. Probably both factors contribute to this pattern. More recently, during this reporting period, there has continued to be recruitment of both species at several sites. Red sea urchin recruitment was greatest at PLC21, PLC18, and PLM18. Note, these are the outer areas of the kelp forest which is known to be the major sites of larval arrival to the kelp forest. High recruitment at the shallower sites is mainly due to the fact that very few sea urchins were observed at those sites and most or all were juveniles. Therefore, both red and purple sea urchins were observed to recruit during this study period but at lower levels than the 2018/19 recruitment events and it is highly unlikely that sea urchin overgrazing will occur in the near future in most areas of the LJKF and PLKF.

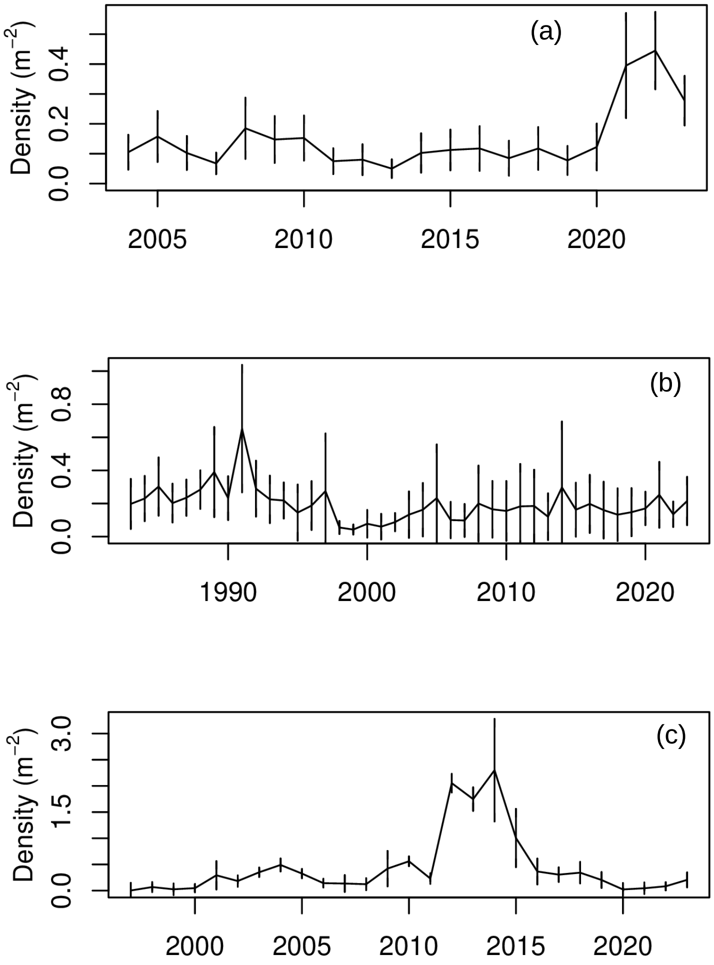

Figure 31. *Time series of the red sea urchin (Mesocentrotus franciscanus) mean densities at the (a) LJN18, (b) PLC18, and (c) PLM18 study sites. Error bars are standard errors.*

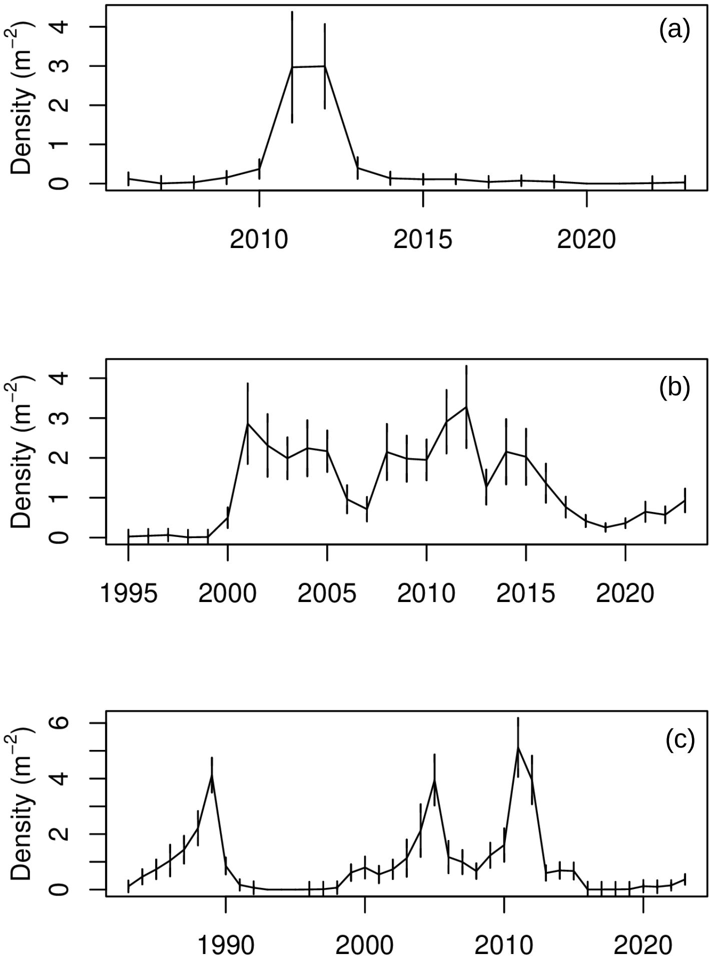

Figure 32. *Time series of purple sea urchin (Strongylocentrotus purpuratus) mean densities at the (a) Cardiff, (b) PLC21, and (c) PLS18 study sites. Error bars are standard errors.*

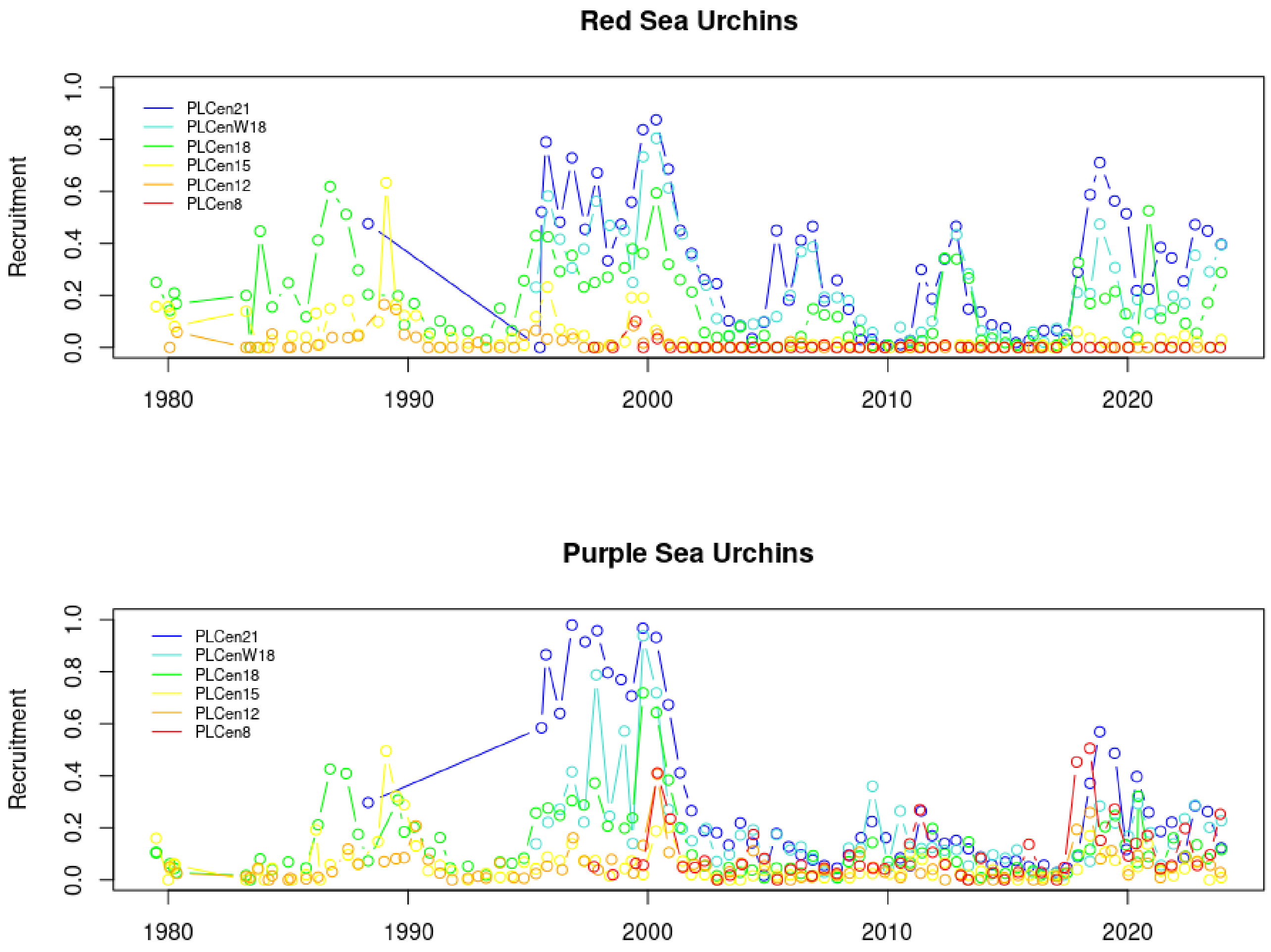

Figure 33. *Time series of red (top) and purple (bottom) sea urchin recruitment (fraction of the population considered in the first year class by size - see Methods) at the central Pt. Loma study sites.*

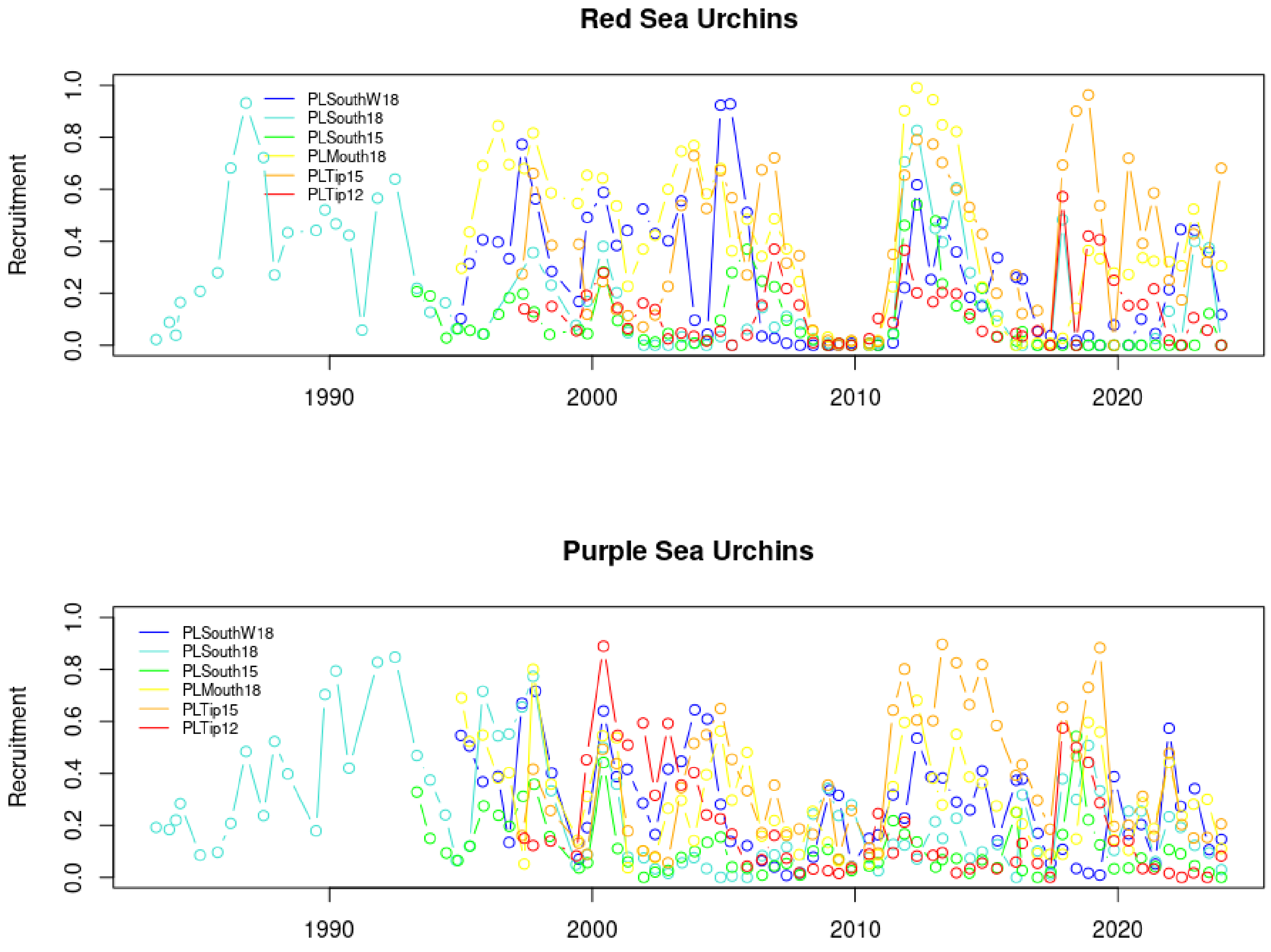

***Figure 34**. Time series of red (top) and purple (bottom) sea urchin recruitment at the southern Pt. Loma study sites.*

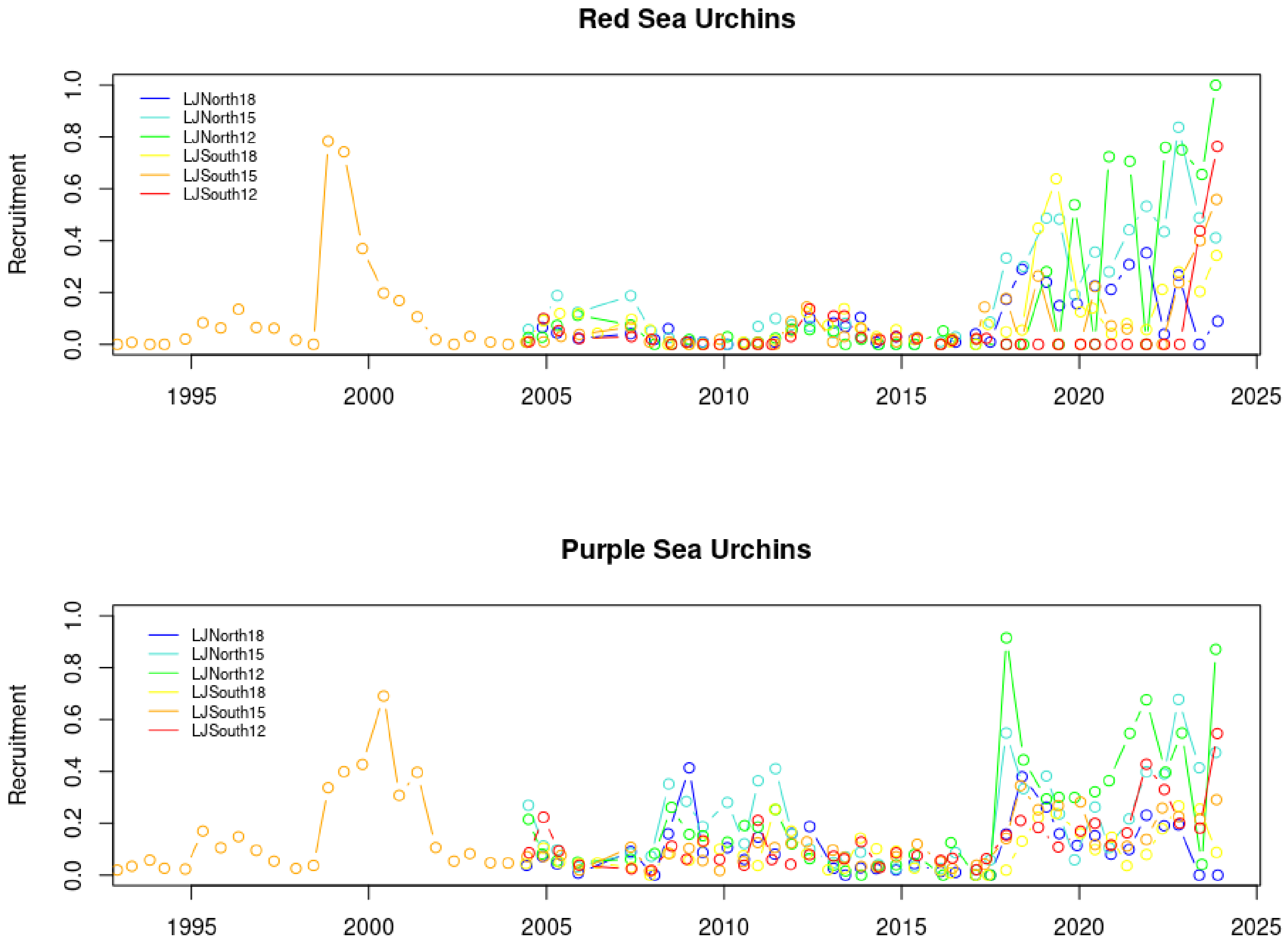

***Figure 35**. Time series of red (top) and purple (bottom) sea urchin recruitment at the La Jolla study sites.*

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. 36) 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, all species of *Pisaster* are still very uncommon or absent at all of the study sites through the end of 2023. *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 (Moitoza et al., 1979). This species has not been observed anywhere off

San Diego County since 2014 even in areas where they were commonly observed. *P. helianthodes* was in decline even prior to the BLOB event and was listed as a threatened species by IUCN (Gravem et al., 2021.

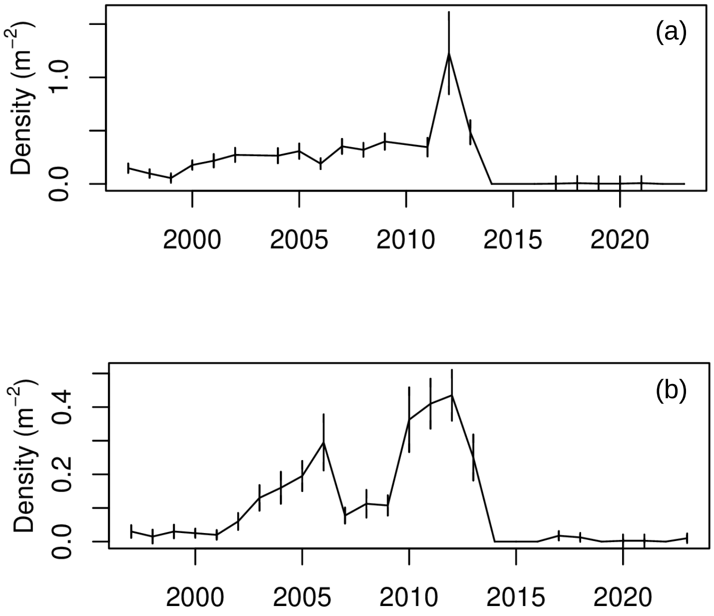

Figure 36. *Time series of the seastar Pisaster giganteus mean density at the (a) PLT12 and (b) PLM18 study sites. Error bars are standard errors.*

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 (Dayton et al., 1992; 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 ephemeral increases in kelp canopy cover since the MHW. However, densities of pink abalone (*H. corrugata*) have increased steadily at PLC08 beginning in the early 2000's (Fig. 37). *H. corrugata* has since increased in density even throughout the warm period reaching peak densities approaching 0.1 m^{-2} but have since decreased by ~60% indicating this population is in general decline despite the favorable ocean climate conditions since 2020. For comparison, densities of pink abalone in the early 70's at similar depths off Catalina were >1 m^{-2} (Tutschulte, 1976).

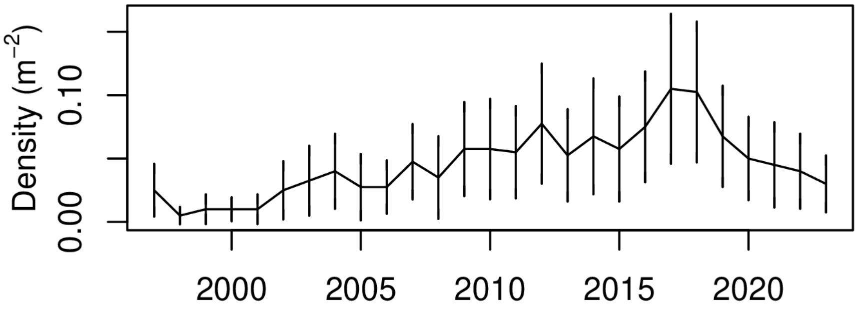

Figure 37. *Time series of pink abalone (Haliotis corrugata) mean densities at the PLC08 study site. Error bars are standard errors.*

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 the sources will be from dredging sediments at deeper depths offshore. Such finer-grained sediments are more susceptible to erosion from beaches than natural sediments. Therefore, potential sediment burial risks to North County kelp forests may be more pronounced than the replenishment of 2012 based on grain sources and proposed 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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