Evaluation of Anthropogenic Impacts on the San Diego Coastal Kelp Forest Ecosystem (2014 to 2019): Final Report

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EXECUTIVE SUMMARY

The kelp forests off La Jolla and Point Loma are the largest contiguous kelp forests off the western coast of the U.S. They host complex marine communities supported by their eponymous species, giant kelp (*Macrocystis pyrifera*), which provides structure and food for hundreds of species of fish and invertebrates. Kelp forests off southern California are subjected to both natural and human-induced disturbance. 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 serve to stress giant kelp and accompanying species of algae. The opposite conditions occur during negative ENSO events (La Niñas) enhancing both the growth and reproduction of kelp species. 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 1970's, and are currently being monitored at twenty permanent study sites located among the Pt. Loma, La Jolla, and North County kelp forests.

During the current study (2014-2019), the kelp forests off California were subjected to severe temperature and nutrient stress beginning in late 2013 which persisted until the spring of 2017. This lengthened period of stress was due the combination of two consecutive ocean climate events. An anomalous surface 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 large scale wind patterns in the NE Pacific. This causative forcing is therefore 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 dissipated. Together these consecutive warm periods resulted in the longest and warmest period ever observed in the 103 year old sea surface temperature time series 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 and 2018 brought cool, nutrient-laden waters up onto the inner continental shelf of southern California creating favorable conditions for giant kelp regrowth. However, it is important to note that the variability of El Niño climate cycles is superimposed onto a larger scale trend of increasing ocean temperatures within the California Current System and the world’s oceans generally, and it is likely that conditions that are supportive of giant kelp growth and reproduction will decrease in frequency and duration over the next century. This will likely result in an increased susceptibility to anthropogenic stress and an overall decreased resilience to disturbances as the century progresses. Presently, there is no evidence of human stress on the marine algae of San Diego County due to wastewater discharge from the Pt. Loma Ocean Outfall.

The recent consecutive warm events and associated decreased nutrient conditions decimated *M. pyrifera* and cohabiting algal species off San Diego. Pooled across 20 kelp forest sites off San Diego, densities of adult *M. pyrifera* were reduced >90%. Unlike previous warm events attributed to El Niño, the BLOB 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 because 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 were 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 another bout of kelp recruitment and recovery occurred over more areas off San Diego County. However, an anomalously warm surface layer, limited to the upper 3-5 meters of the ocean's surface, occurred during the summer of 2018. Sea surface temperature records in the SIO Pier time series were exceeded by at least 2°C when temperatures reached >27°. By contrast, typical summer surface temperatures are ~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. The kelp forests off North County were largely lost during this surface warm period.

Presently, giant kelp densities are ~40% of their all-time historic highs when averaged across all of the study sites. Giant kelp densities are currently the greatest in the northern and central portions of the Pt. Loma kelp forest, and the southern portions of the La Jolla kelp forest. Giant kelp densities are near zero in all of North County kelp forests, including areas off Del Mar, Solana Beach, and Cardiff. Giant kelp that recruited in the spring of 2017 off Solana Beach and Cardiff died during the summer 2018 surface warm pool event and there has been little recovery since due to competition with understory kelp and algal turf species that interfere with giant kelp recruitment.

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. This resulted in the disappearance or near-disappearance of these species from our study sites and from the kelp forests generally. Further, little to no recruitment of sea urchins was observed until the fall of 2017. Sea urchins are primary herbivores of giant kelp and can overgraze giant kelp and associated algal species given the right conditions. They are capable of precluding kelp recovery and overgrazed areas known as barrens that can persist in some areas for decades. The kelp recovery that began in 2017 and continued into 2018 is not being affected by sea urchins because of their low adult densities due to the die-off. However, rates sea urchin recruitment that began in 2017 mean that overgrazing could occur as this cohort emerges from nursery habitats and matures into adulthood. This cohort could lead to overgrazing in some areas of the kelp forests as early as 2020 especially in south Pt. Loma where a unique combination of topography and turbidity emanating from San Diego Bay contribute to resilient sea urchin 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 near zero and it is difficult to predict whether the initial bouts of post-disease recruitment will be adequate to recover their populations 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 associated with warm periods. Abalone off San Diego County suffered further mortality during and after the warm event of 2014-2016 due to lack of food and disease. 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 that began around 2010.

The La Niña conditions that occurred during 2017 and 2018 and resulted in kelp recovery off San Diego County have since shifted to El Niño conditions. However, the present spring upwelling of 2019 has not yet been affected, and bottom temperatures have remained conducive for kelp recruitment and growth. The present El Niño is predicted to last through summer and then shift to ENSO neutral conditions by the fall of 2019. It is not clear at this time whether unusually warm waters will again affect the kelp forests off San Diego during the summer and fall. Conditions for giant kelp recovery may therefore become less favorable during the summer of 2019. Summer is typically an important period for giant kelp growth and reproduction, and warm temperatures could potentially slow or even reverse the rate of giant kelp forest recovery off San Diego. Another source of stress is the accelerating colonization of an invasive algal species, *Sargassum horneri*, first observed in the kelp forests off San Diego in 2014. This species has now become established at 9 study sites and has been observed at 4 others. *S. horneri* can outcompete *M. pyrifera* for space and may further slow the recovery of kelp forests off San Diego, perhaps eventually precluding recovery in some areas altogether. The deeper areas off Northern La Jolla appear most at risk.

INTRODUCTION

Kelp forests are one of 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 food and shelter for a host of fishes and invertebrates as well as cohabiting species of algae. These forests occupy the inner margins of the continental shelf and offshore islands extending from the offshore edge of tidepools to depths as great as thirty meters off 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 the most important fishing grounds for the commercial red sea urchin (*Mesocentrotus franciscanus*) and spiny lobster (*Panulirus interruptus*) fisheries off California.

Kelp forests are susceptible to human disturbance because of their proximity to urbanized coasts exposing them to polluted stormwater runoff and wastewater discharge. 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). The Point Loma Ocean Outfall (PLOO) was extended and deepened in 1993, presently discharging treated wastewater ~7.3 km offshore in marine waters ~98 m deep. The current location of the PLOO is ~5 km offshore of the Point Loma kelp forest. 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 hard bottom kelp supporting habitat as eroded sediments redistribute offshore.

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 less adequate most of the time (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).

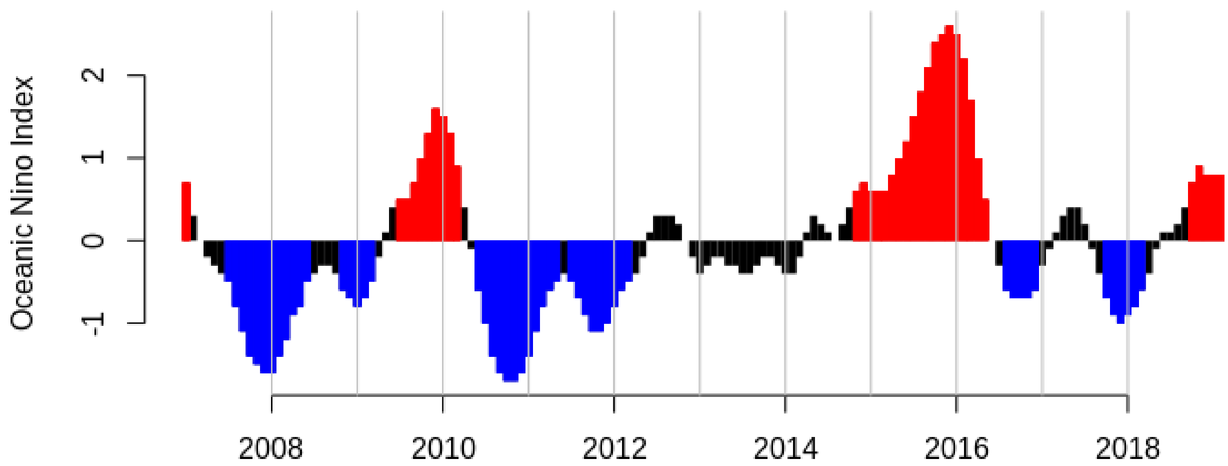

Figure 1. *Barplot of the Oceanic Niño Index (ONI) since 2007. Red bars indicate El Niño conditions, blue bars indicate La Niña conditions, and black bars indicate ENSO neutral conditions (data from NOAA, 2019). The ONI index is based on equatorial sea surface temperatures in the Eastern Pacific.*

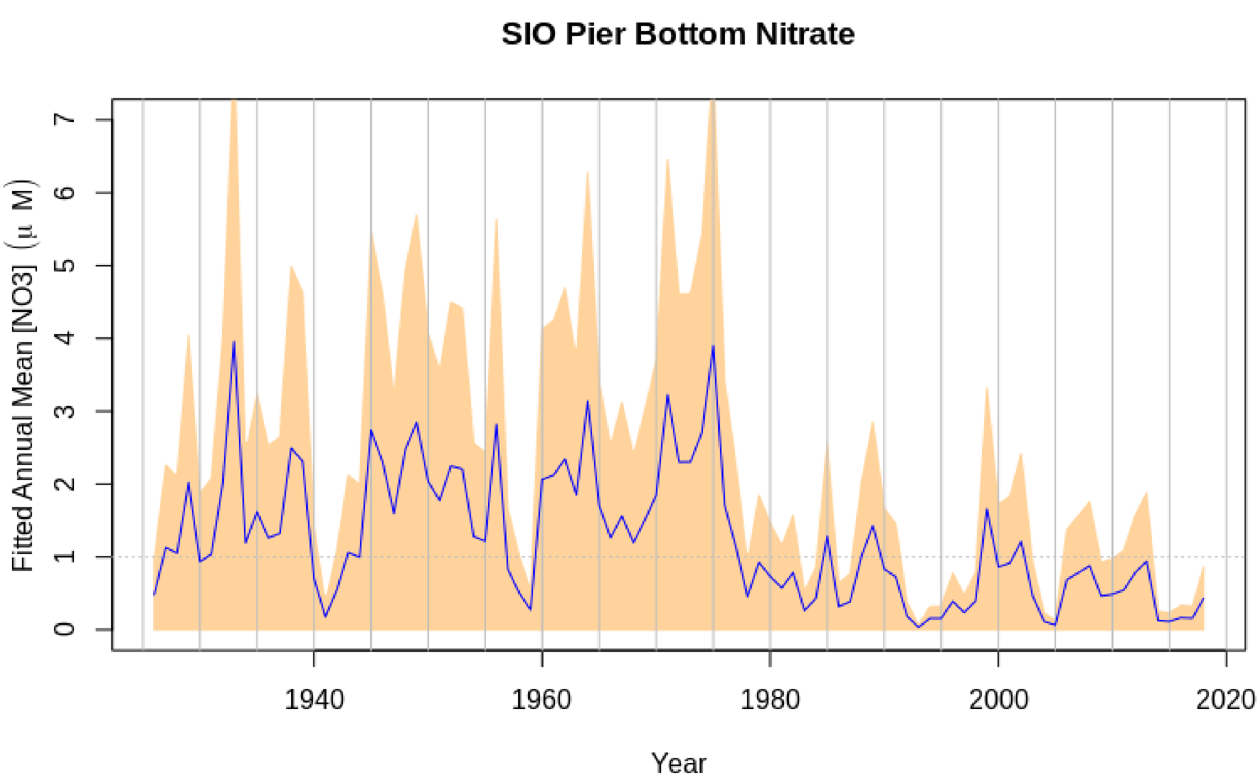

Figure 2. *Time series of annual mean nitrate concentrations estimated from daily temperature and*

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 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). Forests 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 are known as barrens. Barrens and forested modes can be semi-permanent or resilient in some areas such as in the southern portion of the Pt. Loma kelp forest (Parnell, 2015), or the two modes can alternate 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).

Another source of natural disturbance is the increasing establishment 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). *Sargassum horneri* is now establishing itself in many areas of San Diego County including the kelp forests and bays.

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 several 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 assessments 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) sea 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.

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 (≥4 stipes), pre-adults (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). The number of stipes is 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. 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 of each species located near all of the study sites except for the NCKF sites which do not have adequate densities of sea urchins. Sedimentation is monitored along the NCKF sites by measuring the height of permanently established spikes at replicate locations within each of those forests. Bottom temperature is recorded at 10 min intervals using ONSET Tidbit recorders (accuracy and precision = 0.2˚C and 0.3˚C (respectively). All field work was conducted using SCUBA.

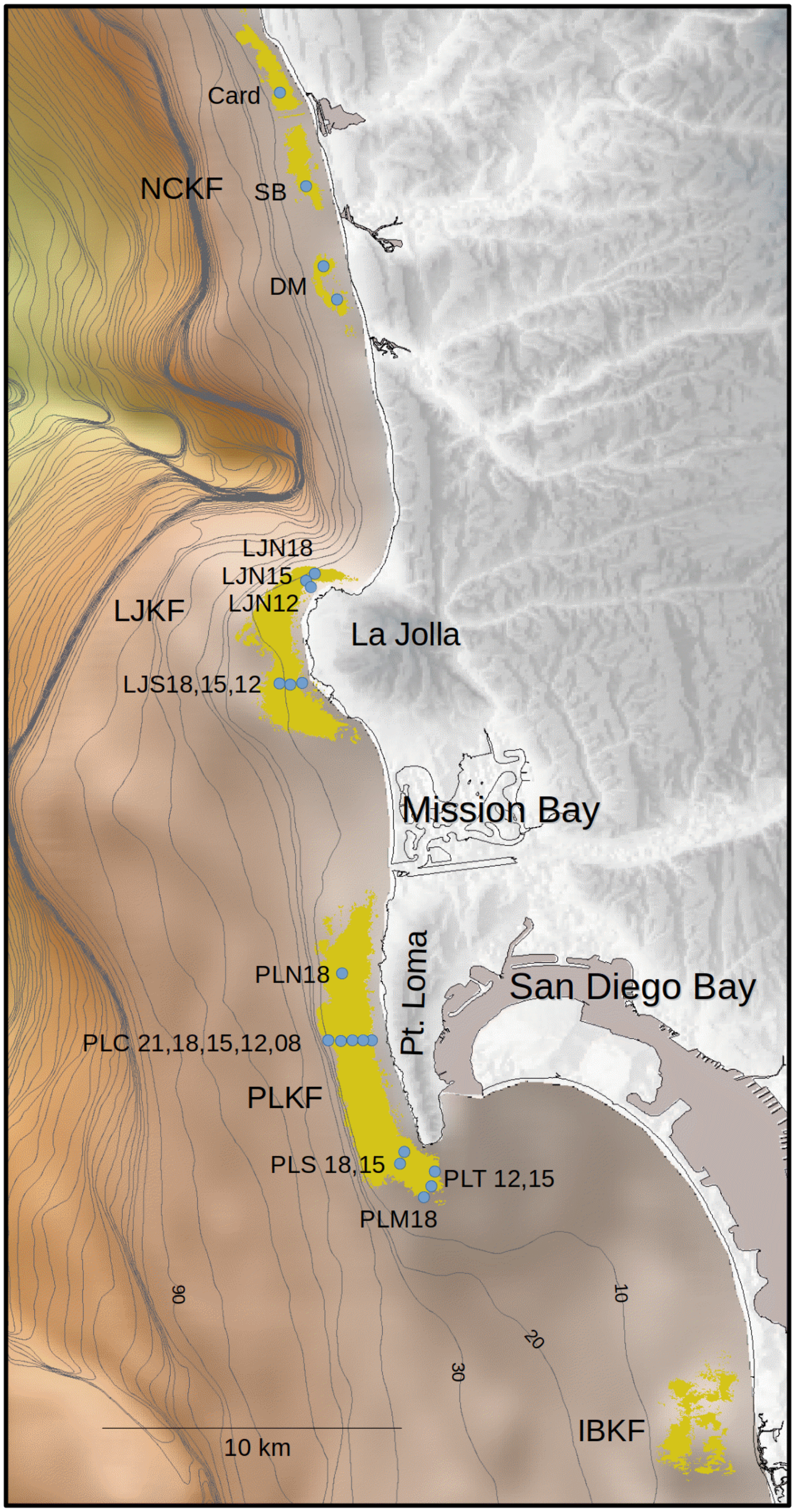

Figure 3. *Map of the San Diego inner shelf showing locations of the Point Loma, La Jolla, North County, and Imperial Beach kelp forests (indicated by PLKF, LJKF, NCKF, and IBKF, respectively). Permanent study site locations are indicated by blue circles and corresponding study site names. Depth contour 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* was determined by the method of DeWreede (1984). A 6mm diameter hole is punched in the midrib of the terminal blade ~30mm 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 100mm from the base of each blade, which 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.

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 placed back where they were collected.

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 dimension that can then be plotted to determine community composition differences 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.

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.*

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 2. *Qualitative reproductive scores used for grading algal reproductive states.*

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 zoospores

RESULTS AND DISCUSSION

Bottom Temperature

The ENSO index (ONI – Oceanic Niño Index) 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 each El Niño/La Niña event penetrates higher latitudes differently. Therefore, while correlated, the magnitudes of ENSO events at the equator and temperatures along the SCB can be somewhat uncoupled.

The bottom temperature record at the central Pt. Loma study sites extends back to 1983 just as 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 2014-2015 that occurred during the present study and was associated with a large scale anomalous NE Pacific warm event (DiLorenzo and Mantua, 2016) termed the BLOB. This was immediately followed by a strong El Niño in 2015/2016 (Figs. 1 and 4). The ONI (Fig. 1) and the Pt. Loma bottom temperature time series (Fig. 4) are strongly concordant for the largest ocean climate events over the present study period (2014-2019), including the onset of the coupled BLOB/El Niño warm event beginning in late 2014 which began to ebb by the spring of 2016. The ONI and bottom temperatures off Pt. Loma indicate rapid cooling at that time with the onset of La Niña conditions which were then followed by another warming event beginning late 2017. An anomalous temperature event occurred during the summer of 2018 in 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 and included the warmest temperatures ever observed in the 103-year 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 waters at the study sites where recovery from the BLOB/El Niño warm event had occurred, because bottom temperatures remained relatively cool during the summer of 2018.

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 the understory and canopy kelps. Strong El Niños such as the 1997/98 El Niño and the 2014-2016 BLOB/El Niño penetrate 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 increasing understory domination at the expense of giant kelp canopy cover.

Currently, bottom temperatures have been cool since the spring of 2018 (<15°C) leading to recruitment and growth at many of the study sites. Warming occurred during the fall and winter of 2018/2019 but temperatures have cooled since, with bottom temperatures at study sites deeper than 12 m typically <13°C much of the time. A mild El Niño is presently occurring along the equator (Fig. 1), and is likely to continue through summer and is predicted to be followed by ENSO neutral conditions (NOAA, 2019). Presently, it is not clear what, if any, impact the current mild El Niño will have on kelps in the SCB, but growth conditions continue to be conducive for kelp growth due to normal spring upwelling conditions.

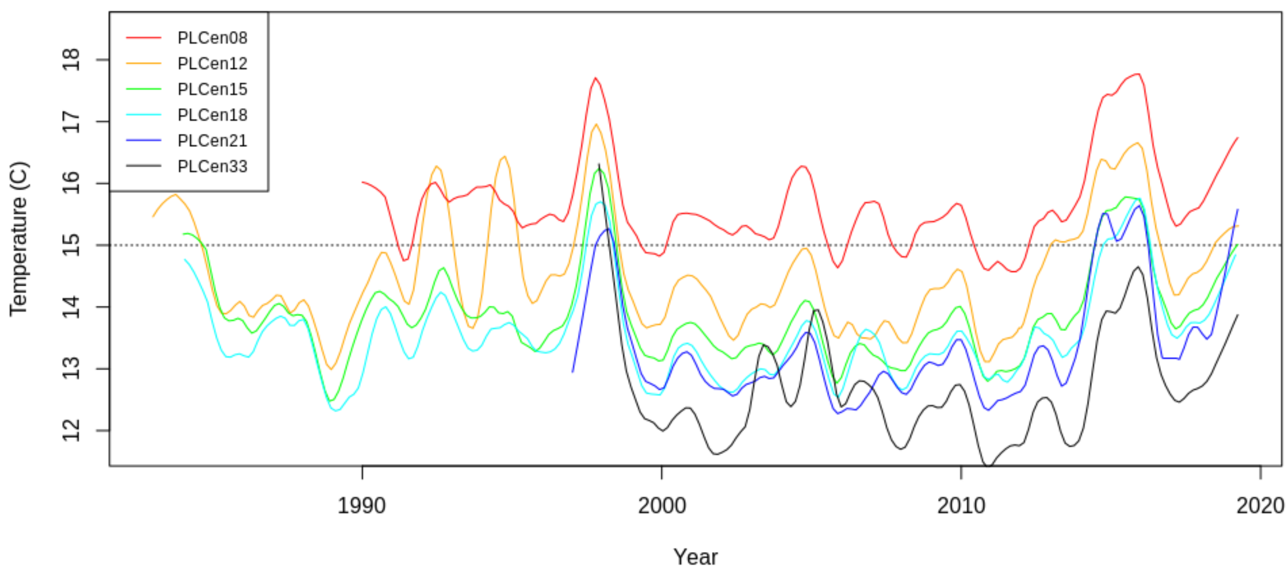

Figure 4. Ocean bottom temperature trends along the central Pt. Loma study sites. Horizontal gray line indicates the temperature above which nitrate concentrations are typically limiting for giant kelp growth.

Giant Kelp Status and Reproduction

The primary abundance pattern for *M. pyrifera* since the 1980's includes rapid declines associated with El Niños followed by step increases in plant and stipe density due to mainly discrete pulses of recruitment leading to varying levels of recovery or failed recovery if a cohort fails to reach adulthood. Recruitment, maturation, and establishment of adult giant kelp plants are highly variable spatially even within a single kelp forest. Densities of all life stages and stipes are shown in Figs. 5-9. Densities for these life stages at all of the 18 m deep sites off La Jolla and Pt. Loma, with the exception of bifurcates, are plotted in Fig. 10 for comparisons among these outer kelp forest sites where bottom temperatures are cool relative to shallower sites, and conditions are therefore more conducive for the recruitment and growth of early giant kelp life stages.

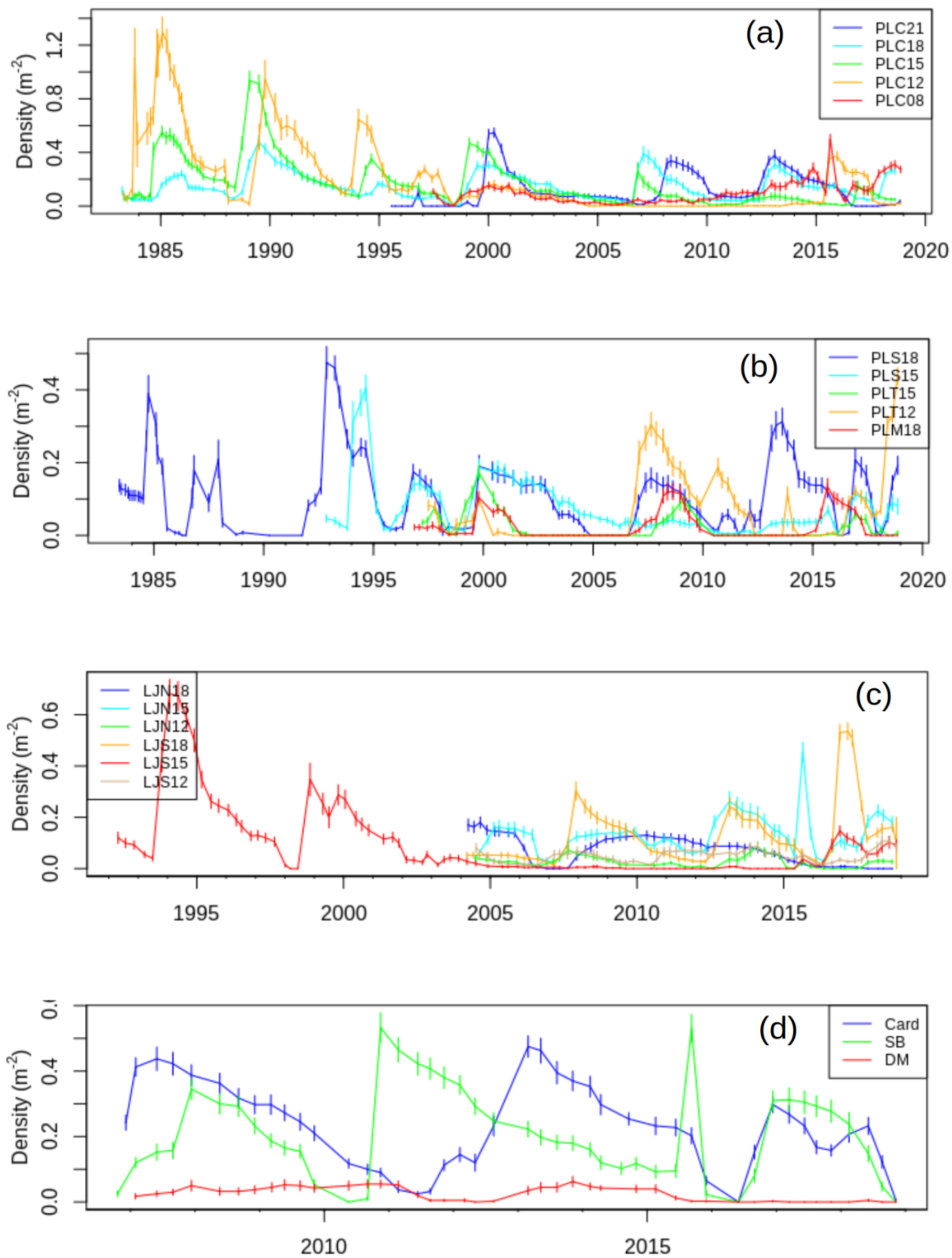

Figure 5. Mean densities of adult Macrocystis pyrifera among study site groups: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County. Error bars indicate standard errors.

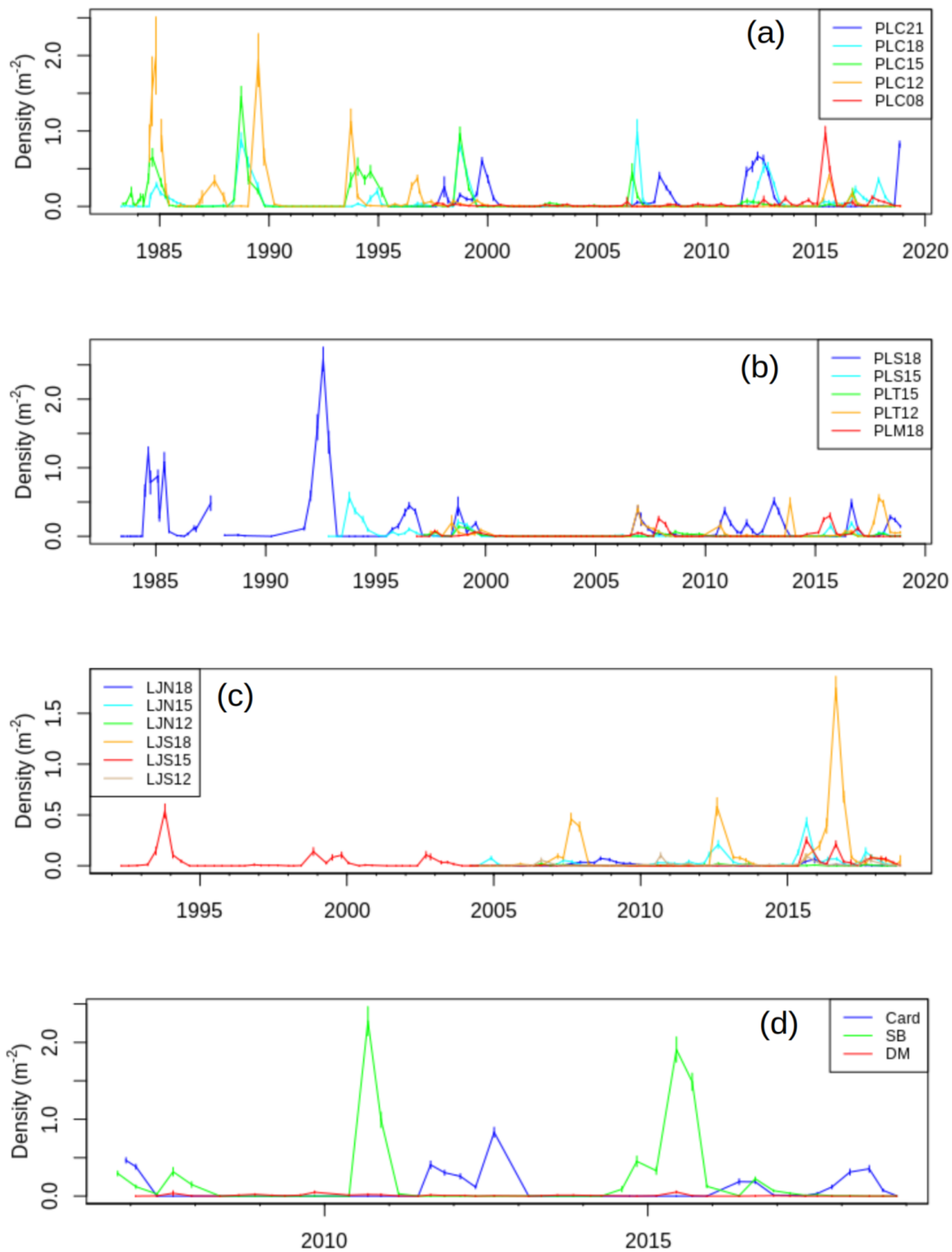

Figure 6. Mean densities of Macrocystis pyrifera pre-adults (≤4 stipes): (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

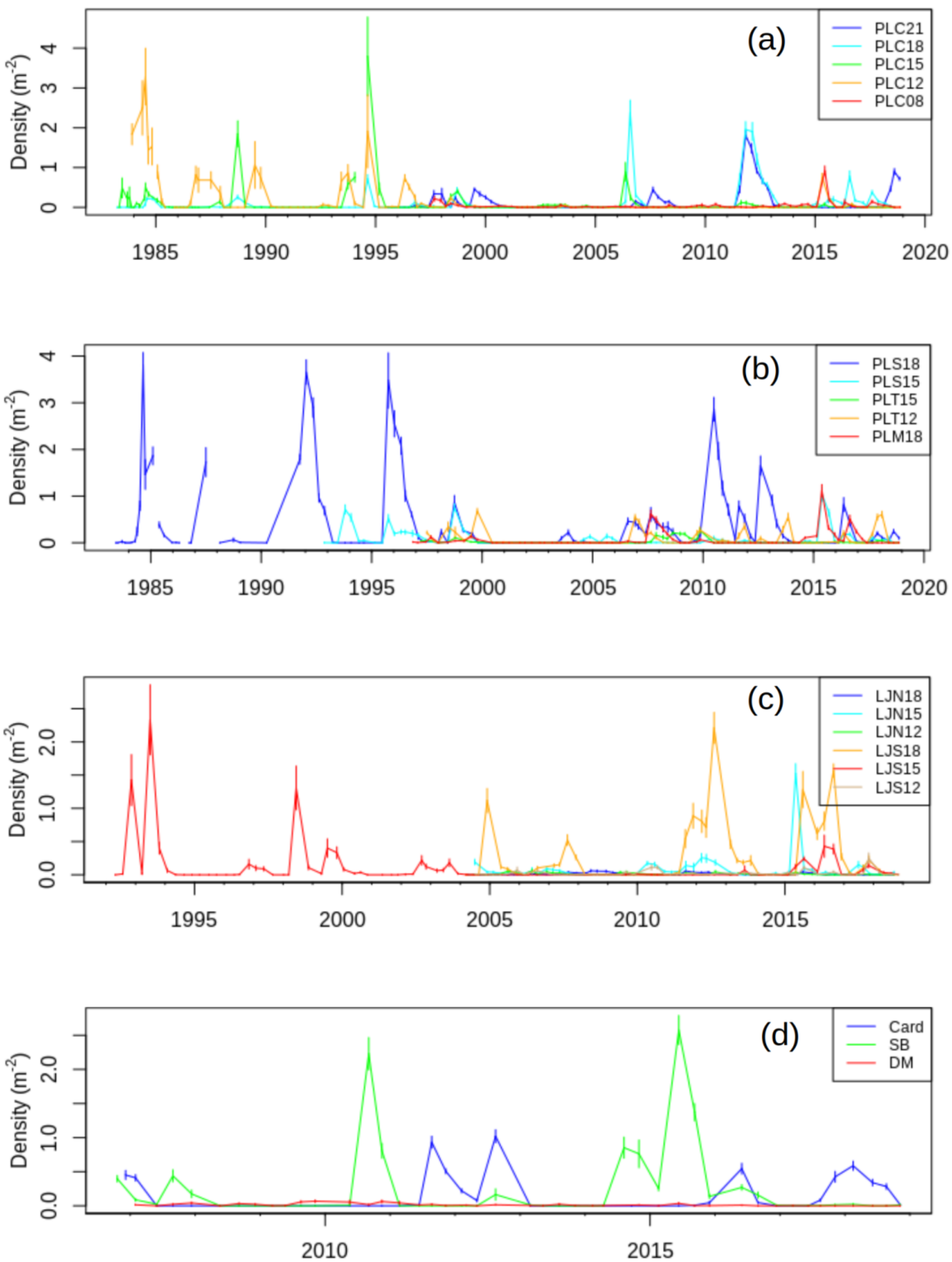

Figure 7. Mean densities of Macrocystis pyrifera bifurcates: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

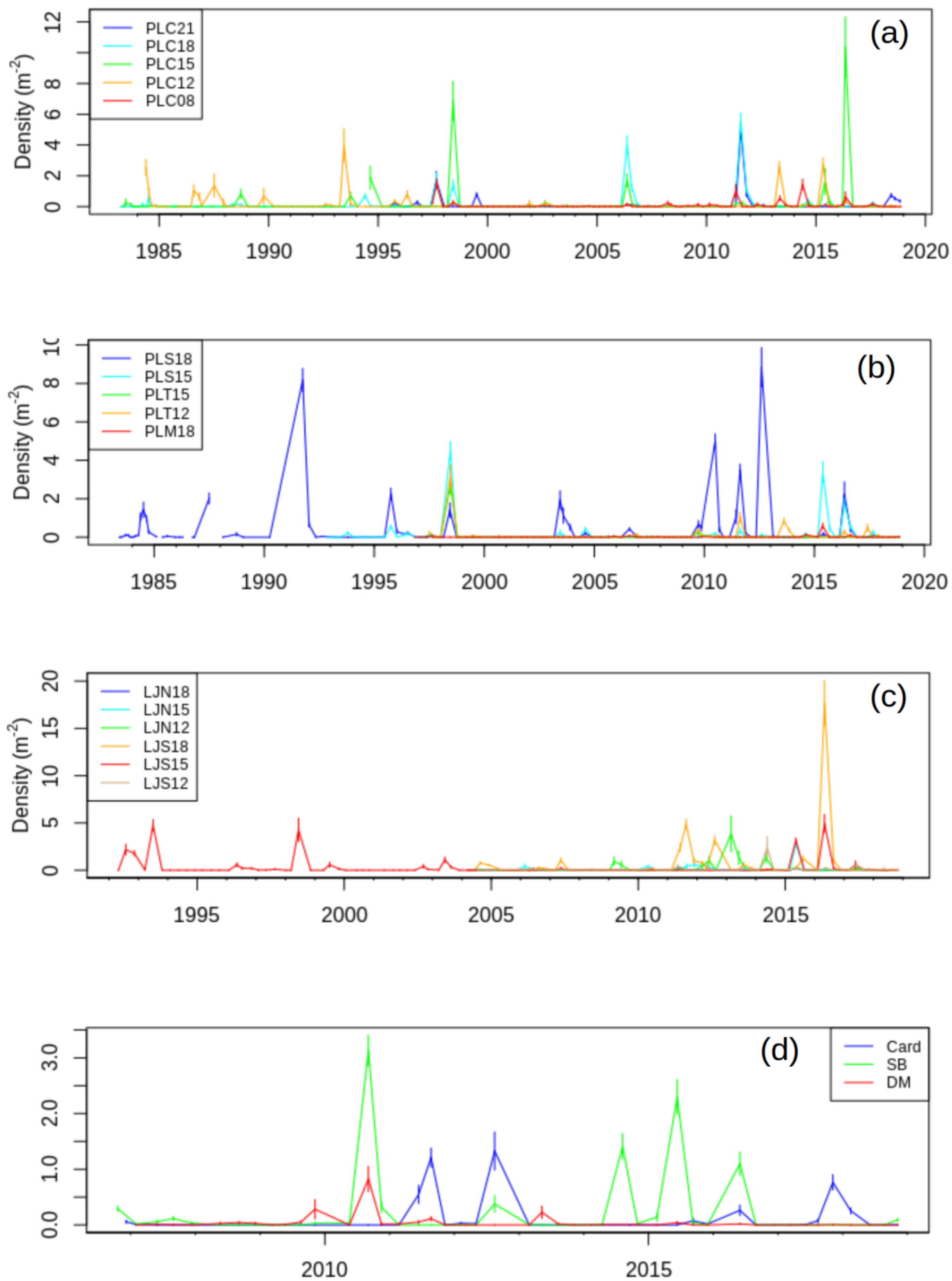

Figure 8. Mean densities of Macrocystis pyrifera pre-bifurcates: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

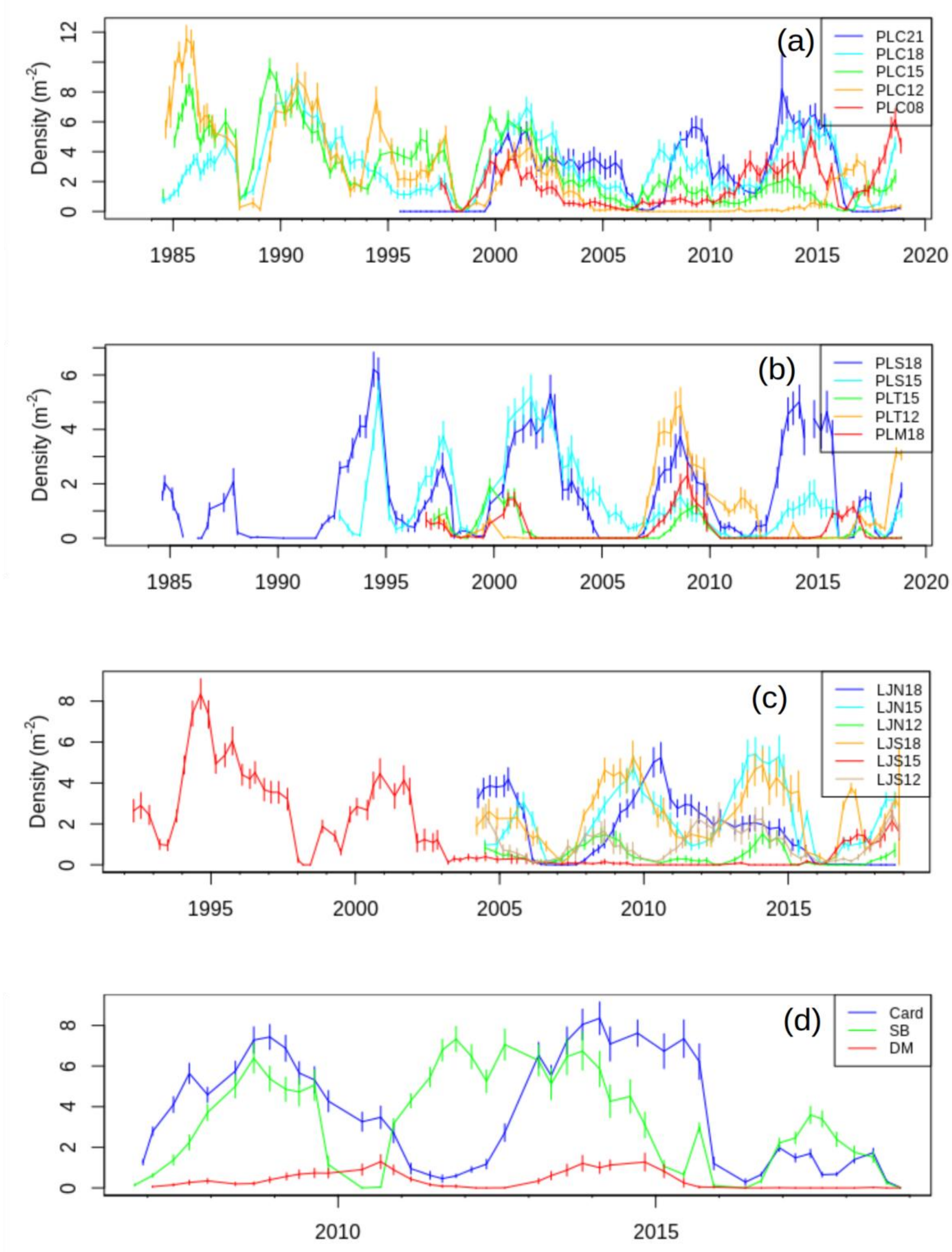

Figure 9. Mean densities of Macrocystis pyrifera stipes: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

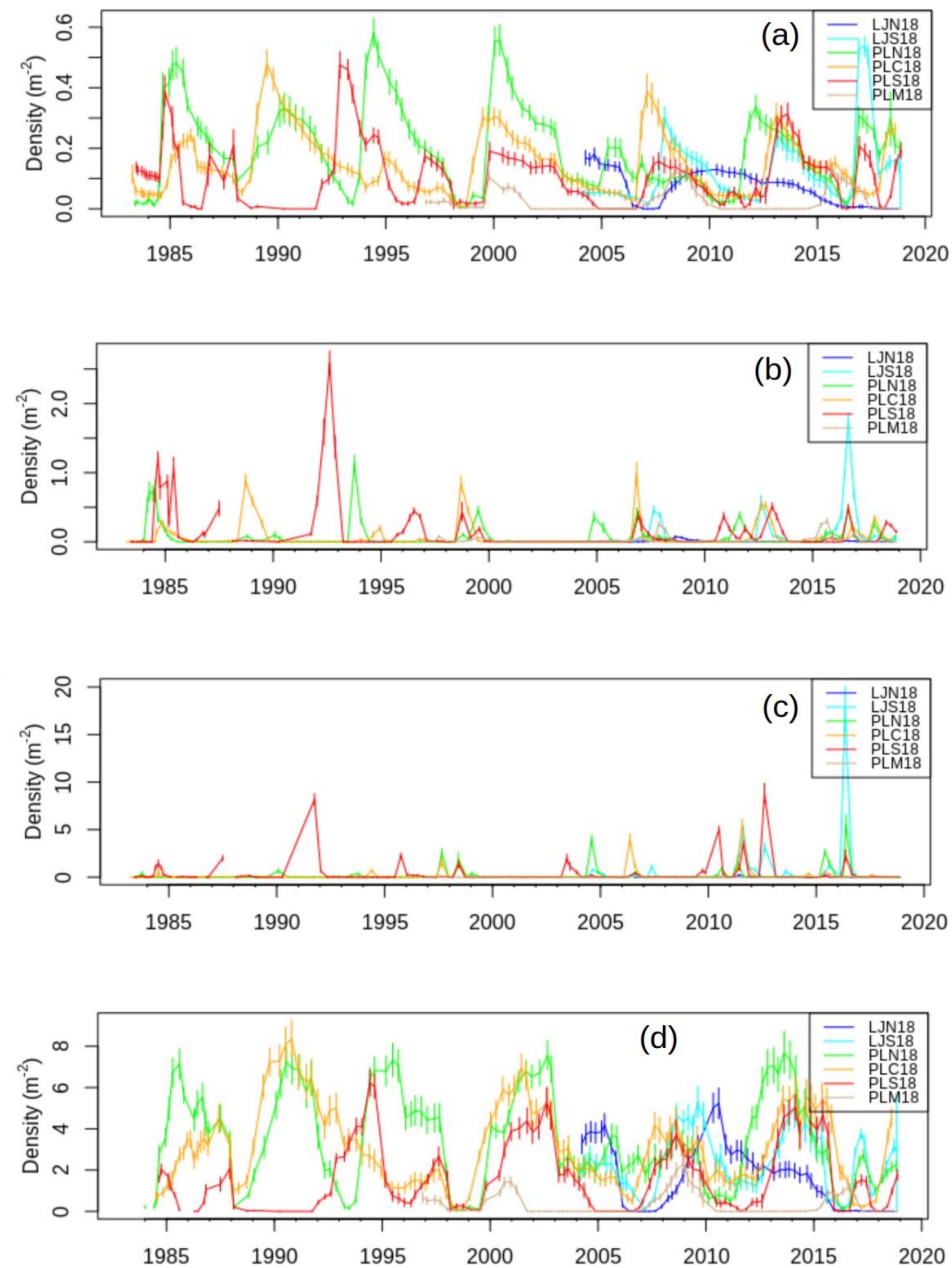

Figure 10. Mean densities of Macrocystis pyrifera (a) adults, (b) pre-adults, (c) pre-bifurcates, and (d) stipes along the 18 m sites off La Jolla and Pt. Loma. Error bars indicate standard errors.

The 2014-2016 warm period directly 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. 5) and stipes (Fig. 9) decreased dramatically at all study sites off San Diego. *M. pyrifera* has since recruited in some areas of the forests beginning as early as 2016 with subsequent recruitment cohorts observed in 2017 and 2018. Some of the 2016 cohorts at least partially matured into pre-adults and adults at a subset of the sites. At other sites recruitment failed such that there are presently very few or no adult plants remaining. Presently, sites with the greatest densities of giant kelp include: the northern La Jolla site at 15 m; the southern La Jolla sites at 15 and 12 m; the central Pt. Loma sites at 18 and 8 m; the southern Pt. Loma sites at PLT12, PLT15, and PLS18.

No adult giant kelp plants remain at the North County sites even though significant recruitment occurred off Cardiff in 2017. An earlier cohort that recruited in 2016 near the end of the El Niño off Solana Beach, has died off entirely. No giant kelp has been observed off Del Mar since early in the study period (2015).

Post warm-event recruitment was observed at the La Jolla study sites including LJN15, and all 3 of the southern La Jolla sites. Recruitment off southern La Jolla was by far the greatest at the 18 m site. Moderate densities of giant kelp are now present at the LJN15, LJS18, and LJS15 study sites.

Giant kelp recovery at the Pt. Loma study sites has been highly variable among study sites. Recruitment occurred during the 2015 warm event at PLC12 but that cohort died completely by late 2017. At other sites where giant kelp adults currently exhibit moderate densities (>$0.1 m^{-2}$), recruitment occurred beginning as early as 2016 and some sites experienced additional recruitment in 2017 and 2018. These sites include PLC21, PLC8, PLT12, PLS15, and PLS18. Recruitment occurred but did not successfully mature into adult stands at PLC18, PLC15, PLT15 and PLM18. An early colonizing post disturbance brown alga, *Desmerestia ligulata*, has dominated the PLT15 and PLM18 study sites interfering with giant kelp recovery at those sites. Limited recovery at the deeper sites during this period could also be partly due to decreased light levels reducing rates of kelp germination. However, light penetration data are not available.

The reproductive state of giant kelp along the central Pt. Loma study sites was greatly diminished by the end of the 2016 El Niño (Fig. 11). 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 and indicator of how stressful the warm water events of 2014-2016 were for the species, but also limited the rate at which giant kelp has been able to recover since then.

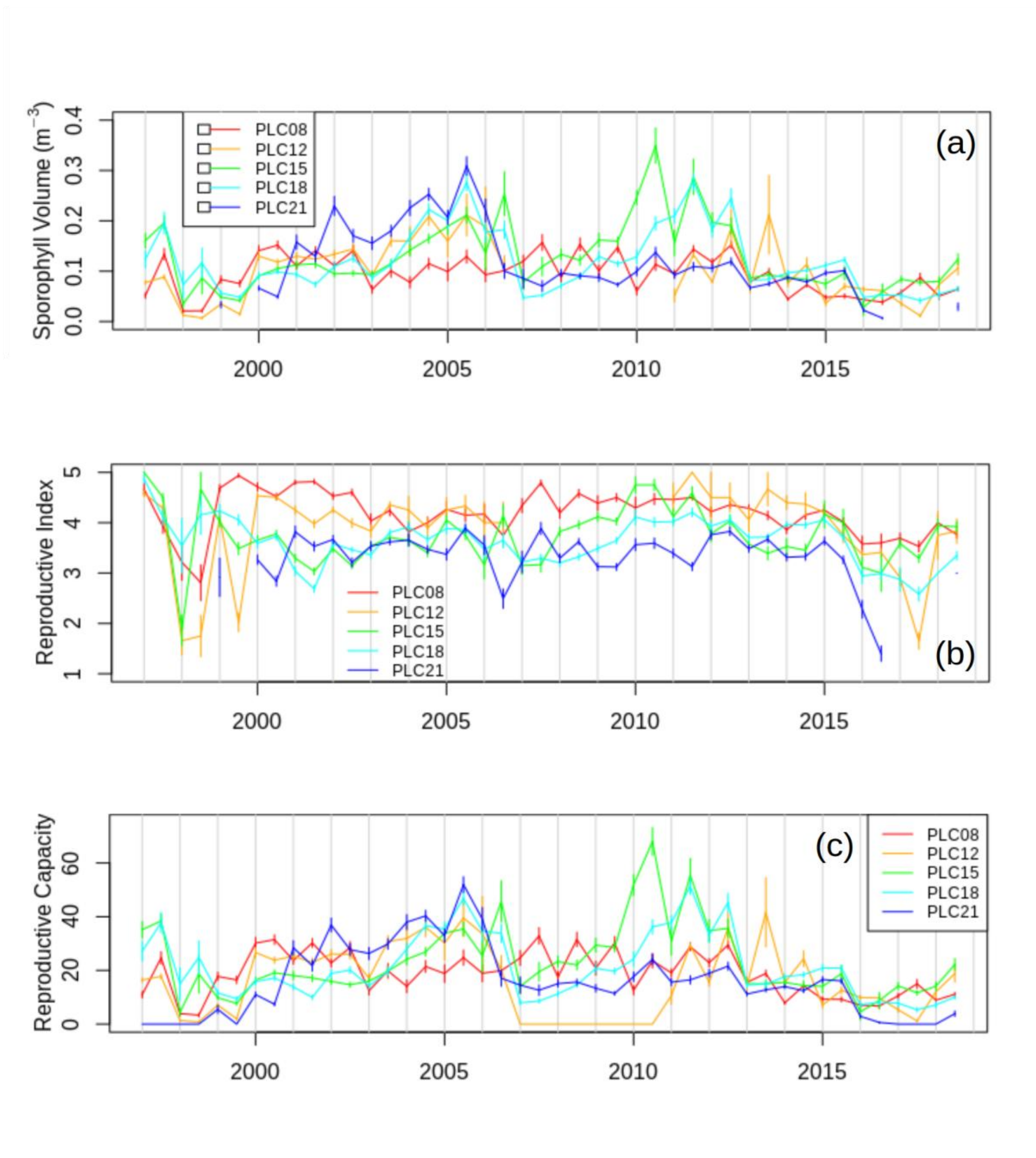

Figure 11. Reproductive states of Macrocystis pyrifera at the central Pt. Loma study sites: (a) sporophyll volume, (b) reproductive index (see Table 2), and (c) reproductive capacity (derived index of relative among-site reproductive potential - see Methods). Means are plotted and error bars indicate standard errors.

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. Warm and nutrient deplete 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 as giant kelp is stressed by low nutrient and high temperature conditions. By contrast the understory and turf canopy guilds are exposed to cooler and more nutrient replete waters. And as the surface canopy kelps begin to lose tissue and die off, 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 differentially affected by the consecutive warm periods. The main effects of the warm periods on *P. californica* were exemplified by two groups of sites (Fig. 12). The first group included sites where densities decreased dramatically with the BLOB and remained low during and after the 2016 El Niño (PLC21, PLC18, PLC12, PLC08, LJN15, LJN12, LJS12). Densities of *P. californica* at the second set of sites decreased during the BLOB then increased rapidly through 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 LJS18, LJS15, PLC15, and PLT12 study sites.

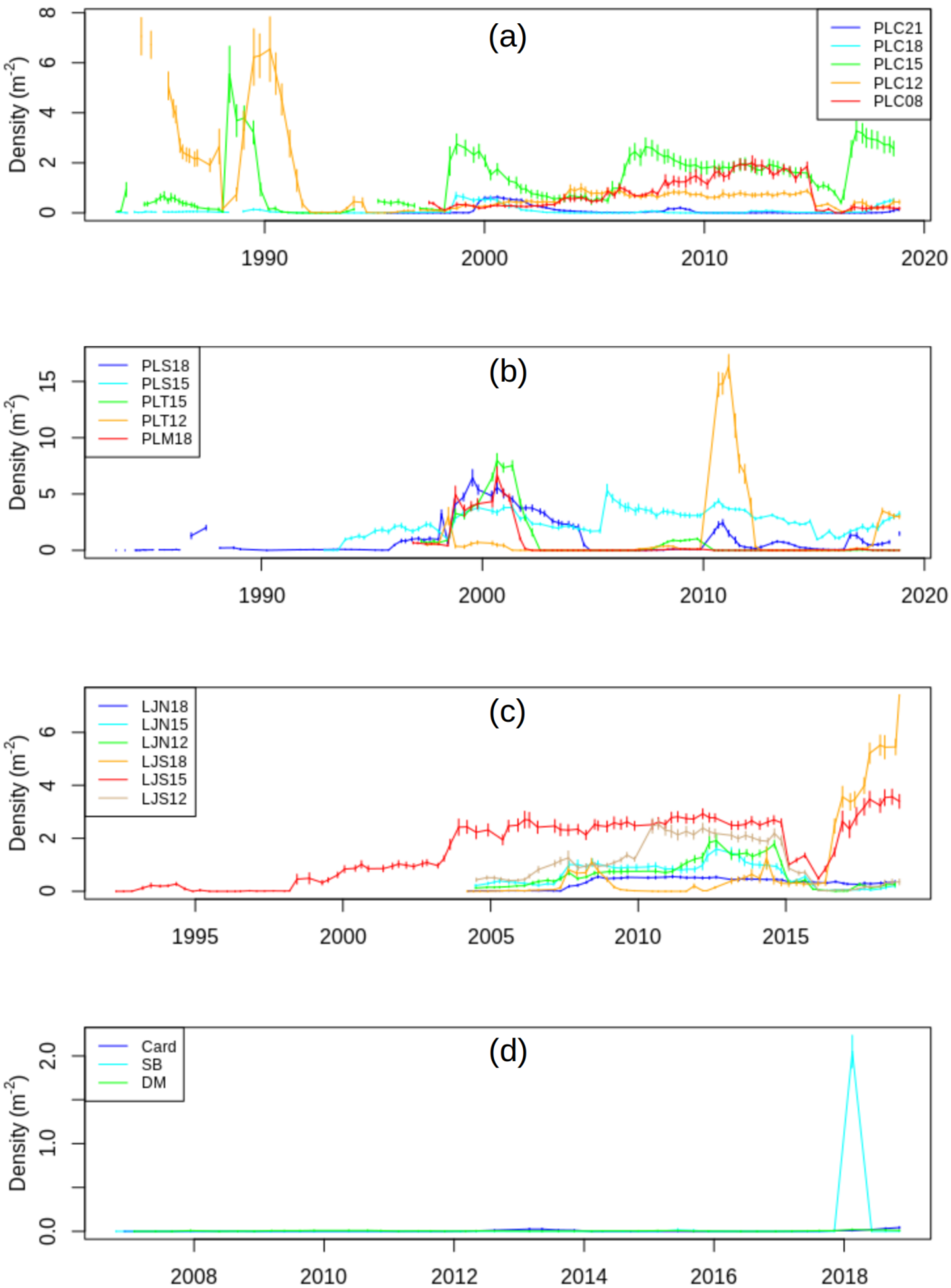

Figure 12. Mean densities of the understory kelp Pterygophora californica: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

The response of *L. farlowii* to the recent consecutive warm periods was more variable among study sites (Fig. 13). Three types of responses were observed. First, previously high densities at many sites quickly decreased during the BLOB with subsequent increases during the 2016 El Niño (e.g., PLC15, LJS18, and LJS15). Relatively high cover at other sites decreased due to the BLOB and remained reduced through the 2016 El Niño. These mainly include the sites in La Jolla and Del Mar. The third response occurred at PLS15 where cover was increasing prior to the BLOB when it decreased slightly followed by a rapid increase during and after the 2016 El Niño. Currently, *L. farlowii* is present at densities of at least 1 m^{-2} at all of the central and south Pt. Loma study sites with the exception of PLM18 and PLT15, and all of the La Jolla study sites. *L. farlowii* densities continue to be very low in North County. Densities have decreased to a third of pre-warm period densities off Del Mar and it is nearly absent from the other two North County study sites.

The complex trajectories of understory kelps 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 low understory, (2) lush understory with low surface canopy, and (3) lush to moderate canopy with low fractional cover of understory. A fourth ephemeral mode was also observed during the consecutive warm periods with sparse canopy and understory 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. 4). This resulted in long periods of nutrient stress for these lower canopy species, and effectively limited their recovery even when light limitation decreased during periods of low surface canopy.

Growth and reproductive states of both *P. californica* and *L. farlowii* were reduced during the BLOB and increased afterward (Figs. 14 and 15). Both growth and reproduction of *P. californica* was still depressed at the deeper central Pt. Loma sites until 2017. 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 modes. Such forcing can lead to a hysteresis than can persist for several years until the occurrence of a new major disturbance. Growth and reproduction for both species have recovered at all the study sites where they are present off central Pt. Loma.

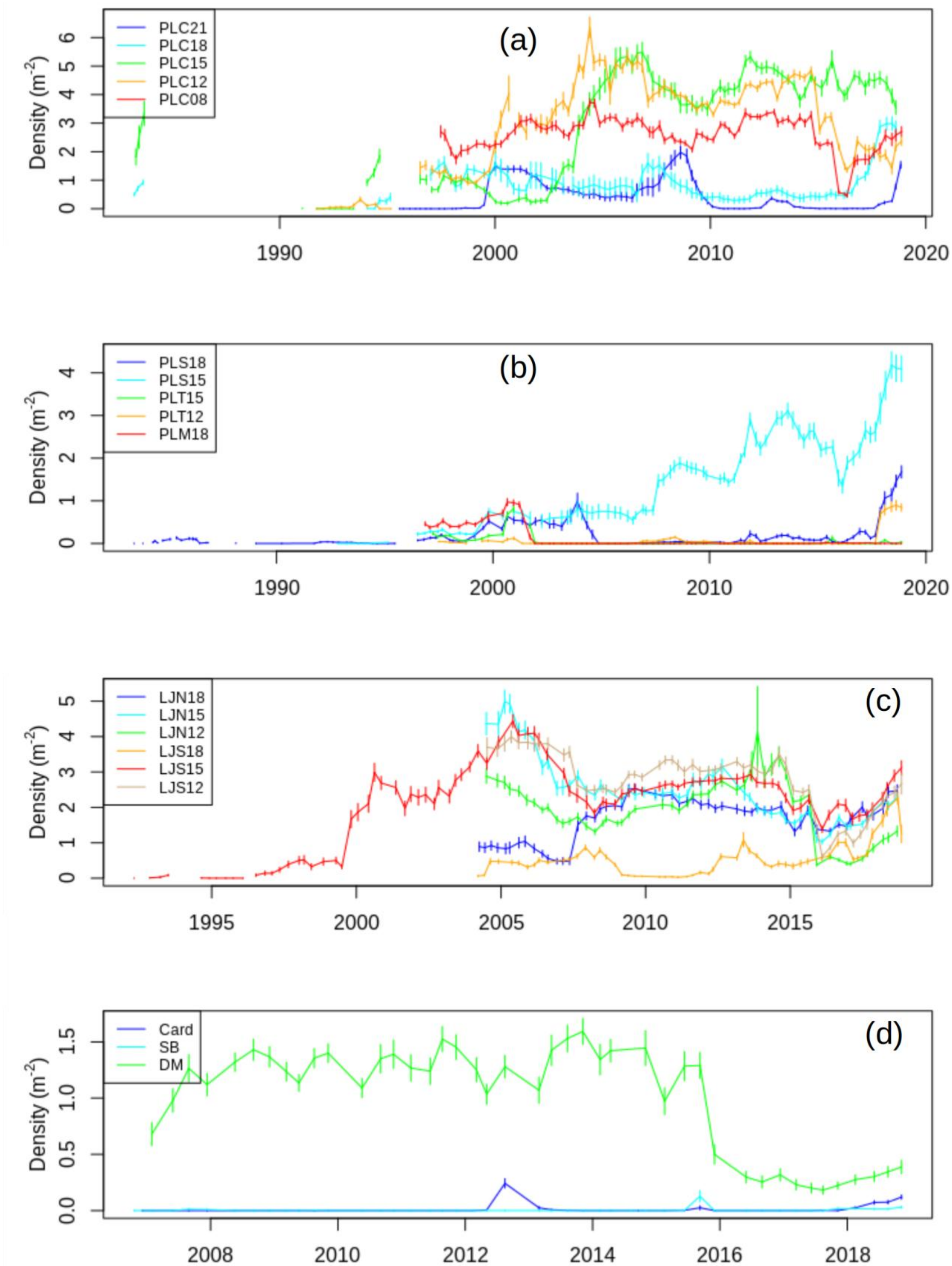

Figure 13. Mean densities of the understory kelp Laminaria farlowii: (a) central Pt. Loma, (b) south Pt. Loma, (c) La Jolla, and (d) North County study sites. Error bars indicate standard errors.

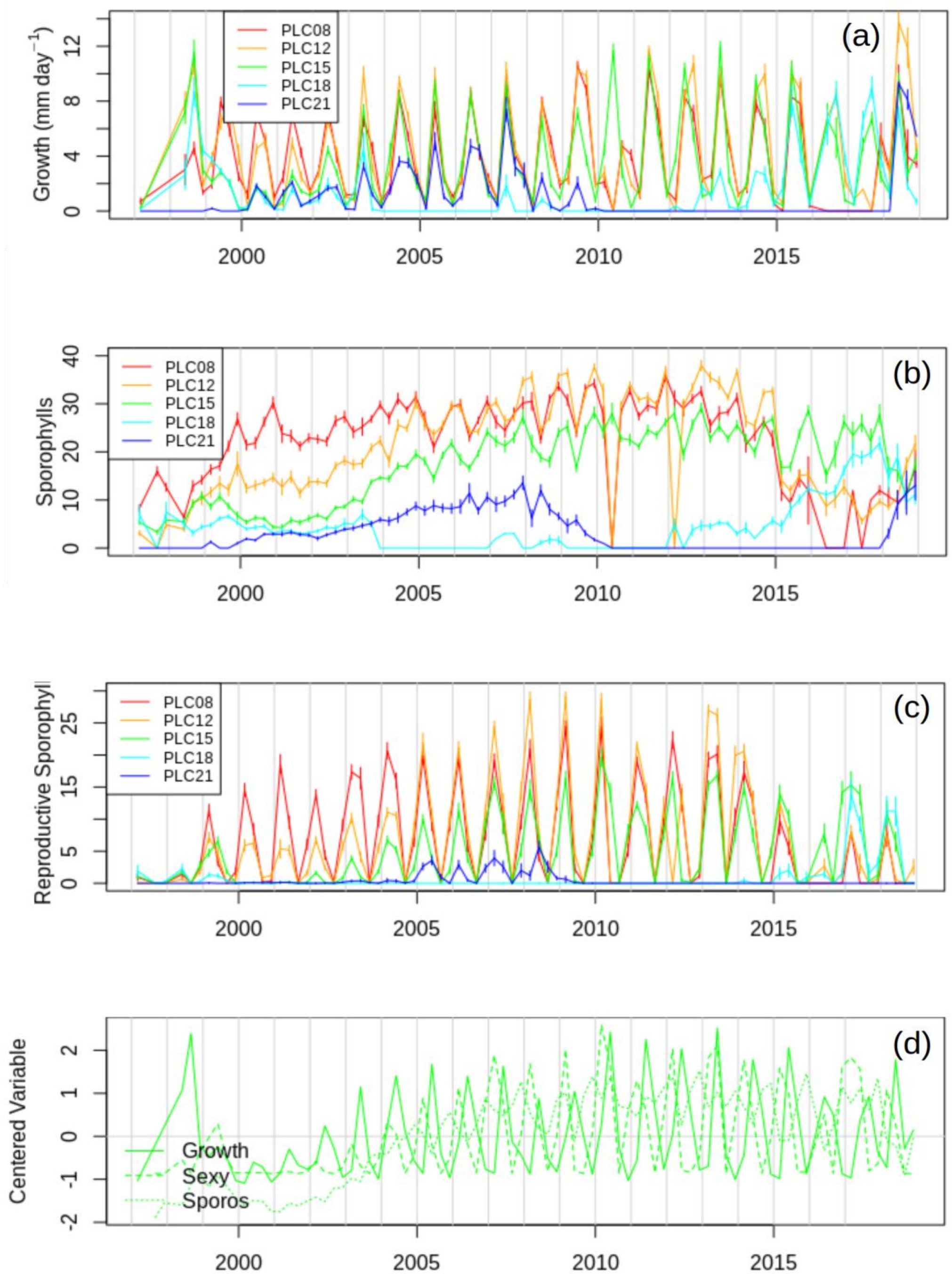

Figure 14. Growth and reproduction of the understory kelp Pterygophora californica at the central Pt. Loma study sites: (a) growth, (b) # sporophylls, (c) # reproductive (sexy) sporophylls, and (d) centered growth and sporophylls for the PLC15 site. Means are plotted and error bars indicate standard errors.

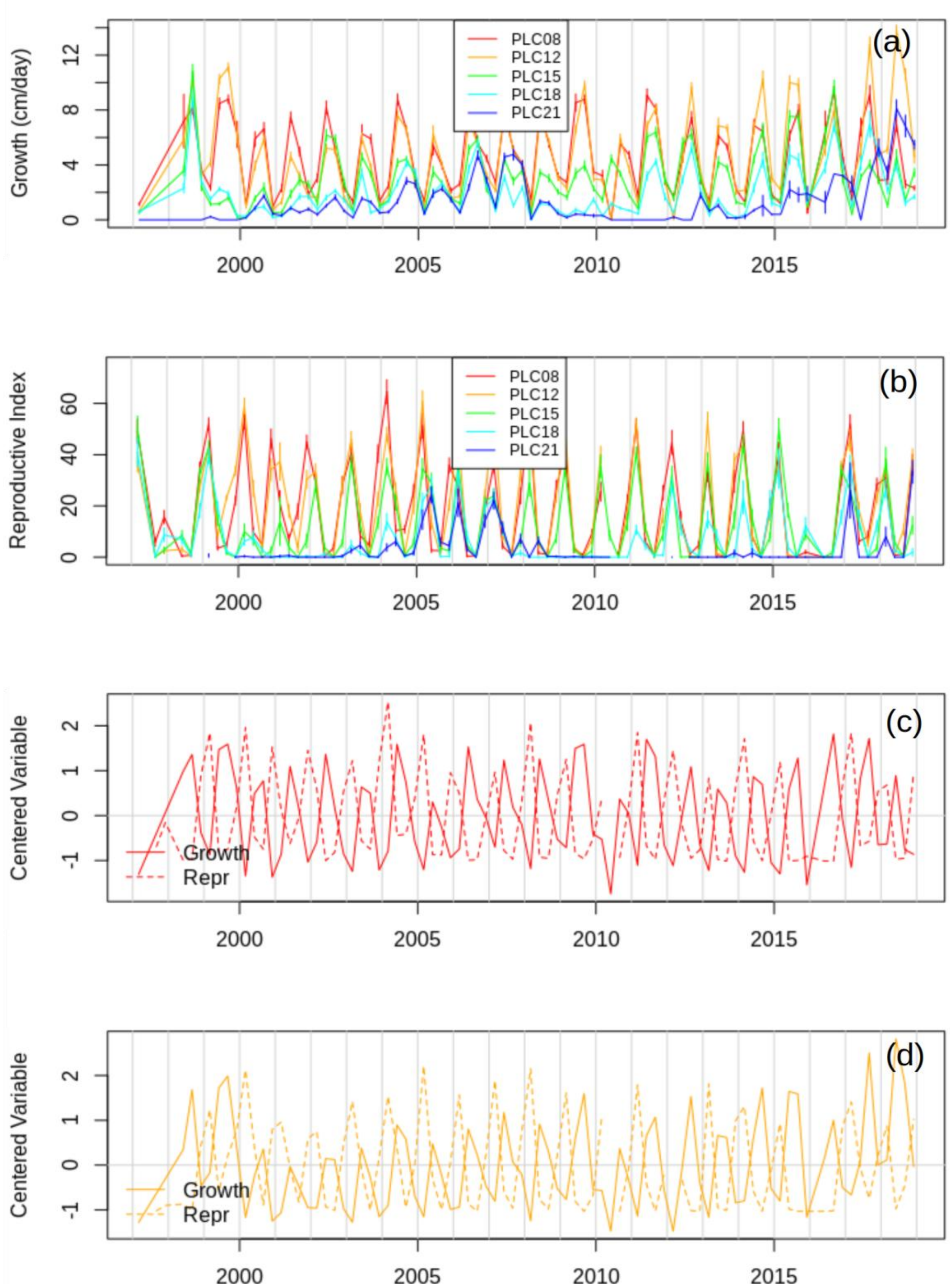

Figure 15. Growth and reproduction of the understory kelp Laminaria farlowii at the central Pt. Loma study sites: (a) growth, (b) % of blade that is sorus (reproductive), (c) standardized growth and reproduction for the PLC8 and the (d) PLC12 study sites. Means are plotted and error bars indicate standard errors.

Algal Community Analysis

Algal community composition among all of the study sites show the dramatic community-wide changes that occurred over the 5 years of the study (2014-2019, Figures 16-20). The results of the factor analysis that includes all algal species and derived bare space plotted in two dimensions clearly portray these changes. The first two factors represent ~31% of the overall variance in the dataset and are therefore a good representation of the algal community over time. Factor 1 indicates a continuum of understory and turf states from bare ground (negative values) to lush turf algae (positive values) with understory canopy species such as *P. californica*, *Eisenia arborea*, *L. farlowii*, and *Agarum fimbriatum* in between these two extremes. 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). The major pattern is a decreasing shift in factor two after 2014 reflecting the loss of giant kelp due to the consecutive warm periods beginning in late 2014. An increase in giant kelp between 2016 and 2017 is indicated by increases in factor 2 for many sites including LJS18, SB, PLN18, and PLC08. There is also a shift away from bare space towards more abundant understory canopy and turf species. *Desmerestia ligulata* is an early colonizing species that competes with both giant kelp and understory species after disturbances for up to several months (Dayton et al., 1992). The fractional cover of this species increased sharply in 2016 at PLT15, PLT12, Cardiff, and Del Mar. *A. fimbriatum* was still abundant at PLT15 in 2017. Fractional cover of *A. fimbriatum* increased after the El Niño of 2016 at PLC21 and PLC18, but was rare at these study sites after the BLOB. This species had the clearest competitive effects on surface and canopy kelp recovery at Cardiff, Del Mar, PLT15, and PLT12. Increases in kelp abundance at many study sites is evident beginning in 2017 and continued through 2018 at these sites with the exception of PLC12 which became dominated by turf algae. Generally, shallower sites tend to be more turf oriented due to increased wave and nutrient/temperature stress on giant kelp. These factors favor the understory guilds and turf algae in their competition for space with giant kelp.

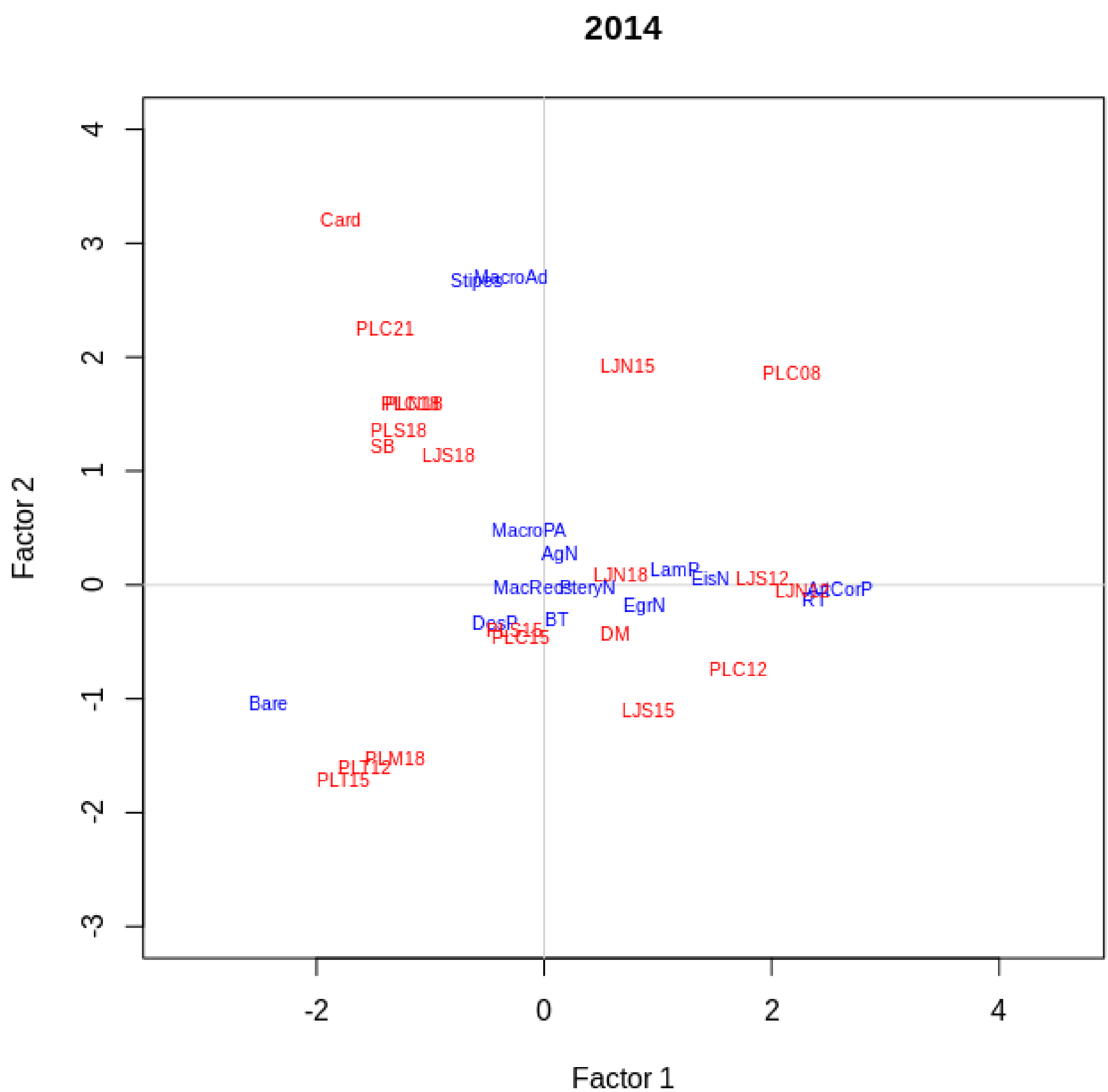

Figure 16. Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2014. Algal group definitions: Bare = derived bare space, MacRecs = M. pyrifera recruit stage (pre-bifurcates + bifurcates), MacroAd = M. pyrifera adult density, Stipes = M. pyrifera stipe density, MarcroPA = 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.

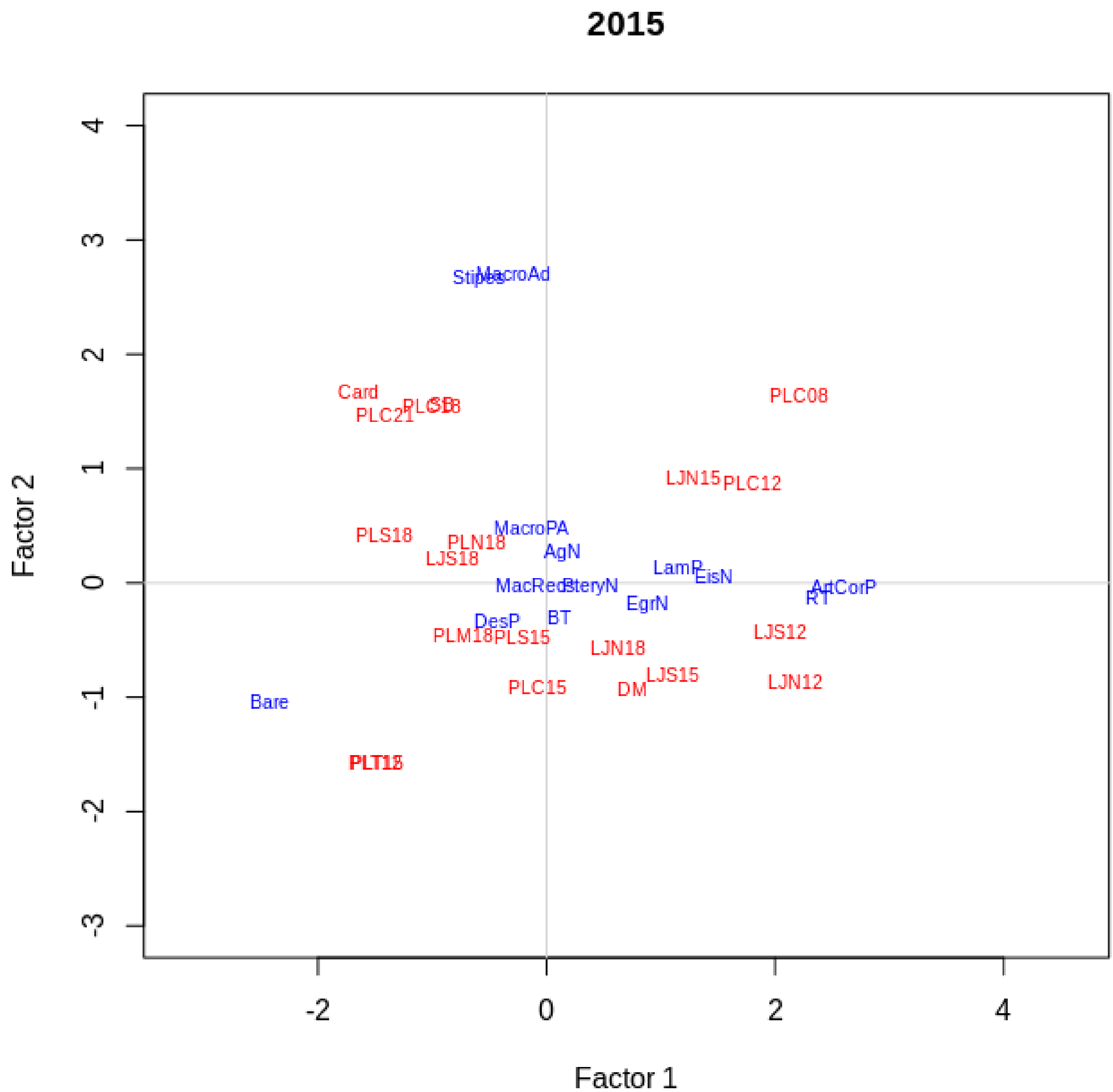

Figure 17. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2015. See Figure 16 for description of plot.*

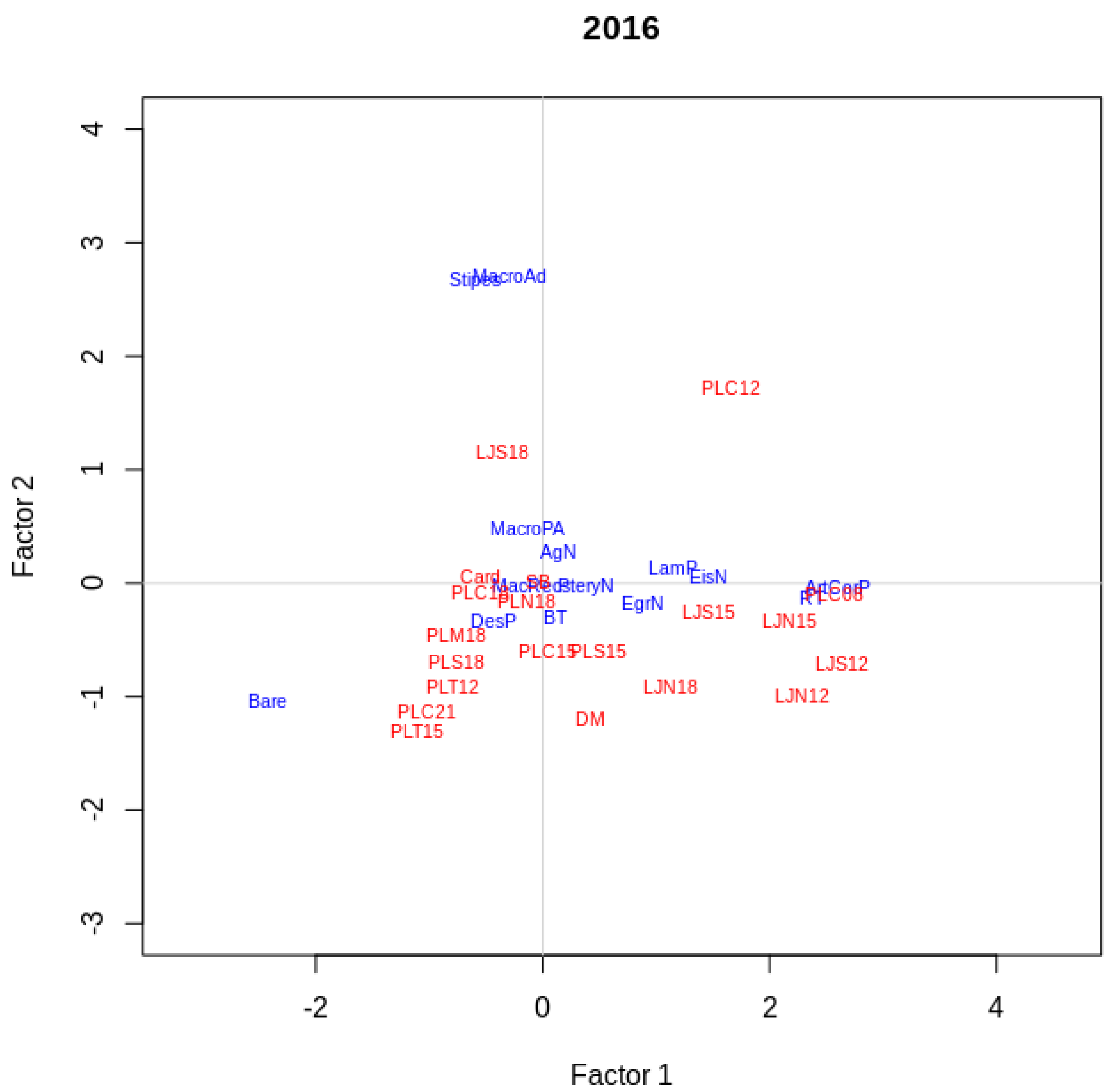

Figure 18. Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2016. See Figure 16 for description of plot.

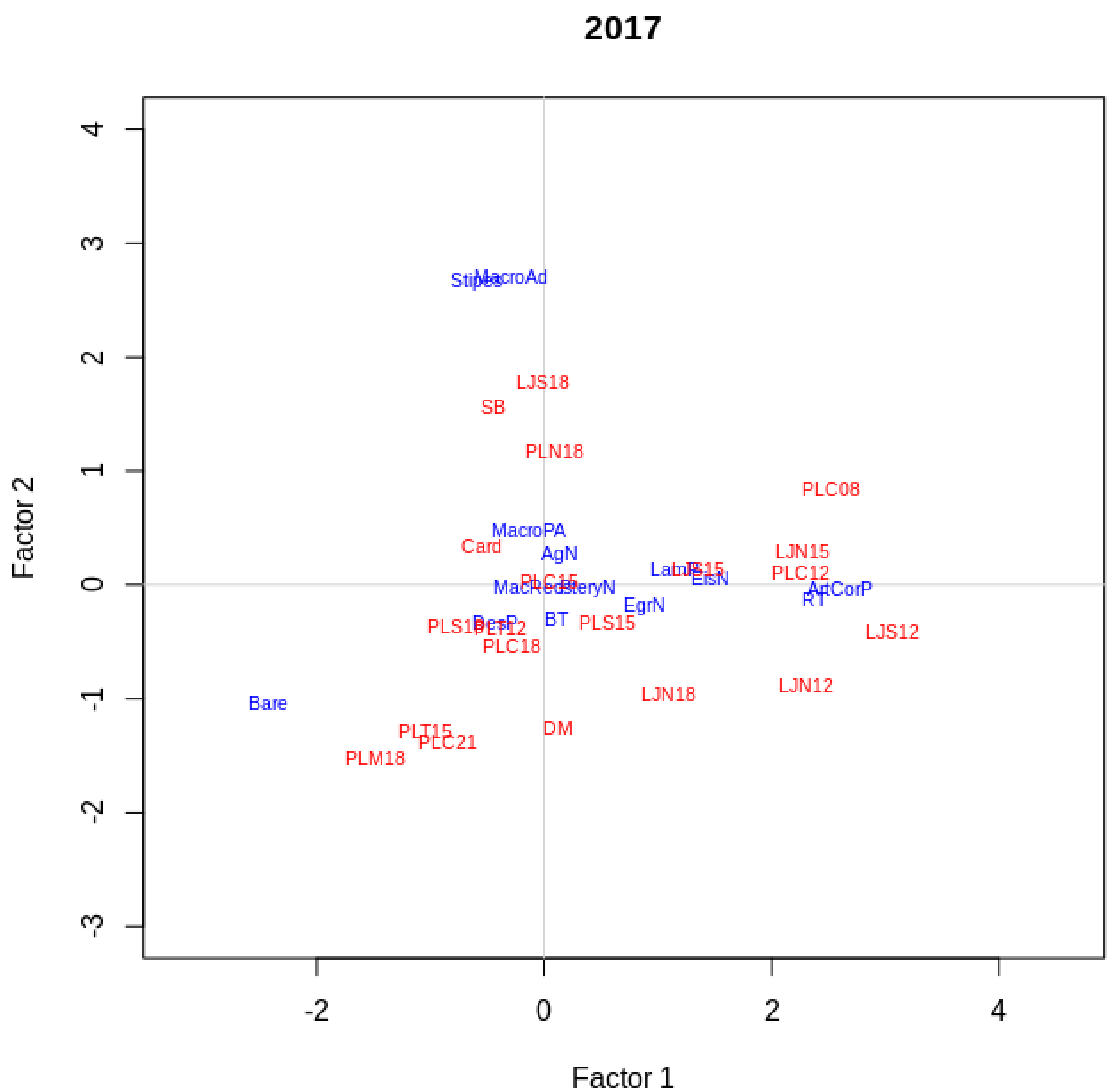

Figure 19. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2017. See Figure 16 for description of plot.*

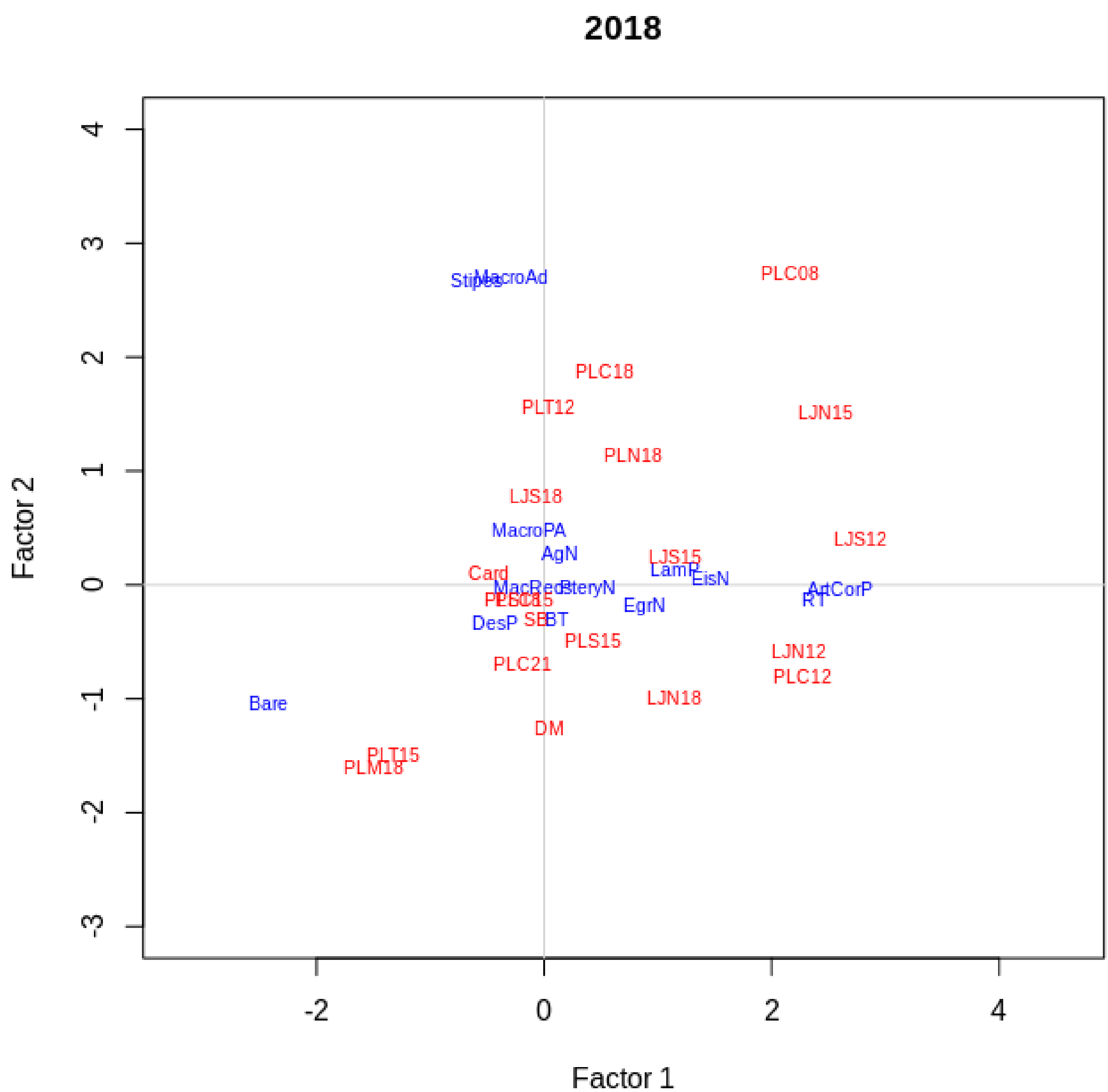

Figure 20. *Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2018. See Figure 16 for description of plot.*

Invasive Algal Species

Sargassum horneri is an invasive alga that invaded southern California in 2006 when it was reported from Long Beach Harbor (Miller et al., 2007). Since that time it has gradually spread along the coast and was observed in Mission Bay by 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 at the beginning of the study period in 2014 and has since spread to 13 of our study sites. Initially, it was observed near the study sites and subsequently established itself within the permanent band transects at several of the study sites. Table 3 lists first sightings within the actual band transects and Fig. 21 shows relative abundances and frequency among the study sites. The greatest percent cover observed thus far was at LJN18 in the fall of 2017 when mean percent cover approached 30%. *S. horneri* has established itself at 9 of the study sites and has been observed at 4 others (Fig. 21).

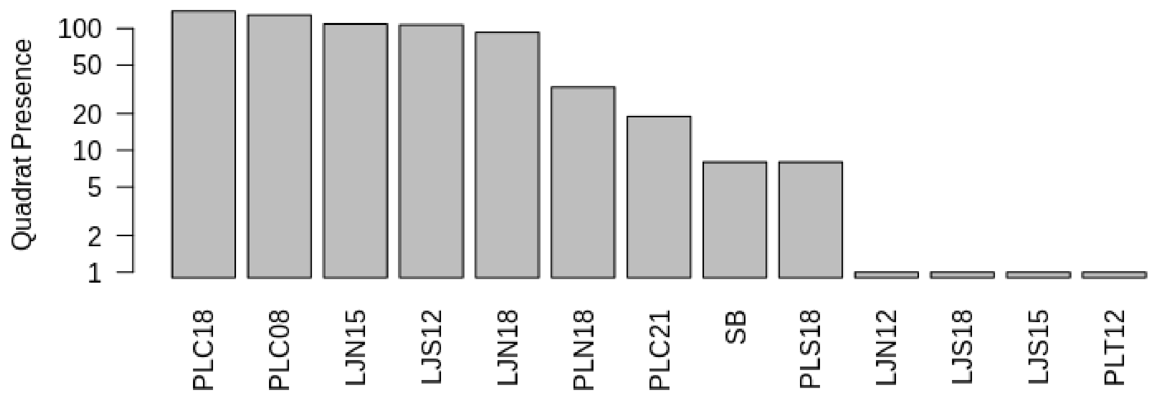

Figure 21. Presence of the invasive alga, Sargassum horneri, among the study sites where it has been observed within the permanent band transects. Quadrat presence indicates the total number of 5x2 m quadrats along the transects where it has been observed over time since first sighting at each individual site.

S. horneri clearly poses a risk to *M. pyrifera* and many other algal species due to its rapid seasonal growth rates. It is not implausible for it to take over some areas of the 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.

Table 3. *List of study sites where the invasive alga, Sargassum horneri, has been observed within the band transects and the dates it was first observed.*

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
PLC8	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

Invertebrates

Many species of invertebrates were also stressed by the 2014-2016 warm event. Sea urchins (Echinoids) and seastars (Asteroids) were affected the most. Both groups have important functions within kelp forests. Sea urchins are major grazers of algae and can overgraze kelp forests if they become too numerous and mobile. Seastars are important benthic predators. Both groups suffered great mortality off San Diego during the warm event.

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 22 and 23 for the sites where these species were most abundant prior to 2013. 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. Presently, there are very 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). Additionally, sea urchin recruitment was absent or extremely limited at all sites until the fall of 2017 (based on semi-annual size frequency sampling). Sea urchin recruitment (percent in the first year age class at a site) for both species increased at several sites (Table 4). The largest increases were observed mainly at the southern Pt. Loma sites, and all sites off La Jolla with the exception of LJS18. Recruitment of RSU was strong at the outer central Pt. Loma stations (PLC18 and PLC21).

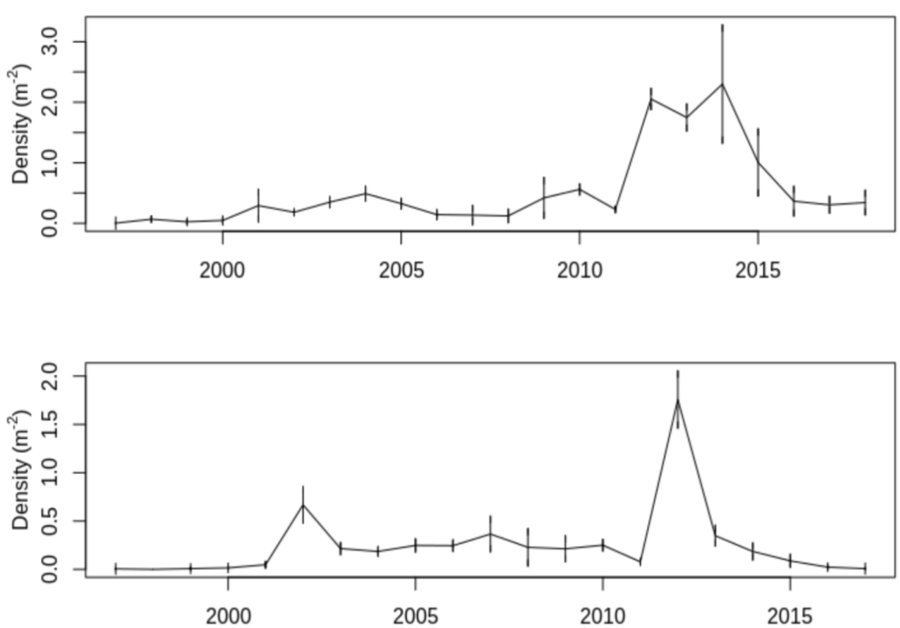

Figure 22. Time series of the red sea urchin (Mesocentrotus franciscanus) mean densities at the PLM18 (top) and PLT15 study sites. Error bars are standard errors.

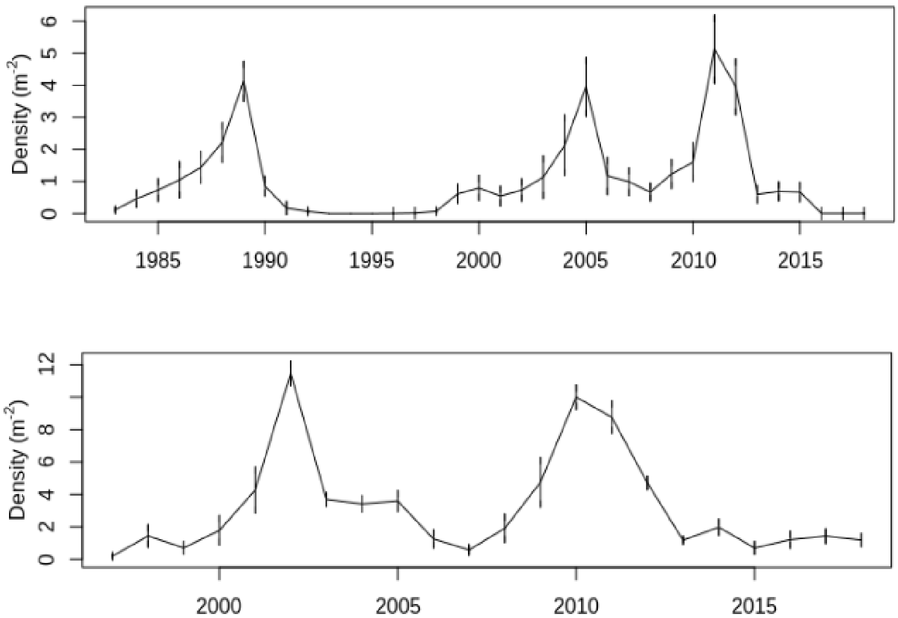

Figure 23. Time series of purple sea urchin (Strongylocentrotus purpuratus) mean densities at the PLS18 (top) and PLT12 study sites. Error bars are standard errors.

Sea urchins are not likely to have any immediate effects on kelp recovery due to their reduced abundance and delayed recruitment. However, the fall 2017 and 2018 sea urchin recruitment events may result in overgrazing at some sites as the sea urchins mature and migrate away from sheltering juvenile habitat and begin to actively seek forage. Sea urchin overgrazing may occur at some sites by 2020 as the fall 2017 cohort matures and begins to actively forage over broader areas.

Table 4. Recruitment rates for red and purple sea urchins (M. fransicanus and S. purpuratus, respectively) during the fall of 2017 and 2018. Recruit percent is the fraction of ~1 year old individuals sampled within quadrats. Size thresholds for RSU and PSU recruits are <35 and <25 mm, respectively. "" refers to sites where too few sea urchins were available for measurement (<75).*

	Fall 2017		***Fall 2018***	
Site	***Mesocentrotus franciscanus***	***Strongylocentrotus purpuratus***	***Mesocentrotus franciscanus***	***Strongylocentrotus purpuratus***
LJN18	17.31	15.84	24.00	26.2
LJN15	33.32	54.84	48.64	38.21
LJN12	64.7	91.49	28.13	29.41
LJS18	4.85	1.94	44.76	22.32
LJS15	17.65	14.17	26.31	25.20
LJS12	50.00	15.38	31.58	18.42
PLN18	15.84	7.94	33.96	16.52

PLCenW18	21.09	9.26	47.36	28.45
PLC21	28.92	8.99	71.05	56.88
PLC18	32.69	9.57	18.81	20.35
PLC15	6.19	4	2.00	10.65
PLC12	*	19.42	*	8.06
PLC08	*	45.35	*	15.21
PLSouthW18	0.84	10.85	3.57	1.67
PLS18	48.25	37.9	50.00	51.81
PLS15	18.75	16.49	44.44	22.12
PLM18	2.73	8.89	36.52	59.67
PLT12	57.14	57.43	42.06	44.42
PLT15	69.33	71.60	96.29	73.10

Diseases affecting echinoderms also caused mass mortality of several asteroid species throughout the Southern California Bight during the consecutive warm periods (Hewson et al., 2014). Species that suffered the greatest mortality at our study sites included *Pisaster giganteus* (Fig. 24) 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. Juvenile *P. giganteus* have been observed recruiting onto giant kelp fronds off Pt. Loma beginning in 2017 and continuing into 2018, thus heralding their recovery. However, disease has also decimated *Pycnopodia helianthodes*, an important sea urchin predator (Moitoza et al., 1979). This species has not been observed anywhere off Pt. Loma since 2014 even in areas where they were once common. *P. helianthodes* was in decline even prior to the BLOB event.

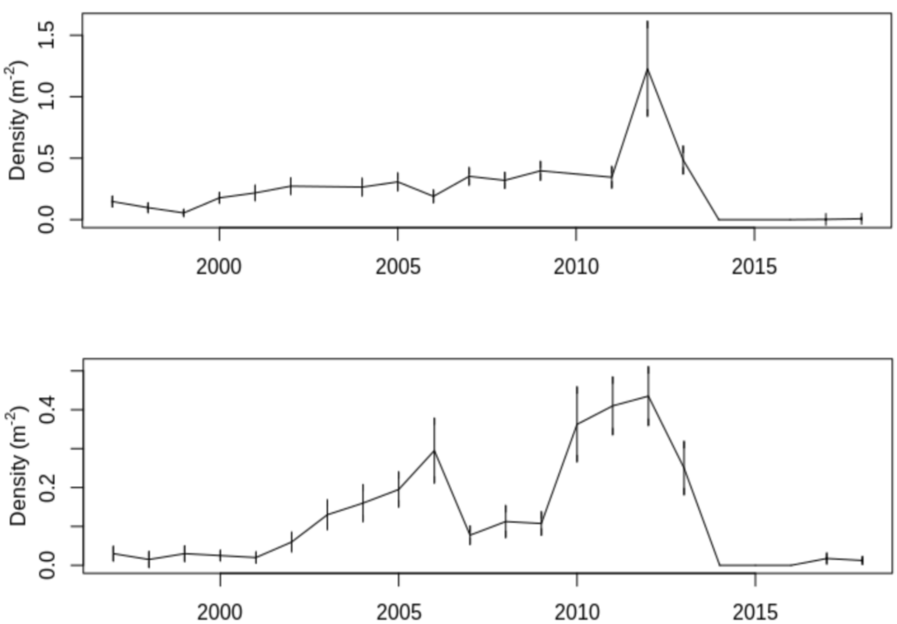

Figure 24. Time series of the seastar Pisaster giganteus mean density at the PLSC12 (top) and PLM18 study sites. Error bars are standard errors.

Abalones are marine mollusks and 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 warm periods. At the same time, densities of pink abalone (*H. corrugata*) have been steadily increasing at PLC8 since 2012 (Fig. 25), exhibiting steady population increases throughout the warm period

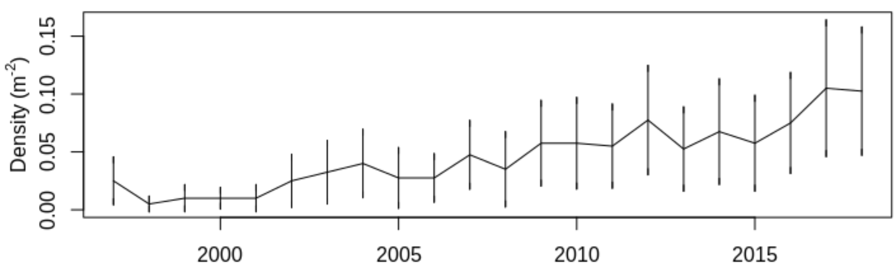

Figure 25. Time series of pink abalone (Haliotis corrugata) mean densities at the PLC8 study site. Error bars are standard errors.

North County Sedimentation

Sediments at the NCKF sites have been relatively stable since 2008. Sediment horizons have varied less than 10 cm since 2008 when the sediment time series began. This period included the significant replenishment of beaches inshore of the study sites in 2012. North County beaches are presently undergoing a larger sand replenishment project that is slated to last four years. The grain size of sediments used for beach replenishment is an important determinant of beach stability. The 2012 replenishment event utilized coarser sediments than previous replenishment efforts, and therefore erosion of those beaches did not appear to affect NCKF reefs. The source of sediments for the present beach replenishment effort is San Elijo Lagoon, as part of an effort to restore the estuary to more marine conditions. The grain size composition of these sediments is not clearly defined and therefore the potential impact of this most recent replenishment project on North County reefs is presently uncertain.

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