Appendix A

Status and Trends of San Diego Kelp Forests

2016 – 2017

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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 United States. They host complex marine communities supported by their eponymous species, the giant kelp *Macrocystis pyrifera*, which provides structure and food for hundreds of species of marine fishes and invertebrates. Kelp forests off southern California are subjected to both natural and human-induced stress. For example, the El Niño Southern Oscillation (ENSO) represents the primary ocean climate mode that affects the abundance, growth, and reproduction of kelp along the western Americas. Positive ENSO events 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. The opposite conditions occur during negative ENSO events (La Niñas). Together, these two modes drive the greatest amount of annual variability in surface canopy cover of *M. pyrifera*. El Niño periodicity 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 periods afterwards. Rates of kelp recovery depend on growth conditions after each El Niño ebbs. The kelp forests off San Diego have been studied by researchers at the Scripps Institution of Oceanography (SIO) since the 1970s, and are currently being monitored at twenty permanent study sites located among the Point Loma, La Jolla, and North County kelp forests as part of a long-term project presently funded by the City of San Diego Public Utilities Department in order to enhance its ocean monitoring efforts for the Point Loma and South Bay ocean outfall regions. This report summarizes the findings from the last several years of the SIO kelp forest monitoring project with an emphasis on calendar years 2016 and 2017.

California kelp forests have been subjected to severe temperature and nutrient stress that began in late 2013 and persisted until the spring of 2017. This lengthened period of stress was due to the combination of two consecutive ocean climate events. First, an anomalous warm pool of surface ocean waters extended across much of the NE Pacific from 2013–2015. This warm pool, unique in the climate record of the NE Pacific, was coined the BLOB and resulted from completely different forcing events than ENSO. Second, a strong El Niño occurred just after the BLOB dissipated, and together these consecutive warm periods resulted in the longest and warmest period ever observed in the >100 year ocean temperature time series data collected at the SIO pier.

The consecutive warm events described above and associated low nutrient conditions decimated populations of *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 water events attributed to El Niño, the BLOB resulted in warming and low nutrient exposure of understory kelp species as well for prolonged periods of time leading to dramatic reductions in those species. 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. Since these two events affected kelps at the study sites differently, the classic pattern of a real synchronized mortality and recovery has been disrupted. More recently, growth conditions returned to normal with the onset of mild La Niña conditions in the spring of 2017. Rates of giant kelp recovery since that

time have been variable among study sites and are now either slower than previous recovery periods or near zero. Additionally, surface canopy cover has been precluded by increases in understory species in some areas. Some of these areas are likely to remain devoid of giant kelp canopy for years since understory species are long-lived and competitively 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 sea urchins (*Mesocentrotus franciscanus*), 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 has been observed until recently in 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. Kelp forest recovery in the coming year (2018) is not likely to be affected by sea urchin overgrazing given their recent die-off. However, overgrazing may occur in some areas by the following year (2019) as recruits grow large enough to migrate out of juvenile refuge habitats.

Present La Niña conditions are predicted to shift to ENSO neutral conditions by the spring of 2018, and if so, this will occur during the season of maximal nutrient delivery up onto the nearshore coastal shelf off San Diego. Conditions for giant kelp recovery may therefore become less favorable at a critical time for their growth and reproduction and could potentially further slow the rates of giant kelp forest recovery off San Diego. Another source of stress is the gradual colonization of an invasive algal species, *Sargassum horneri*, first observed in the kelp forests off San Diego in 2014. This species has become established at several study sites. *Sargassum horneri* can outcompete *M. pyrifera* for space and may further slow the recovery of kelp forest canopies off San Diego, perhaps precluding recovery in some areas altogether.

Introduction

Kelp forests are one of the most charismatic marine communities off southern California. 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 marine fishes and invertebrates as well as many cohabiting species of understory algae. These forests occupy the inner margins of the continental shelf and offshore islands extending from the outer edge of tidepools to depths as great as 30 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. For example, the 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 disturbances because of their proximity to urbanized coasts exposing them to polluted stormwater runoff and wastewater disposal. Perhaps the largest effect is that due to increased turbidity in coastal waters that limits light penetration for kelps to grow, germinate, and reproduce (Clendenning and North 1960). Dramatic reductions in kelp forest canopy cover 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). However, nearshore turbidity due to wastewater discharge has long been mitigated by increasing the offshore distances and depths of discharge sites and improved outfall design (Roberts 1991). The Point Loma Ocean Outfall (PLOO), for example, was extended and deepened effective in late 1993, presently discharging treated wastewater ~7.3 km offshore in waters ~98 m deep. The current location of the PLOO discharge is ~5 km offshore of the western edge 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 as the replenished sediments erode from beaches and partially bury low relief hard bottom habitat as eroded sediments redistribute offshore.

Kelp forests in southern California are also disturbed naturally by ocean climate variability that occurs at interannual (e.g., El Niño Southern Oscillation - ENSO) and decadal (e.g., 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 necessary for kelp growth. These modes are also associated with increased storm 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 1970s in which the main ocean thermocline deepened, resulting in a step reduction in nitrate concentrations that still persists (see Figure 1, Parnell et al. 2010). Concentrations of nitrate, the main limiting nutrient for kelp growth in southern California, switched from being conducive for kelp growth most years, 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 *M. pyrifera* individuals (Parnell et al. 2010).

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 sea urchin barrens. Such barrens and forested modes can be semi-permanent or resilient in some areas such as in the southern Point 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 *M. 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 less protected areas along the mainland including San Diego County.

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 Kelp Forest (PLKF) and La Jolla Kelp Forest (LJKF) and continue at several of the sites established in the 1970s and 1980s (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 (NCKF). PLKF and LJKF are the largest contiguous kelp forests off the western United States coast and together historically represent one of the most studied kelp forest ecosystems in the world.

Materials and Methods

A variety of marine algae and invertebrates and bottom temperatures are monitored at 20 permanently established study sites in the kelp forest off San Diego (Figure 2). Algae and invertebrates are monitored along four replicate parallel permanent band transects oriented perpendicular to shore (25 x 4 m bands

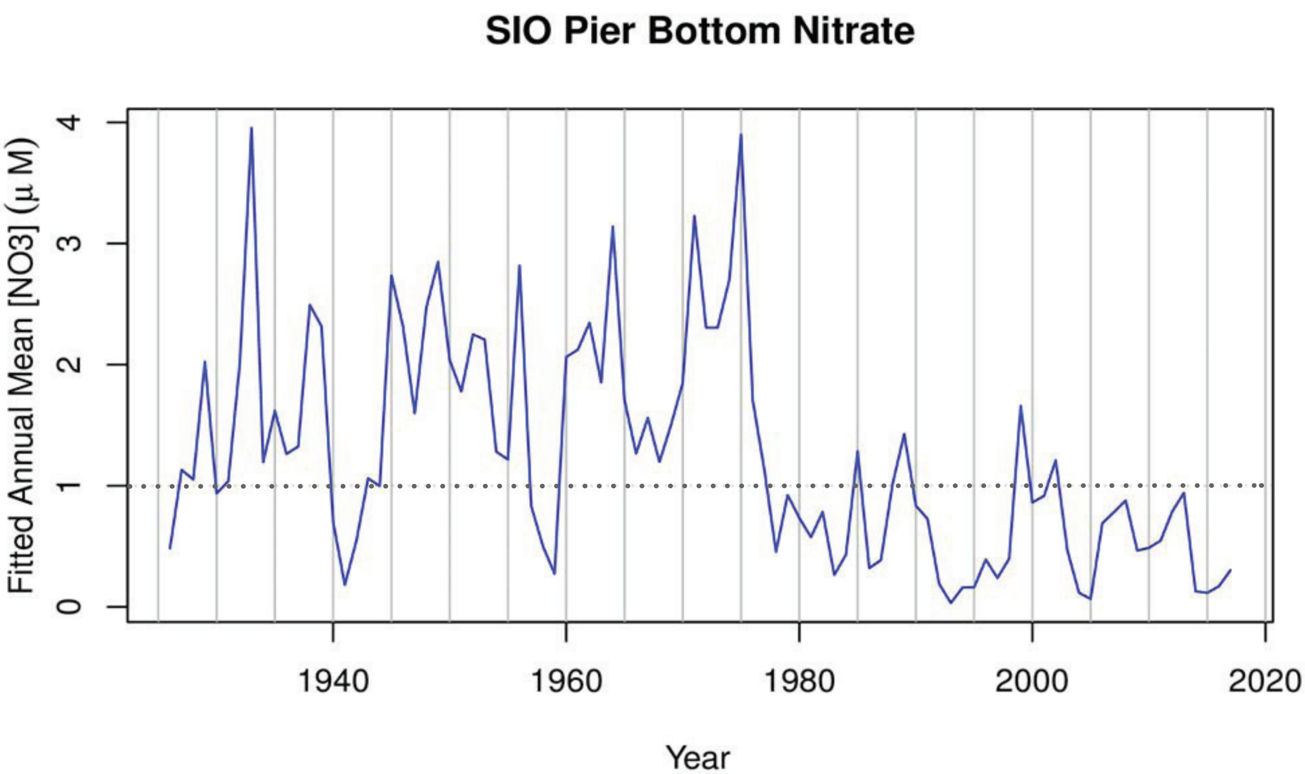


Figure 1
Time series of annual mean nitrate concentrations estimated from daily temperature and salinity data at the base of the Scripps Institution of Oceanography Pier (see Parnell et al. 2010 for details). Dotted gray line indicates the minimum nitrate threshold for growth of *Macrocystis pyrifera*.

separated 3–5 m apart) except at the Del Mar (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) 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.

Conspicuous macroalgal species/groups are enumerated or percent cover is estimated within 5 x 2 m (10 m^2) continuous quadrats along the band transect lines at all sites. Reproduction and growth of giant kelp *Macroscystis pyrifera*, and the understory kelps *Pterygophora californica* and *Laminaria farlowii,* are measured on permanently tagged plants along the central PLKF study sites. All conspicuous sessile and mobile invertebrates are enumerated annually within the 10 m^2 quadrats during spring. Size frequencies of red sea urchins (RSU - *Mesocentrotus franciscanus*) and purple sea urchins (PSU - *Strongylocentrotus purpuratus*) are recorded for >100 individuals of each species located near all of the study sites except within the NCKF where there are not 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 minute intervals using ONSET Tidbit recorders (accuracy and precision = 0.2˚C and 0.3˚C, respectively). All field work was conducted using SCUBA.

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

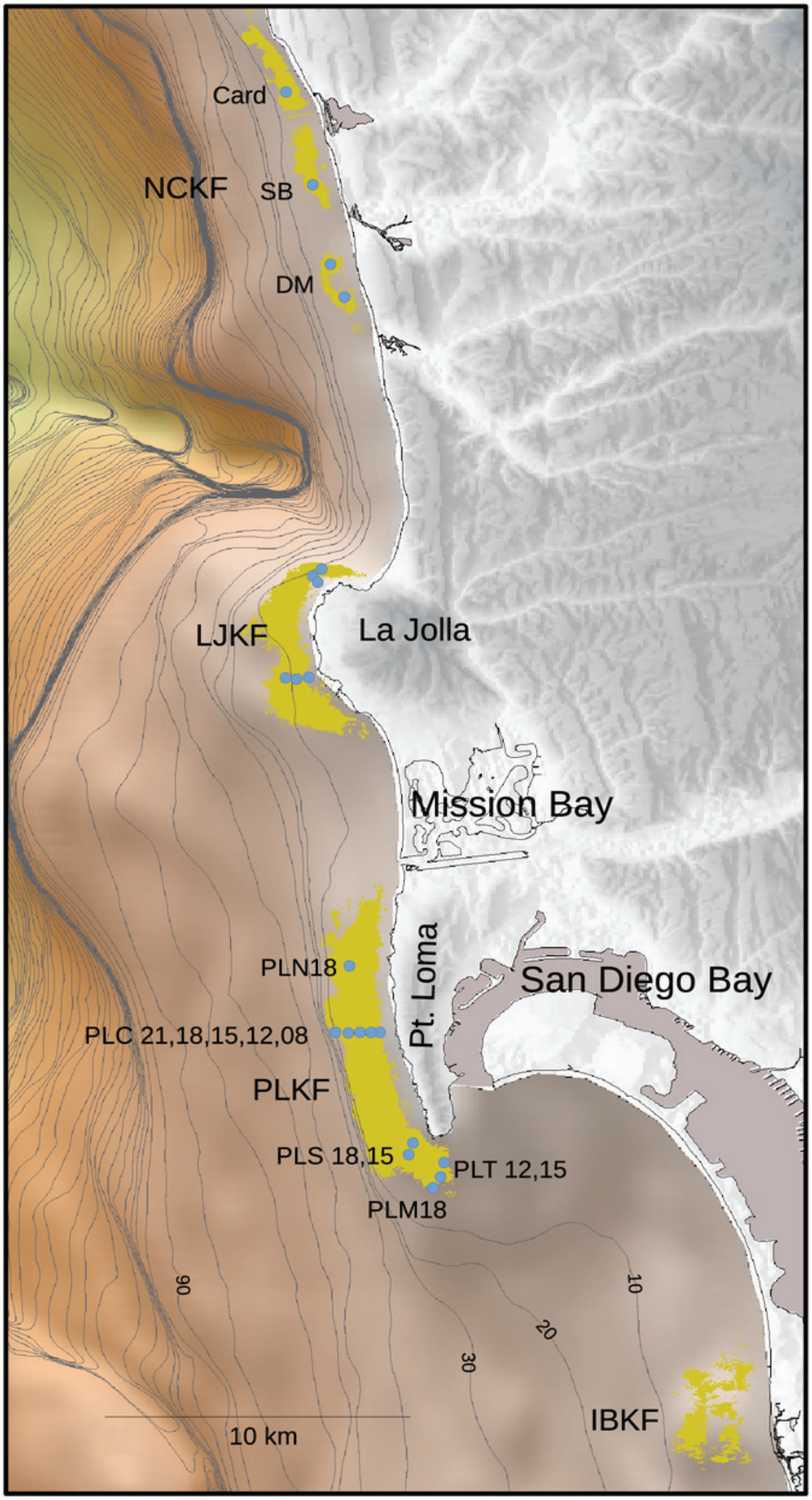


Figure 2

Map of the San Diego marine shelf showing locations of the Point Loma (PLKF), La Jolla (LJKF), North County (NCKF), and Imperial Beach (IBKF) kelp forests. Permanent study sites are indicated with blue circles with study site names clustered with site clusters. Depth contour units are meters.

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)

height and diameter of each bundle. This is an indirect measure of reproductive effort, and 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 following ordinal scale:

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.

Growth of *Pterygophora californica* was determined by the method of DeWreede (1984). A 6 mm diameter hole is punched in 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.

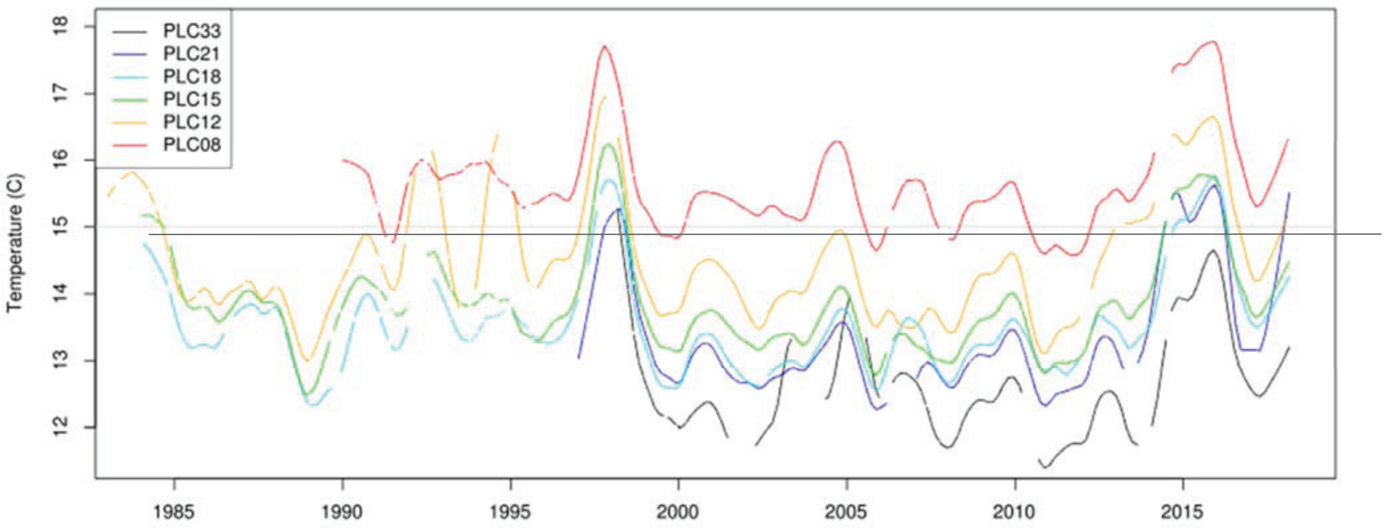


Figure 3
Sea bottom temperature trends at the central Point Loma study sites. The horizontal gray line indicates the temperature above which nitrate concentrations are typically limiting for giant kelp growth. Gaps indicate missing data due to instrument loss/malfunction.

Reproductive effort for *P. californica* is evaluated by a count of the total number of sporophyll blades on each plant and the number with sori.

Growth of *Laminaria farlowii* is determined in a similar manner to *P. californica*. A 13 mm diameter hole is punched 100 mm 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 PLKF and LJKF study sites. Sea urchins are exhaustively collected in haphazardly placed 1-m^2 quadrats in suitable substrate within 50 m of each study site. Suitable substrate includes ledges and rocks which can be fully searched for sea urchins as small as 2 mm. 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. 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 10-m^2 quadrats) with the least amount of total algae (density or percent cover) were ranked highest for bare space.

Results and Discussion

Bottom Temperature

The bottom temperature record at the central PLKF study sites extends back to 1983 when the strong 1982/1983 El Niño was ebbing. The largest temperature signals in the time series include the 1997–98 El Niño and the extended warm period (2013–2015) associated with the large scale anomalous NE Pacific warm event (DiLorenzo and Mantua 2016) termed the BLOB and was immediately followed by a strong El Niño (Figure 3). Relatively less pronounced warm periods have 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 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 2014-2017 BLOB/El Niño penetrate to the bottom for extended periods even at the offshore edge of the forest stressing all kelps. 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 only the surface canopy kelps (mainly *M. pyrifera*) more than the understory kelps where temperatures are cooler. Repeated cycles of mild El Niños over many years in the absence of large storm waves leads to increasing understory domination at the expense of giant kelp canopy cover. The bottom temperature climate off San Diego during the present reporting period encompasses the end of the unprecedented warm event of 2013–2017, and bottom temperatures have since cooled but appear to be increasing again. Currently, unseasonably warm winter sea surface temperatures with anomalies as great as 2ºC are being observed at the SIO pier despite this period being categorized as a La Niña (Climate Prediction Center, NOAA).

The ENSO index is based on equatorial sea surface temperatures in the Pacific Ocean. ENSO warming and cooling of western American coasts propagates poleward from the tropics, and each El Niño/La Niña events penetrate higher latitudes differently. Present sea surface temperature anomalies off San Diego during the current La Niña indicate that dynamic forcing of the temperature and nutrient climates off southern California may have changed over the observational time period of available temperature records in the region. The NOAA Climate Prediction Center forecasts a return to neutral ENSO conditions from the present La Niña by spring. This portends a less favorable growth climate for the kelp forests off San Diego, potentially interrupting the recent improvement in kelp growth conditions present at the end of 2017 (Figure 1).

Kelps and Algal Reproduction

The effects of the 2014–2017 warm period on the kelp forests off San Diego were clearly negative. Densities of adult *M. pyrifera* (Figure 4) and giant kelp stipes decreased dramatically at all study sites. *Macroscystis pyrifera* was entirely lost from several study sites and has not yet recovered at many of the study sites, especially the deeper sites including PLC21, PLS18, PLM18, and LJN18. Giant kelp surface canopy was nearly entirely lost off most of San Diego, Orange, and Los Angeles counties during 2016 (MBC Applied Environmental Sciences 2017). These losses are set against an overall declining trend of *M. pyrifera* density observed at the long term study sites off central Point Loma.

The primary abundance pattern for *M. pyrifera* since the 1980's includes rapid declines associated with El Niño's followed by step increases as giant kelp recovers afterward (e.g., Figure 4a). Densities then typically slowly decrease from post El Niño recoveries. The most recent declines observed between 2015 and 2017 contrast with this primary pattern. Whereas previous losses associated with El Niño have been nearly simultaneous among sites, the most recent die-off affected giant kelp differently among sites because they were previously impacted by the BLOB. Densities at some sites such as PLC08 declined quickly and began recovery with two episodes of moderate recruitment (Figure 5). Other sites, such as PLC18, PLC15, and PLC12 experienced at least one bout of *M. pyrifera* recruitment between the ebbing of the BLOB and the onset of the 2016 El Niño (Figure 5). The fates of these cohorts differed among sites with the greatest recovery observed at PLC08 and LJN15. Generally, giant kelp at the deepest sites off Point Loma and La Jolla has decreased to zero or near zero with little recovery despite cooler temperatures. These areas have also experienced diminished cover of competing understory algae (Figures 6 and 7) suggesting that the lack of recovery at the deeper sites is likely due to decreased reproductive capacity of *M. pyrifera* (Figure 8) prior to the mass mortality of giant kelp during the El Niño of 2016. Limited recovery at the deeper sites during this period could also be partly due to decreased light levels reducing rates of kelp germination. Light penetration data are not available. Reproductive capacities of giant kelp at all of the central Point Loma sites are presently at historic lows suggesting that recoveries from the two warm events between 2014–2017 are less

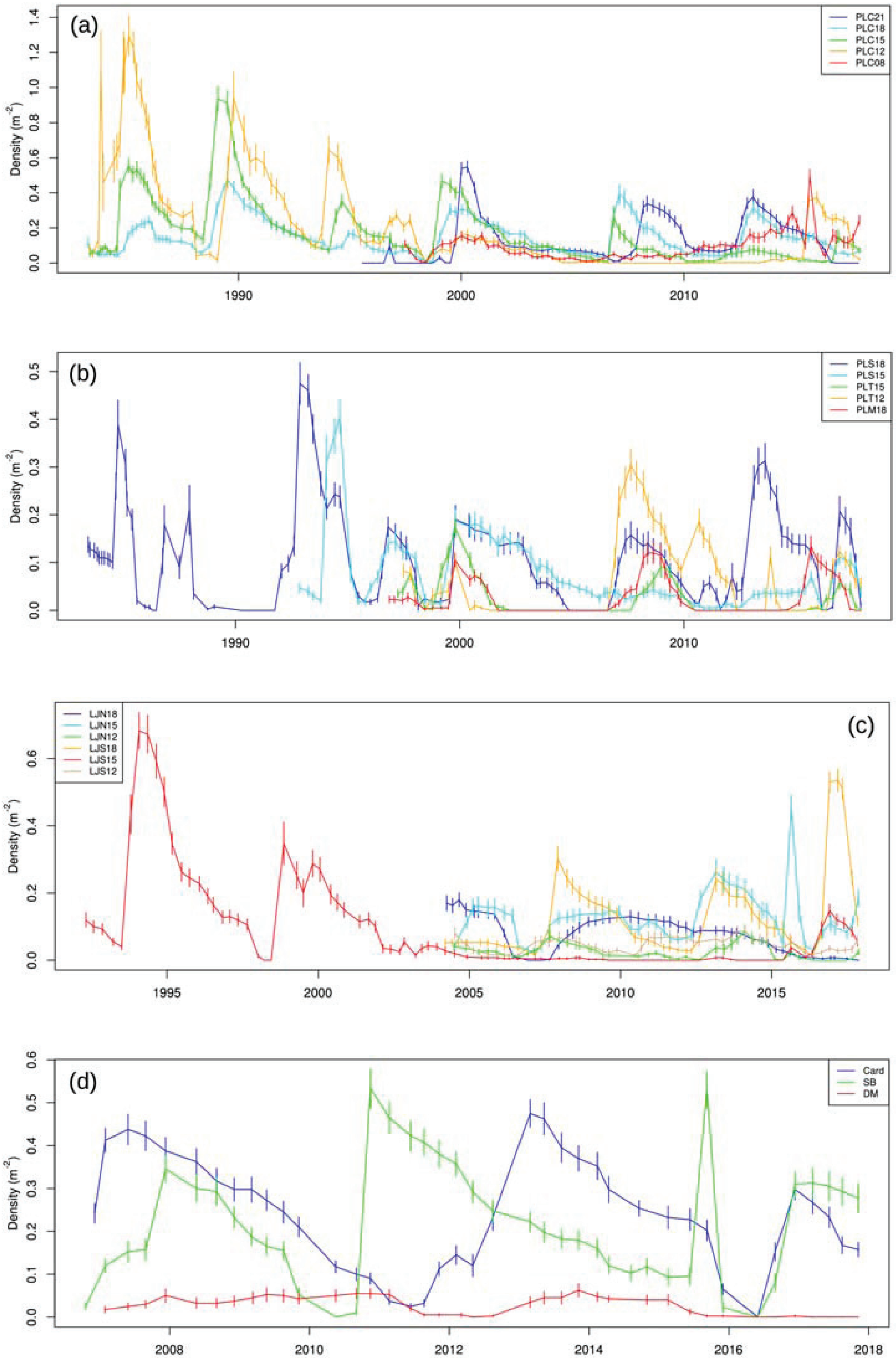


Figure 4

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

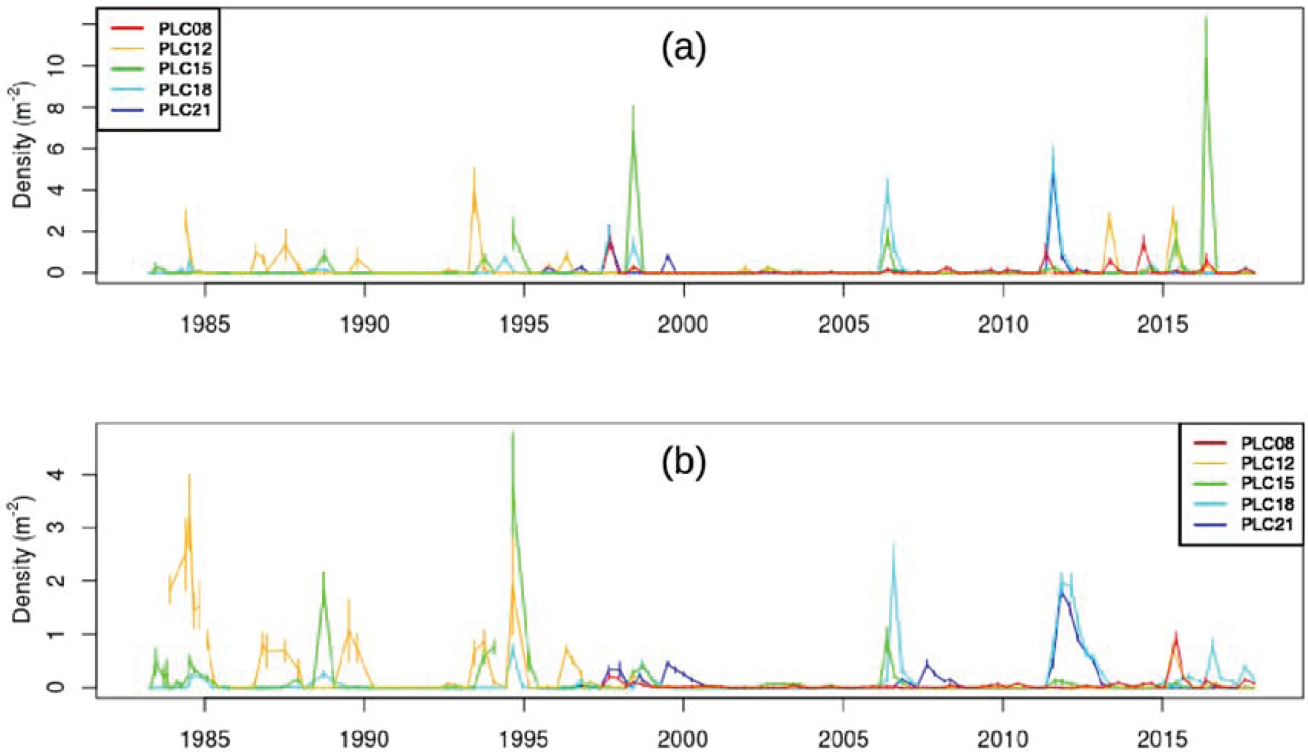


Figure 5
Mean densities of *Macrocystis pyrifera* recruit stages: (a) pre-bifurcate stage, (b) bifurcate stage. Error bars indicate standard errors.

supported by reproductive output than at any other time since the 1980's. Therefore, rapid increases in giant kelp density will likely be muted this spring (2018) and may not follow the rapid post-El Niño patterns observed in the past.

Understory Kelps

Understory kelps, *Pterygophora californica* and *Laminaria farlowii*, were affected differentially by the consecutive warm periods. The main effects of the warm periods on *P. californica* were exemplified by two groups of sites (Figure 6). The first group included sites where densities decreased dramatically with the BLOB and remained low during and after the 2016 El Niño (i.e., 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 (i.e., PLC15, LJS18, LJS15). Densities of *P. californica* at the North County sites have been persistently low and remain low at present. The response of *L. farlowii* to the warm periods was more variable among sites. Three types of responses were observed. First, previously high fractional cover at many sites quickly decreased during the BLOB with subsequent increases during the 2016 El Niño (e.g., PLC15, LJS18, and LJS15). Relatively high fractional cover at other sites decreased due to the BLOB and remained reduced through the 2016 El Niño to the present. These mainly include the sites in La Jolla and Del Mar. The third response occurred at PLS15 where fractional cover was increasing prior to the BLOB when it decreased slightly followed by a rapid increase during and after the 2016 El Niño.

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

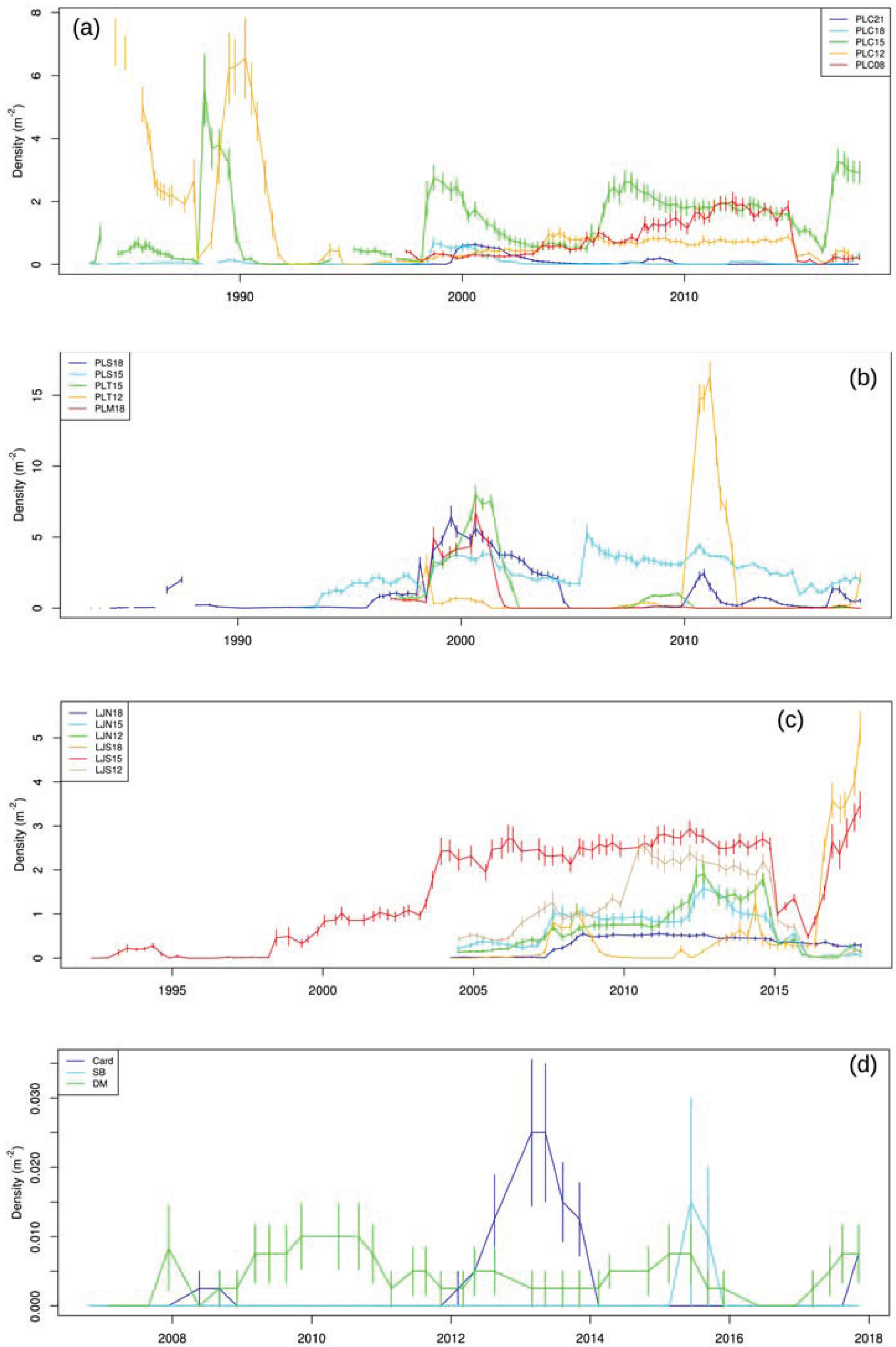


Figure 6

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

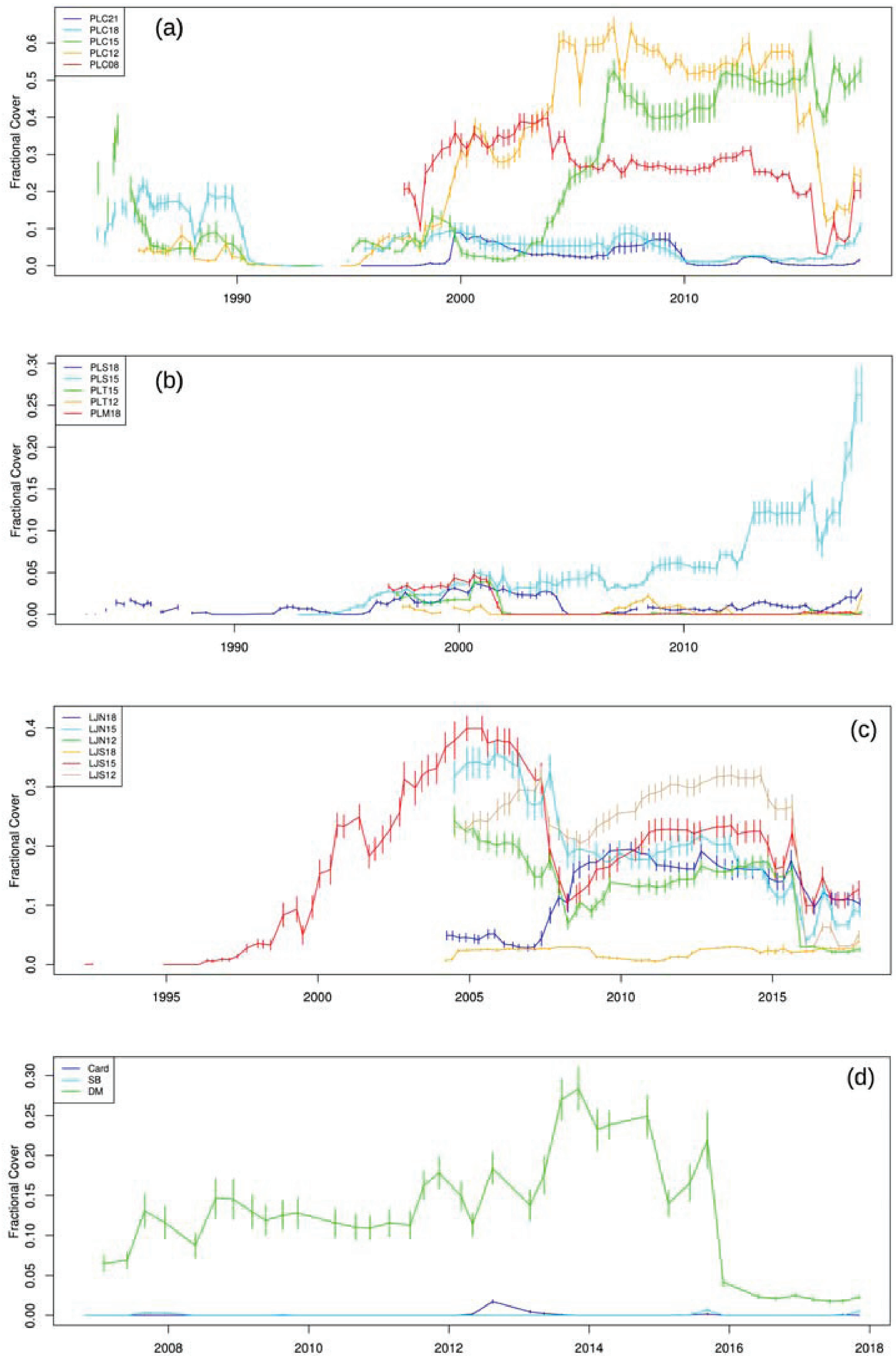


Figure 7

Mean fractional cover of the understory kelp *Laminaria farlowii*: (a) central Point Loma, (b) south Point Loma, (c) La Jolla, and (d) North County. Error bars indicate standard errors.

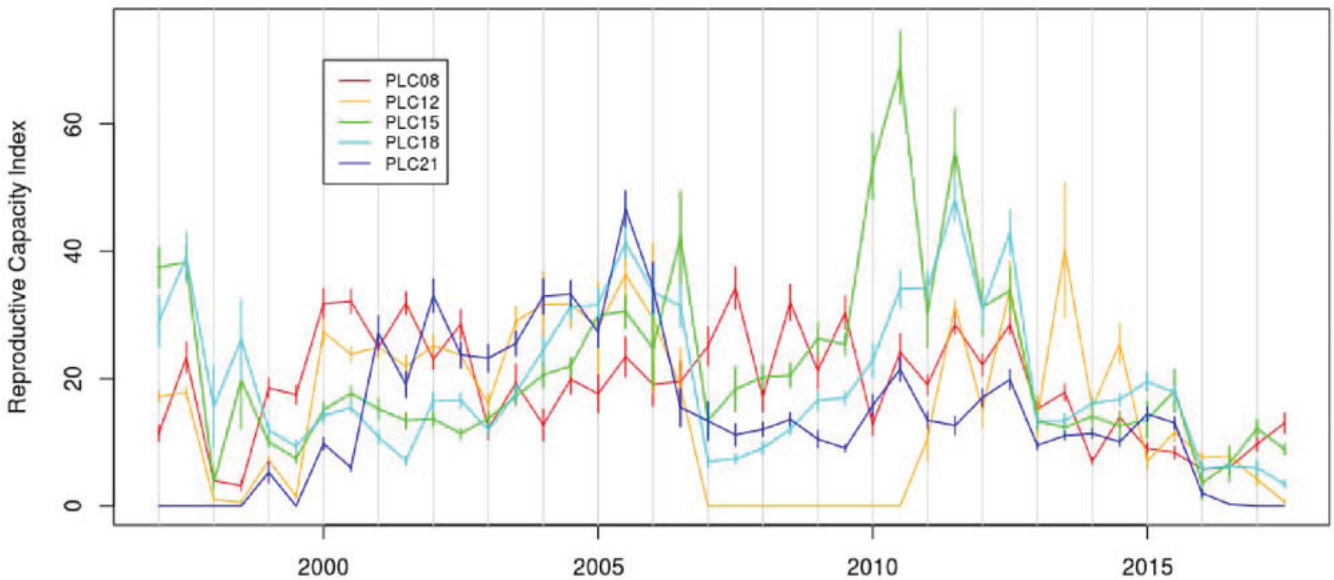


Figure 8

Mean reproductive capacity (see text for derivation details) of *Macrocystis pyrifera* at the central Point Loma study sites.

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 (Figure 3). 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 understory kelps was reduced during the BLOB and increased afterward, though both growth and reproduction of *P. californica* is still depressed at the deeper central Point Loma sites (Figures 9 and 10). 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 states that we currently observe. Such forcing can lead to a hysteresis that can persist for several years until the occurrence of a new major disturbance.

Algal states among all of the study sites for 2016 and 2017 are shown in Figures 11 and 12, respectively. The first two factors resulting from the factor analysis of all algal data represent >82% of the overall variance and therefore are a good representation of the data. Factor 1 indicates a continuum of understory and turf states from bare ground to lush turf algae 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 or young recruits and pre-adults (<4 stipes). The 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 between the two years towards more abundant understory canopy and turf species. For example, *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. *Agarum 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.

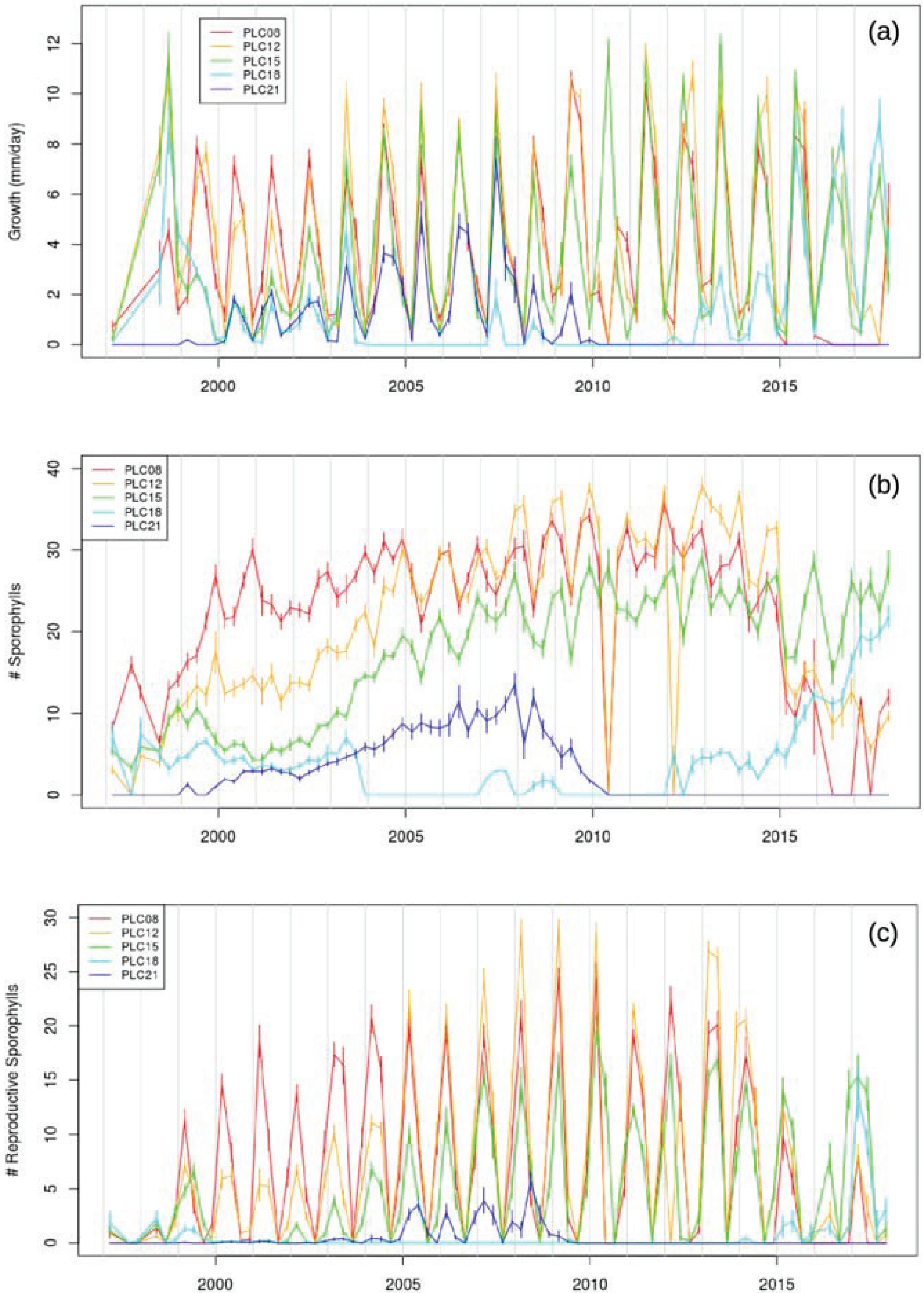


Figure 9

Time series of (a) mean growth, (b) mean sporophyll count, and (c) mean count of reproductive sporophylls for the understory kelp *Pterygophora californica*. Error bars indicate standard errors.

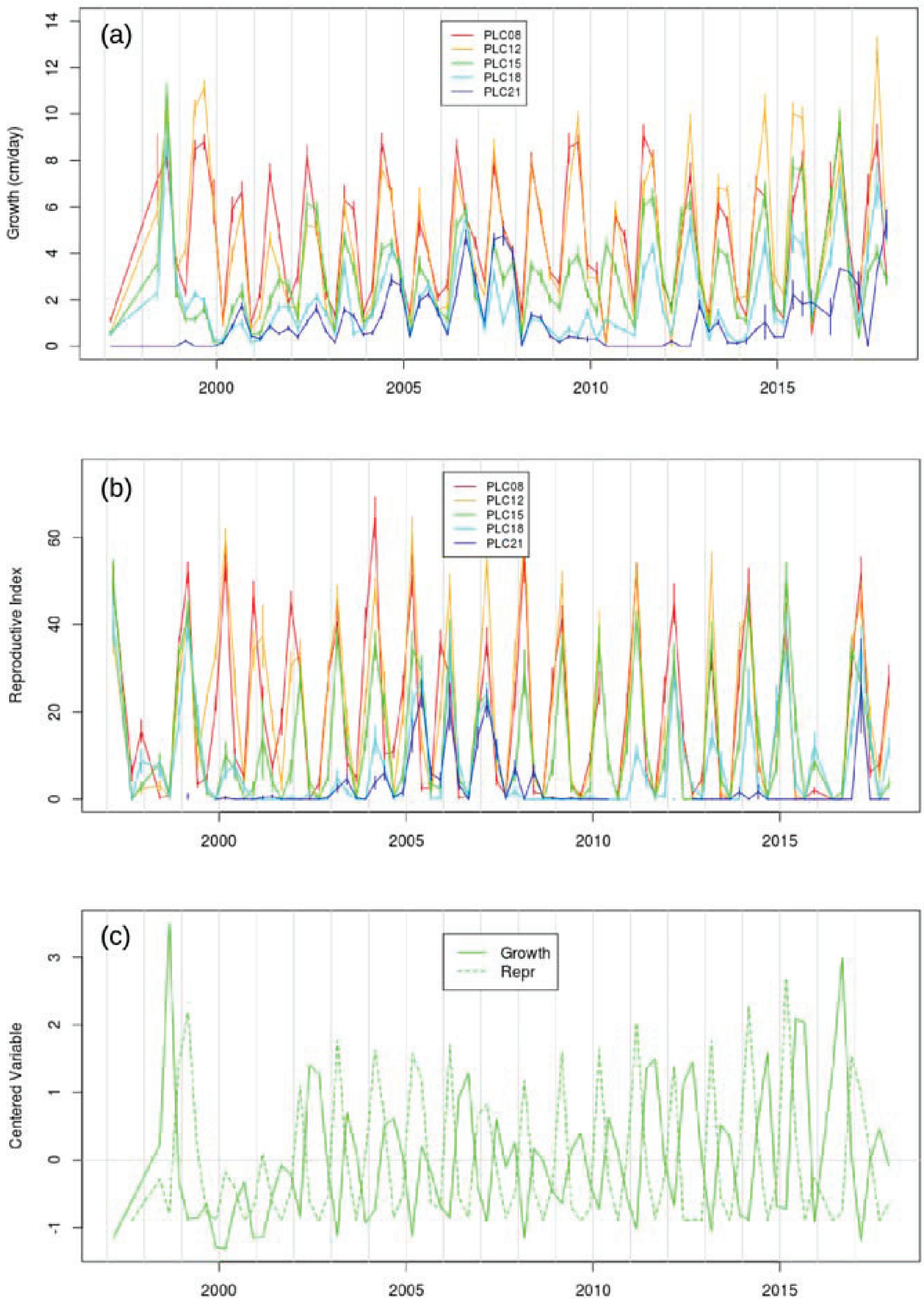


Figure 10
Mean growth (a) and reproductive index (b) of *Laminaria farlowii*, and (c) centered growth and reproduction of *L. farlowii* at the PLC15 study site showing relative seasonal phasing of growth and reproduction.

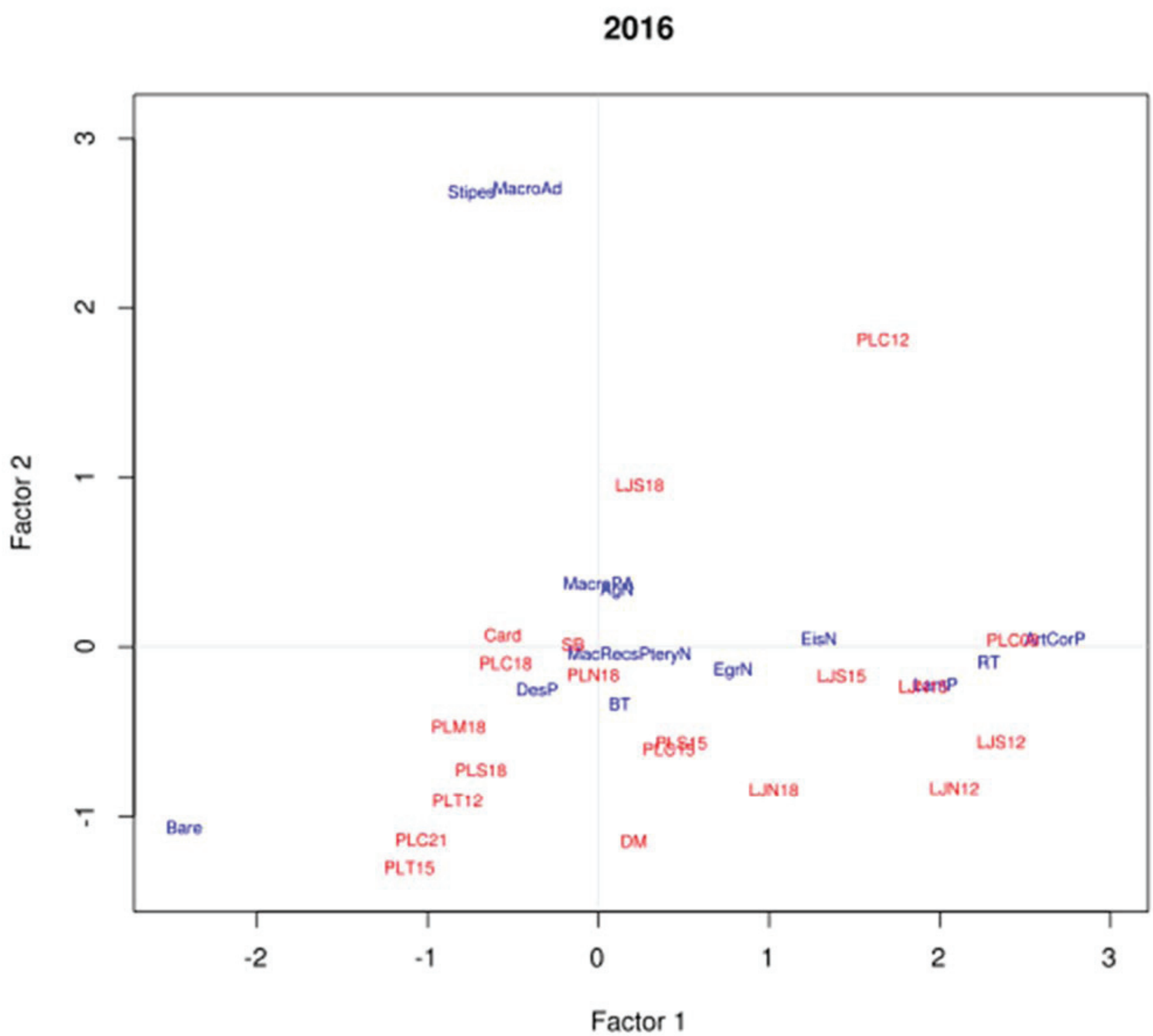


Figure 11
Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2016. Algal group definitions: Bare = derived bare space, MacRecs = *M. pyrifera* recruit stage (pre-bifurcates + bifurcates), MacroAd = *M. pyrifera* adult density, Stipes = *M. 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.

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. *Sargassum horneri* dominates some areas formerly dominated by *M. pyrifera* including areas off Santa Catalina Island and the Northern Channel Islands off Santa Barbara. This species was first observed in the kelp forests off San Diego in 2014 and has spread slowly, first observed near study sites and subsequently established onto the permanent band transects at several of the study sites. The greatest percent cover observed thus far was at LJN18 in the fall of 2017 when mean percent cover approached 30%. This species has also been observed on the permanent transects at (in order of decreasing percent cover) PLC18, PLC08, LJS12, LJN15, and PLN18.

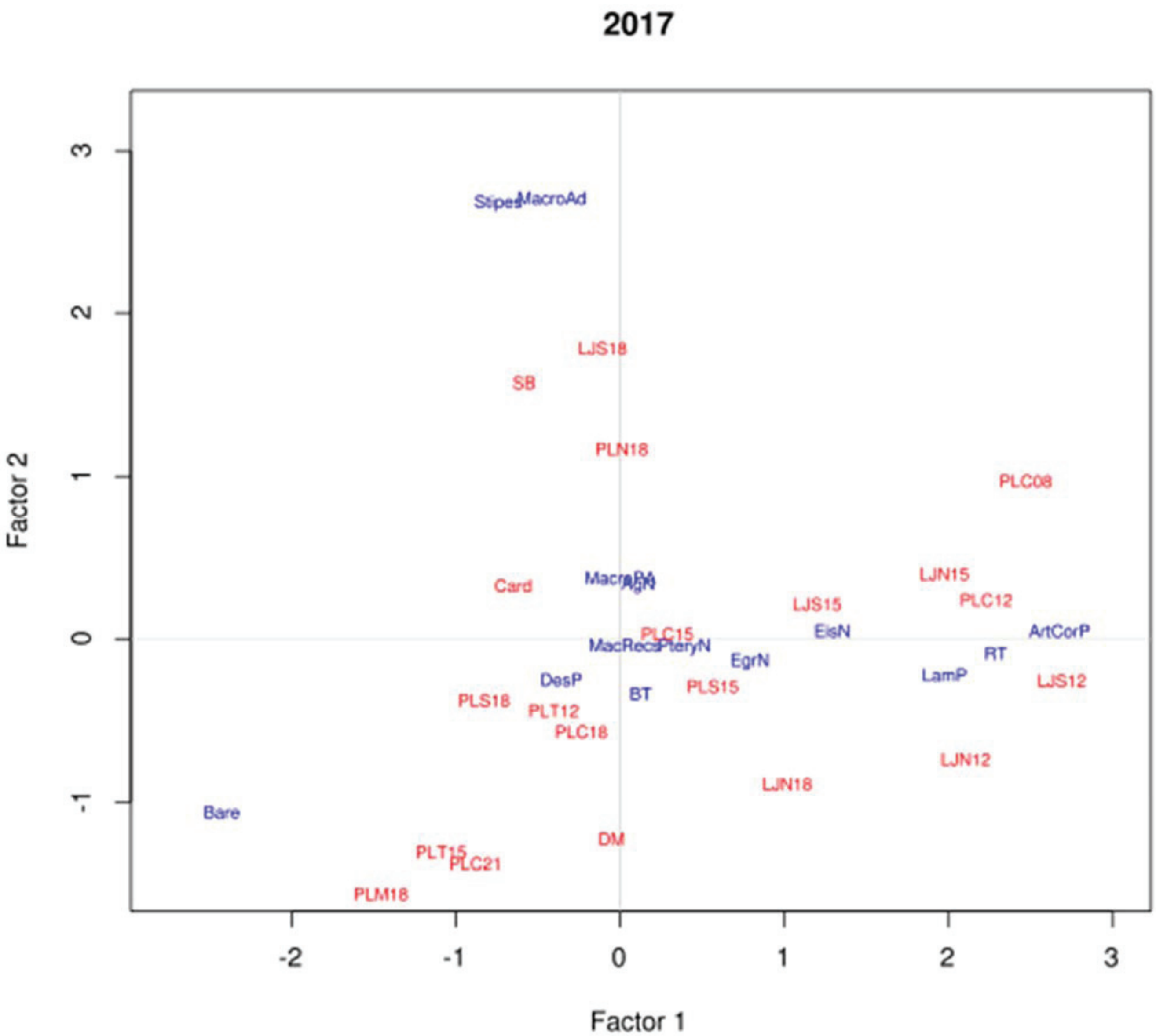
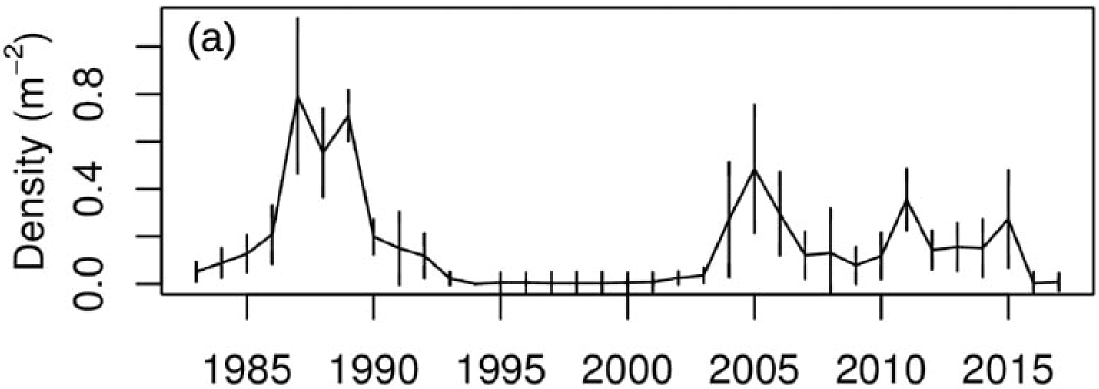


Figure 12
Plot of first two factors resulting from the factor analysis of algal groups among the 20 permanent study sites in 2017. See Fig. 11 caption for definitions of algal groups.

Sargassum 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 San Diego kelp forests especially after a future major disturbance that reduces the densities and cover of native algal species.

Invertebrates

Densities of both red and purple sea urchins (RSU and PSU, respectively) either crashed in response to the consecutive warm periods or were already at or near zero. Sea urchin densities are shown in Figures 13 and 14 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 Point Loma where sea urchin overgrazing has been historically resilient (Parnell 2015). Additionally, sea urchin recruitment was absent or extremely limited at all



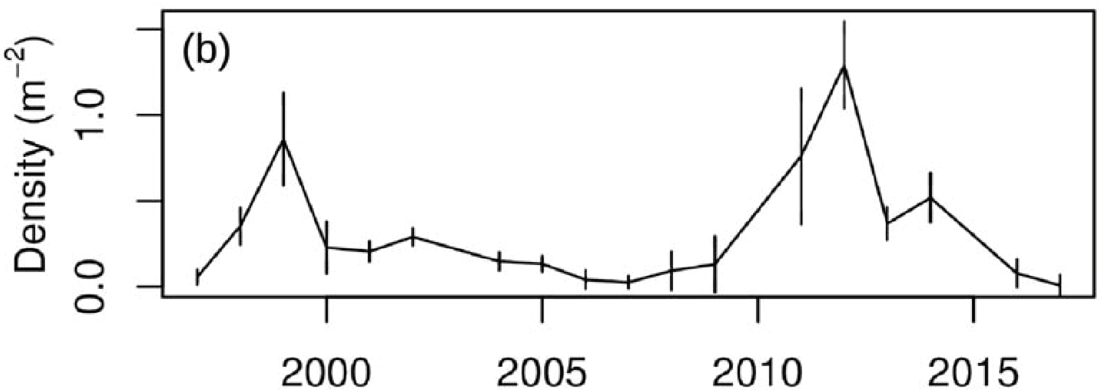


Figure 13
Time series of red sea urchin (*Mesocentrotus franciscanus*) densities at the (a) PLS18, and (b) PLT12 study sites. Error bars indicate standard errors.

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 2). The largest increases were observed mainly at the southern Point Loma sites, and all sites off La Jolla with the exception of LJS18. Recruitment of RSU was strong at the outer central Point Loma stations (PLC18 and PLC21). Sea urchins are not likely to have any significant effects on kelp recovery in 2018 due to their reduced abundance and delayed recruitment. However, the fall 2017 recruit cohort may result in overgrazing at some sites as they mature and migrate away from sheltering juvenile habitat and actively forage over larger areas. Sea urchin overgrazing may occur at some sites by 2019 as the fall 2017 cohort matures and begins to actively forage over broader areas.

Diseases affecting echinoderms has 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* and *P. brevispinus* (Figure 15) 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* were observed recruiting onto giant kelp plants off Point Loma as early as 2017, 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 Point Loma since 2014 even in areas where they

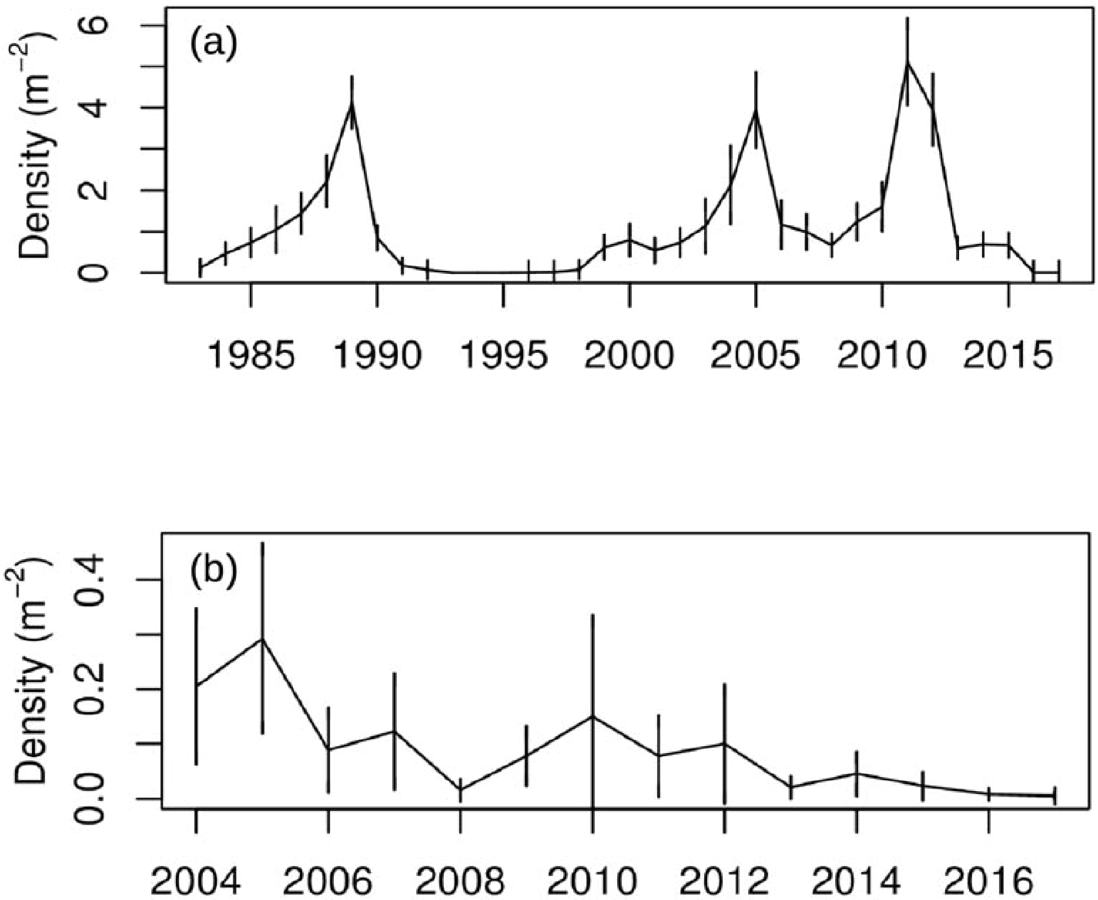


Figure 14
Time series of purple sea urchins (*Strongylocentrotus purpuratus*) at (a) PLS18, (b) LJN12, and (c) Cardiff study sites. Error bars indicate standard errors.

were once common. *P. helianthodes* was in gradual decline even prior to the BLOB event.

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 Point Loma crashed in the 1980's (Tegner and Dayton 1987). However, *H. rufescens* persisted in low numbers near PLS18 and LJS18. Those few individuals were lost during the recent prolonged warm periods. At the same time, densities of pink abalone (*H. corrugata*) have been steadily increasing at PLC08 since 2012 (mean density in 2017 = 0.12 m^2), exhibiting steady population increases throughout the warm period.

Sedimentation among North County Kelp Forests

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

Table 2

Recruitment rates for red and purple sea urchins (*M. franciscanus* and *S. purpuratus*, respectively) during the fall of 2017. 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).

Site	*Mesocentrotus franciscanus*	*Strongylocentrotus purpuratus*
LJN18	17.31	15.84
LJN15	33.32	54.84
LJN12	64.7	91.49
LJS18	4.85	1.94
LJS15	17.65	14.17
LJS12	50.00	15.38
PLN18	15.84	7.94
PLC21	28.92	8.99
PLC18	32.69	9.57
PLC15	6.19	4
PLC12	*	19.42
PLC08	*	45.35
PLS18	48.25	37.9
PLS15	18.75	16.49
PLM18	2.73	8.89
PLT12	57.14	57.43
PLT15	69.33	71.60

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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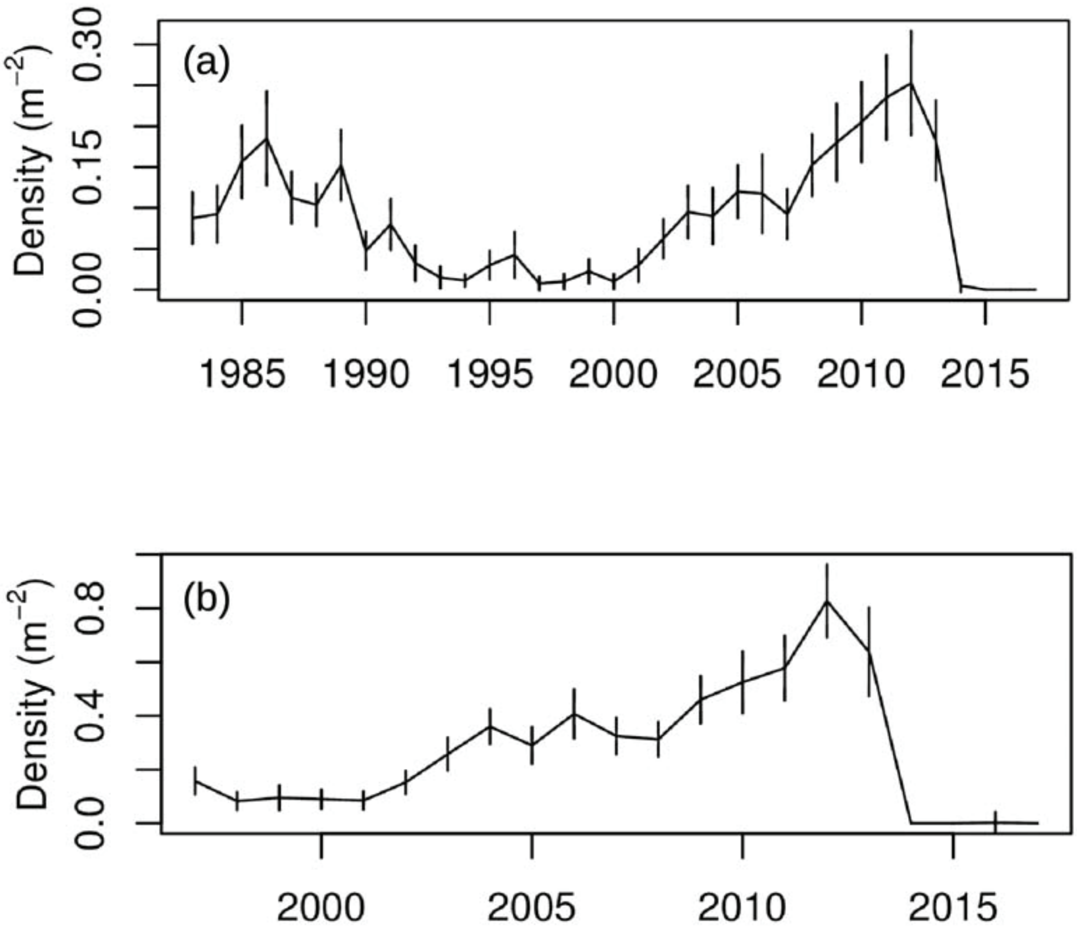

Figure 15
Time series of seastar density (*Pisaster giganteus* and *P. brevispinus* combined) at (a) PLS18 and (b) PLT15 study sites. Error bars indicate standard errors.

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