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Searching for multidecadal change in the San Diego rocky intertidal

A Thesis submitted in partial satisfaction of the requirements for the degree of

Master of Science

in

Biology

by

Christina Bonsell

Committee in charge:

Professor Paul Dayton, Chair  
Professor Elsa Cleland, Co-Chair  
Professor Jonathan Shurin

2013

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The Thesis of Christina Bonsell is approved and it is acceptable in quality and form for publication on microfilm and electronically:

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2013

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ABSTRACT OF THE THESIS

Searching for multidecadal change in the San Diego rocky intertidal

by

Christina Bonsell

Master of Science in Biology

University of California, San Diego, 2013

Professor Paul K. Dayton, Chair

Professor Elsa E. Cleland, Co-Chair

Determining the ecological impacts of long-term change versus those caused by shorter-term variation is important for making predictions and managing ecosystems. Historical surveys offer potentially valuable baseline data for the evaluation of long-term change. This study is based on two historical ecological surveys at two rocky

intertidal sites (Dike Rock and Ocean Beach) in San Diego, California. The historical surveys are notable in that they overlap with or predate a major oceanographic climate shift in Southern California in the late 1970s. Although the 2012 surveys showed that the invertebrate communities at both sites had changed since the historical surveys, the changes were dissimilar. While both sites lost and gained a few invertebrate species, notably losing the predatory whelk *Nucella emarginata* and gaining another in *Mexacanthina lugubris*, species abundances at Dike Rock increased while those at Ocean Beach decreased. This may be due to the different substrates at the sites: the sandstone of Ocean Beach may have been more impacted by a changing wave climate than the basalt of Dike Rock. Data on the percent cover of macroalgae at Ocean Beach demonstrated changes in seven out of ten morphological groups. However, the lack of dramatic changes overall indicates the resilience of rocky intertidal communities to human impacts and the effects of climate change.

## **Introduction**

Episodic events often structure ecosystems for long periods and occur across multiple time scales. In the Northeast Pacific, modes of variability in climatic forcing influence the long-term temporal patterns seen in both coastal benthic and pelagic communities. In the California Current Ecosystem, El Niño Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and North Pacific Gyre Oscillation (NPGO) influence larval recruitment to the intertidal zone (Menge et al. 2011). In the rocky intertidal, the temporal dynamics of certain algal species can also be indirectly related to ENSO (e.g. Gunnill 1985, Vinueza et al. 2006). Furthermore, these communities are also influenced by seasonal storms and sand inundation (Littler et al. 1983). The characteristics and causes of long-term variability in intertidal communities can only be fully understood through long-term ecological study.

Overlying these cyclical climate variations are the long term trends due to anthropogenic climate change. Studies of rocky intertidal communities are revealing shifts that may be instigated by these changes. Barry et al. (1995), when replicating a sixty year old rocky intertidal community survey in Central California, found changes in faunal abundance that correlated with increased sea surface temperatures: southern species increased and northern species decreased in abundance. Climate-driven community changes are not always so clear-cut. Increased temperatures, sea level rise, ocean acidification are all expected to affect coastal marine organisms, but in unequal ways depending on their life history (Hurley et al. 2006). These complexities can obscure attempts to make predictions about ecosystems for management purposes. Furthermore, ecological forecasting using climate models necessitates in-depth understanding of how

climate affects physiology and species interactions at a variety of scales (Helmuth et al. 2006). Trend prediction and ecosystem management are therefore limited for natural systems without the support of observations over decadal timescales. Current monitoring programs can be effectively bolstered by historical data that provides context for the variability inherent in such studies.

Long-term monitoring of multiple climatic and biological variables revealed that a "step-like" climate regime shift occurred in 1976 (Ebbesmeyer et al. 1991). This affected many biological aspects of the coastal marine environment in the Southern California Bight (e.g. Roemmich and McGowan 1995, Tegner et al. 1996). However, there is little published information on how it affected intertidal communities. Parnell et al. (2010) report that the climate shift impacted nutrient dynamics, and thus the kelp community, immediately adjacent to the intertidal community studied for this paper. The shift in nutrient regime and wave climate (Seymour 1996) may also have affected the intertidal community.

Ecological monitoring over a long time period is the ideal means of investigating the effects of climate change. However, such data are rare and in most cases we are lucky to have even a crude baseline study to evaluate temporal change. Thus, ecologists have sought early baseline data, however crude, often relying on old photographs as the only measure of early baselines. These types of "historical science" (sensu Francis and Hare 1994) use current and past observations to evaluate hypotheses about possible change. Historical surveys have often proven extremely valuable in evaluating ecological community changes over time (e.g. Barry et al. 1995, Gibbs et al. 2005, Moritz et al. 2008). In these situations, the main conclusions suggest range shifts related to long-term

temperature increases in both marine (Barry et al. 1995) and terrestrial fauna (Moritz et al. 2008), and localized extirpations due to land use change (Kelly et al. 2005). These surveys demonstrate the importance of historical baseline data in interpreting current ecological patterns.

The population of San Diego County has increased by 128% since 1970 (U.S. Bureau of the Census 2010). The San Diego Association of Governments projects a further 48% growth in population from 2000 to 2050 (sandag.org). As the pressures from anthropogenic coastal impact and climate change increasingly influence marine systems, it is important to assess the changes of those systems by comparing past and present data. This thesis seeks to compare two sets of historical surveys of rocky intertidal communities in San Diego County with modern surveys, as well as create a baseline for future studies. These historical surveys either precede or overlap with the 1970s regime shift, therefore providing an opportunity for historical comparisons to draw inferences about long term change in the face of multidecadal variation. The first set of surveys used in this study came from Scripps Institution of Oceanography (SIO) graduate students, led by Professor E.W. Fager, in 1961 and 1963. The students examined the intertidal invertebrate community found on Dike Rock, a large boulder in a small strand of rocky shore just north of the SIO pier (Fig. 1A-B). The data and associated reports from these trips eventually found their way into the Fager archives at the SIO Library. Although the focus of the exercise was to demonstrate how physical factors affect rocky intertidal community composition, the data collected by the class offers a baseline of the state of that community at that time. This site is now part of the Scripps Coastal Reserve, part of the University of California Natural Reserve System. The second set of surveys began in

1975 when the Bureau of Land Management (BLM; now the Bureau of Ocean Energy Management) commissioned a survey of the biotic communities of the California coast "to determine ambient, pre-oil development conditions" as part of the Outer Continental Shelf Research Program (Callahan and Shokes 1977). Intertidal surveys were conducted at ten sites along the mainland coast of the Southern California Bight and four of the Channel Islands, investigating the invertebrate and algal communities from 1975 to 1978. The only site in San Diego County is located in Ocean Beach, south of the Ocean Beach pier (Fig. 1A,C).

Here I compare these historical surveys to current surveys to test the null hypothesis that both sites show no effect of time on the composition of these communities. Specifically, the null hypotheses are: 1) no change in species composition at either site over time; 2) no change in abundances of each species at either site over time; 3) The two sites will have the same direction of change in species composition and/or abundances, if hypotheses 1 and/or 2 are false. If long term trends were affecting these assemblages, I should expect to observe changes in abundances of certain species, and maybe even extirpations. I could also see the appearance of new species, driven by range expansions. These two sites are very different in terms of their physical characteristics, so I also wanted to see if the communities at each site responded similarly to large scale changes.

## **Methods**

### Historical Surveys

*Dike Rock:*

Dike Rock is a large basalt boulder, part of the large Scripps Reef rocky intertidal area located in what is now Scripps Coastal Reserve in La Jolla, California (Fig. 1B). The intertidal community was studied as part of a class exercise in March of 1961 and 1963 for the Marine Ecology graduate class at Scripps Institution of Oceanography, taught by E.W. Fager. Students determined community composition along many transects across the rock using 10x10 cm and 5x5 cm quadrats. Much of the transect area has a vertical, cross-shore orientation. This thesis only examines the data from transects that were oriented cross shore as surveys with this orientation were the most numerous. The Fager class's data were not collected uniformly from transect to transect (Table 1).

*Ocean Beach:*

The BLM surveys were located on a shoreline of sloping sandstone in Ocean Beach, San Diego, California (Fig. 1C). In the upper intertidal, the sandstone levels out into a broad shelf, below which the habitat is sloped and cut by terraces and shallow water channels, pockmarked with homescars from chitons and limpets. These conditions make the sandstone in the area, which is rather soft, quite friable. At mid low-low water (MLLW) the slope levels out again to a shelf covered by fleshy red algae and surf grass, with a few scattered deep pools. The low intertidal shelf at this location is 2-4 m wide and drops off into deeper water. The high intertidal shelf lies below a sloping cliff.

Two transects, 4 m apart and following 312° NNW, were laid out from where the slope leveled out at high intertidal to where it leveled out at low intertidal. A total of thirty-nine 0.15 m<sup>2</sup> quadrats were placed along the transects "at regular intervals", nineteen on the south transect and twenty on the north transect. Species densities were

quantified in the field. Photographs of each quadrat were taken and analyzed later for percent cover of flora and fauna using point intercept of 1,176 regularly spaced points projected over the photo (Littler 1978).

Data were collected from September 1975 to April 1978 in the months of February, April, September, and November. The reports were separated into four main time groups: 1975-1976, 1976-1977, 1977-1978, and April 1978. The data reported in the main volumes of the final reports consisted of mean density and mean percent cover of flora and fauna for the entire study area. The 1977-1978 appendix, which contains mean densities and percent cover of all species sampled by tidal height in table format (therefore providing actual numbers for the data), was the only appendix from the intertidal surveys that could be located and is the source of the historical data for Ocean Beach used in the present study. The sampling dates in the appendix are October 1977, November 1977, February 1978, and April 1978. No variance or estimate thereof accompanied the reported means.

The BLM collected percent cover data that included mobile and active species. Because these species move to avoid desiccation or high temperatures, the percent cover data for mobile species do not have much ecological significance. Thus, I only examined changes in percent cover for barnacles, mussels, anemones and urchins.

## 2012 Surveys

### *Dike Rock:*

The quadrats used by Fager's class were far too small to sample more rare species, so I used 0.25 m<sup>2</sup> square quadrats that reflect most surveys that sample intertidal species



of varying densities (Murray et al. 2002). I quantified invertebrates every meter along four transects that followed transects 1-4 used by Dr. Fager's class (Table 1). The two northernmost transects were surveyed on November 27, 2012. The southernmost transect was surveyed on December 11, 2012. The remaining transect was surveyed December 12, 2012. At each quadrat, I quantified invertebrates without moving aside any algae that were present (following the protocol of the Littler Ocean Beach surveys), and took a photograph using a Panasonic Luminix TS20 16.1 MP digital camera. All invertebrates easily distinguishable to the naked eye were counted in the field, excluding crabs and worms, for which only presence was recorded. I identified invertebrate species using The Light and Smith Manual to Intertidal Invertebrates, Central California to Oregon (Carlton 2007), and online photos from D. Eernisse (biology.fullerton.edu) and J. Watanabe (seanet.stanford.edu). I lumped all *Littorina spp.* together to preclude misidentification and to expedite field counts. I marked limpets that were too small to identify with certainty as 'Juvenile *Lottia*'.

#### *Ocean Beach:*

I placed two transects along approximately the same lines used in the BLM surveys, located using the BLM map and photos from the site. The north transect was surveyed on November 12, 2012; the south transect was surveyed on November 13, 2012. I placed 0.25 m<sup>2</sup> quadrats every meter, with 28 quadrates per transect. I quantified invertebrates, as described above, and photographed each quadrat for later percent cover analysis. I later analyzed these for percent cover using Coral Point Count with Excel extensions using 225 stratified random points (CPCE; Kohler and Gill 2006). The

historical surveys at this site also recorded percent cover by algal species, so I analyzed percent cover of surf grass and algae groups using CPCE. . The sandcastle worm *Phragmatopoma californica* was included in the percent cover analysis, along with barnacle species, mussel species, and *Strongylocentrotus purpuratus* that are relatively immobile. I identified algae and plants based on gross morphology: articulated coralline (ACA), other brown (BRWN), non-coralline crust (CRST), crustose coralline (CCA), non-crustose *Scytosiphonaceae* (ENDR), filamentous (FILA), other green (GRN), other red (RED), and *Phyllospadix* (PHYL).

### Statistical analysis

I normalized all abundance data to number per 1 m<sup>2</sup>. These data did not meet assumptions of homogeneity of variance, even when transformed, so to compare community data from the different sampling dates, I used permutational multivariate analysis of variance (PERMANOVA). I compared historical invertebrate abundances to the 2012 Dike Rock data via two-sample permutation tests (replicates=1000,  $\alpha=0.05$ ). I calculated 95% confidence intervals for the 1977-1978 mean invertebrate abundances of invertebrates at OB using maximum likelihood estimates of variance to estimate the underlying distribution of the data. In calculating this, the normalized means per tidal height data were weighted per the number of quadrats surveyed at that height. The same was done with the historical percent cover data for sessile invertebrates and macroalgae at Ocean Beach. I performed analyses using R version 3.0.1 (R Core Team 2013).

## **Results**

The historical Dike Rock and Ocean Beach data show communities at the two sites differed (Fig. 2; PERMANOVA,  $df = 1$ , pseudo  $F = 11.329$ ,  $p < 0.05$ ). In general, limpet species were more abundant at Ocean Beach while barnacle species were more abundant at Dike Rock.

### Dike Rock

Invertebrate communities from the 1961 and 1963 surveys were not significantly different (PERMANOVA,  $df = 1$ , pseudo  $F = 1.9615$ ,  $p > 0.05$ ). These communities were consequentially lumped and compared to the 2012 survey data. The community at Dike Rock during the Fager study was significantly different from the one during the 2012 survey (PERMANOVA,  $df = 1$ , pseudo  $F = 1.6336$ ,  $p < 0.05$ ).

Presence and absence data from Dike Rock show that species composition has not changed very much in the past 50 years (Table 2). Species that appeared in the 1960s that did not appear in 2012 were: *Megabalanus californicus*, *Mopalia mucosa*, *Pegurus samuelis*, and *Tegula funebris*. Species that appeared in 2012 that did not appear in the 1960s were: *Acanthinucella spirata*, *Lottia scabra*, *Mexacanthina lugubris*, *Pisaster ochraceus*, and *Tegula eiseni*. However, *L. scabra* and *L. conus* are notoriously difficult to tell apart, and probably were lumped by Fager's class. For consistency, I lumped these species for comparison of abundances at Dike Rock.

Mean densities of the majority of invertebrates from Dike Rock, along with  $p$ -values from the two way permutation tests, are presented in Table 3. All species with significant changes at Dike Rock represented increased abundances. The anemone *Anthropleura elegantissima* has increased in the area, as has the small mussel *Septifer*

*bifurcatus* and several *Lottia* limpets. Other conspicuous and important species that have increased over the last half a decade include two *Mytilus* species and the large barnacle *Tetraclita squamosa*.

### Ocean Beach

The results from the October 1977, November 1977, February 1978, and April 1978 surveys were not significantly different from each other in invertebrate density (PERMANOVA,  $df = 3$ , pseudo  $F = 1.2371$ ,  $p > 0.05$ ), sessile invertebrate percent cover (PERMANOVA,  $df = 3$ , pseudo  $F = 0.96457$ ,  $p > 0.05$ ), or macroalgae percent cover (PERMANOVA,  $df = 3$ , pseudo  $F = 1.0431$ ,  $p > 0.05$ ). When lumped, the historical data are significantly different from the 2012 survey data in terms of invertebrate density (PERMANOVA,  $df = 1$ , pseudo  $F = 7.9321$ ,  $p < 0.05$ ), sessile invertebrate percent cover (PERMANOVA,  $df = 1$ , pseudo  $F = 5.319$ ,  $p < 0.05$ ), and macroalgae percent cover (PERMANOVA,  $df = 1$ , pseudo  $F = 3.3509$ ,  $p < 0.05$ ).

Presence/ absence data for Ocean Beach of the species shows the appearance (2 out of 34) and disappearance (9 out of 34) of 11 out of 34 species (Table 2). Some of the species not present in the 2012 survey were only found in one or two survey dates from 1975-1978: *Aplysia californica*, *Pugettia producta*, and *Tegula funebris*.

The differences in mean abundance per species between the 2012 data (plotted with 95% confidence intervals) and the 1978-1979 data (plotted with maximum likelihood estimates of the 95% confidence intervals) are plotted in Figure 3. This plot shows a reduction in the *Lottia* population (except for *Lottia gigantea*), and as well as in mussels (*Septifer bifurcatus*, *Mytilus galloprovincialis* and *Mytilus californianus*), gooseneck

barnacles (*Pollicipes polymerus*), keyhole limpets (*Fissurella volcano*), species of chitons (*Cyanoplex hartwegii* and *Nuttalina fluxa*), and the purple sea urchin (*Strongylocentrotus purpuratus*). In fact, unlike at Dike Rock, all of the significant changes represent decreased densities.

Changes in percent cover of largely non-motile species can be seen in Figure 4. As with the abundance data, no statistical tests can be conducted with the original data to compare densities of individual species between the time periods, but some species exhibit obvious density differences. In particular, the data show a marked crash in *Phragmatopoma californica* cover. Large patches of *P. californica* were visible on the seaward vertical face of the lowest sandstone terrace, but this area was not surveyed by either study. *Pollicipes polymerus* has also decreased. This species, which is often found in large aggregations, was only present in small groups of a handful of individuals, or with a few individuals interspersed in a patch of mussels.

The plot of macroalgae percent cover with 95% confidence intervals shows that brown algae has increased, while non-coralline crusts, crustose corallines, non-crustose *Scytosiphonaceae*, and filamentous algae have decreased in percent cover (Fig. 5).

## **Discussion**

The goal of this study was to determine if these communities had changed over time and if these changes might reflect the massive oceanographic changes that have occurred between the original surveys and this survey. I evaluated the null hypothesis that the changes to oceanographic climate that affected San Diego kelp forests (Tegner et al. 1996, Parnell et al. 2010) did not affect the adjacent intertidal community. While Barry et

al. (1995) demonstrated faunal changes correlated with increased sea temperature in Northern California, I did not observe such dramatic changes at both of the sites I studied, although there were some similar findings. These studies are not necessarily directly comparable, as the "northern species", as defined by Barry et al. (1995), did not have a defined range south of Point Conception. A few species disappeared altogether, but in the case of Ocean Beach where we have reliable early data, the abundances of many species have simply declined, though sometimes sharply. At Dike Rock, where the historical data are less reliable, only a few species changed in abundance, all of which were increases. The multidecadal scale of this study and the changes observed indicate long term changes to this community regardless of seasonality.

*Phragmatopoma californica*, whose population over time was only comparable at Ocean Beach, decreased in percent cover over the past forty years. This species reproduces during periods of high wave action, making it relatively resilient in highly disturbed areas (Barry 1989). However, this species also experiences high mortality during these events. With the increased frequency of large wave events after the regime shift (Seymour 1996), it may be that *P. californica* populations were hit too hard and too often for recruitment to keep populations constant.

Some of the other changes in species composition might be real shifts in distribution. These include *Megabalanus californicus*, a cold water species that was found at both Dike Rock and Ocean Beach in the historical surveys, but not found in 2012, so it is likely that its absence today is real. *Mexacanthina lugubris*, a southern species of carnivorous whelk, has expanded its range into southern California at least twice in the past 100 years (Radwin 1974, Hertz 1995). Its first recorded range expansion

was noted in 1974, when it was found at the Cabrillo National Monument, and although the author reported it had been collected in San Diego as late as the 1930s, it had not been found since (Radwin 1974). There were no other reported sightings until 1994, when it was found at Cabrillo National Monument and Ocean Beach (Hertz 1995). By the early 2000s, it had expanded to Dike Rock. This latest expansion northward coincided with a retraction by *Nucella emarginata* from its southern range (B. Pister, personal communication). These predatory whelk species are of similar size and have similar prey, thus the dramatic range shifts might reflect resource competition. However, the populations of the potentially limiting resources, barnacles and mussels, wax and wane, and they do not appear low enough to result in competitive exclusion. It seems to me that this is not a likely explanation for the loss of *N. emarginata* from such a large area. On the other hand, in the Gulf of California, the presence of *M. lugubris*'s congener *M. angelica* plays a key role in shaping the intertidal community through indirect effects derived from a change in barnacle prey morphology in its presence (Lively et al. 1993). The community effects of the expansion of *M. lugubris* should be similarly investigated, especially the response of *N. emarginata*. I suggest that ecologists should look to other explanations for this replacement than competition or water temperature that, while somewhat warmer, is never warm enough to kill this hardy snail. The causes of the apparently cyclical northern range expansion of *M. lugubris* should also be investigated.

While abundances of *Mytilus* mussels did not change at Dike Rock, they decreased at Ocean Beach. Smith et al. (2005) found that a mussel bed adjacent to the Ocean Beach study site, sampled concurrently as part of the broader BLM surveys, had decreased in percent cover and thickness since the 1970s. This coincided with the overall

trend for mussel beds in the Southern California Bight, which the authors speculated could be due to sea surface temperature, pollution, or human visitation, or some combination thereof (Smith et al. 2005). During the 2012 survey at Ocean Beach, the survey transects did not bisect any patch of mussels that was contiguous for more than 0.5 m. The decrease in mean abundance, but not in percent cover of *Mytilus californianus* at Ocean Beach could be a manifestation of a similar reduction in thickness in mussel patches. *M. californianus* and *Pollicipes polymerus* often co-occur in the same clumps and probably share many of the same environmental requirements. Therefore, whatever is responsible for the decline in *M. californianus* might also be causing the declines seen in *P. polymerus*.

Although Table 2 shows that there were changes in species composition at both sites, it is likely that many of these changes are due to sampling artifacts. As discussed above, the presence absence data at Dike Rock show the appearance and disappearance of several species. Certainly many of these observations might be sampling artifacts, especially considering the tiny quadrats used by the Fager classes. However, the absence data from 2012 are more reliable as the site was sampled much more carefully than the brief field trips from the Fager classes. Several species that showed up in 2012 were probably simply missed by the Fager students with the exception of *Mexacanthina lugubris*, as discussed above. The lack of *Pisaster ochraceus* in the historical list is an artifact because it was on the SIO pier pilings and on the artificial reefs Fager studied in the sand habitat near the pier (E.W. Fager to P.K. Dayton, personal communication). The absence of *Nucella emarginata* is also likely an artifact of sampling methods, as it was abundant at the site a decade later (P.K. Dayton, personal communication). The same is



may also be true of *Tegula eiseni*. As discussed above, I believe that the historical absence of *Lottia scabra* is due to its confusion with *L. conus* rather than real absence. The 2012 absence of species found by the Fager class may also be attributed to sampling artifact. *Tegula funebris* can currently be found elsewhere at Scripps Reef, as can *Pegurus samuelis*, although I found neither at Dike Rock itself.

At Ocean Beach, some of the species that were found in the BLM surveys, but not in 2012, are rare in the San Diego rocky intertidal. These include *Aplysia californica*, *Cancer jordani*, and *Pugettia producta*. *Tegula funebris* is motile and follows its drift algal food supply, and thus is patchy in time and space. The pagurid hermit crabs have always been a classical low intertidal species, but may have been missed due to sampling method (not looking under surf grass, cobble or in crevices of pools). The black abalone, *Haliotis cracherodii*, has disappeared in southern California, the victim of systematic poaching and withering syndrome (Altstatt et al. 1996). As at Dike Rock, *Nucella emarginata* is no longer at this site, its shift in distribution correlated with the arrival of *Mexacanthina lugubris*. Barry et al. (1995) found that *Tetraclita rubescens* had increased in abundance at their site in Monterey Bay. They attributed the increases in this "southern" species to climate warming. It is interesting that this "highly reproductive" species did not appear on the Ocean Beach transects, as it is found at Cabrillo National Monument and Dike Rock.

The lack of similar direction change between the two sites indicates that local factors may be more important than regional ones in determining how regional and global patterns are manifested. Even with the conservative analysis forced by the nature of the BLM survey data, these results suggest that many populations at the Ocean Beach site

have crashed. This is a much different result than at Dike Rock, where most of the populations did not show a change, or showed an increase. These sites historically had different communities in terms of species ratios (Fig. 2). The non-synchronous change may be due to differences in human disturbances, or differences in habitat. I propose that habitat differences are the most likely cause for the differences in directional change. One habitat difference is sand inundation. The beach surrounding Dike Rock is inundated with sand in the spring and begins to erode again in the late fall, when I did my survey. While both the historical and current surveys examined the area within this zone of sand inundation, it made up a small percent of the area surveyed (<5%). The differences in habitat substrate also have a large influence on the dynamics of the communities at each site. The nature of the rock that composes rocky shores affects the biological community present through its properties of water retention and heat absorption (McGuinness and Underwood 1986, Barry 1988, Raimondi 1988). The greater water retention and lesser heat absorption of the sandstone that makes up the Ocean Beach site versus the dark basalt of Dike Rock would lead to inherent community differences, as seen in Figure 2. Furthermore, Barry (1988) found that sessile barnacles have lower rates of survival on soft sandstone than on harder substrata due to differences in dislodgement by wave erosion and biotic interactions. Limpets, however, are not as negatively affected by living on soft substrate. These differences in survival, mediated by substrate, also support the patterns seen in Figure 2. Finally, the increase in extreme wave events between the surveys (Seymour 1996) may have affected the disturbance regime at Ocean Beach more than at Dike Rock. Unlike the basalt Dike Rock, the sandstone substrate at Ocean Beach is very friable and therefore prone to erosion by wave disturbance. Dike Rock is also

protected from large surf by local wave refraction patterns associated with the adjacent Scripps Submarine Canyon. The severity of wave disturbance on the biological communities at Ocean Beach may therefore be stronger than at Dike Rock. Thus, the increase in extreme wave events due to the 1976 regime shift likely led to some of the differences in the changes seen at the two sites.

Intertidal algae species can experience large between year variations due to differences in recruitment resulting from variation in the timing and intensity of climatic variables such as storm waves, prolonged warm water periods, and cloud cover (which mediates desiccation stress) (Gunnill 1980, 1985). While this between year variation is especially strong in annual species, cover by perennial species can also vary greatly between years (Klinger and Fukuyama 2011). The fact that the 1977-1978 quarterly samples were not significantly different is likely to be due to lumping species, as there is high seasonality in many of the algae species in San Diego (e.g. Gunnill 1980, 1985, Emerson and Zedler 1978). Furthermore, it is interesting that only one group of algae increased in percent cover at Ocean Beach when there was a reduction in abundance of many of the invertebrate grazers. I did not see a reduction in *Lottia gigantea* or littorine snails, both important intertidal grazers (Lubchenco 1978, Lindberg et al. 1998), but whether these species alone could be contributing to the decreases in algal percent cover, or if this result is due to lumping species, needs further investigation. Intertidal algae are expected to respond to long term changes in climate variables such as UV light, wind stress, and temperature. In central California, a decade of increased water temperature from a power plant thermal outflow resulted in a decline in percent cover by many intertidal macroalgae species and a decrease in algal species richness, but increases in

non-coralline crusts and ephemeral turf species (Schiel et al. 2004). I did not see similar results in the Ocean Beach algae, and it is likely that factors other than temperature are responsible for many of the changes.

Human impact also plays a large role in shaping the communities at each site, and may explain some of the temporal trends described here. Dike Rock has been an ecological reserve since 1929 and is now part of the University of California Natural Reserve System. In principle, it is supposed to enjoy a certain degree of protection. However, the site is accessible from both sides and is a popular area for the public to explore, and the UC NRS has never been able to control access. A separate project viewing photos taken of the area from the Scripps Pier over 115 days (May to August) in 2012 documented a minimum of 292 visitors on the Dike Rock itself and 946 in the adjacent intertidal habitat (S.C. Jarrell, personal communication). Some visitors carried five gallon buckets and presumably were poaching, and certainly all were trampling the habitat. In contrast, the Ocean Beach site has no formal protection beyond the California Department of Fish and Wildlife codes. There are no visitor counts for Ocean Beach, but I did see human activity there during my visits, mainly in the upper intertidal. The upper intertidal shelf is a popular place to watch the sunset, and multiple groups of were observed to be congregating in the general area each time I was present at the site just before sunset, even on overcast days. During the day, individuals were seen fishing in the small coves of the sandstone slope. One such cove is just north of the study site and - despite the high wave stress - is a popular spot for jumping in the ocean. This leads to greater trampling pressure in the mid- and high intertidal areas at the study site compared to adjacent areas. However, given the arguably higher use of the so called protected Dike

Rock site we cannot assert that either site is de facto protected and we have no formal comparison of human impact on either site.

At Ocean Beach, almost all of the invertebrate species that have decreased over the last 40 years are species that are eaten or are vulnerable to trampling impacts (Fig. 3; Ghazanshahi et al. 1983, Brosnan and Crumrine 1994, Murray et al. 1999, Huff 2011). Certainly the absence of *Haliotis cracherodii*, which experienced a population crash in the early 1990s, can be explained in part by overharvesting and poaching (Altstatt et al. 1999). This species has not been found in monitoring surveys at Cabrillo National Monument since 1990, decimated by human harvest and withering disease (Altstatt et al. 1999). Studies of human activities in rocky intertidal areas in Southern California found that mussels, top snails, and limpets were among the species most targeted by collectors (Ghazanshahi et al. 1983, Addessi 1994, Murray et al. 1999). *Mytilus californica* and *Lottia gigantea* are especially targeted for use for food and bait (Ghazanshahi et al. 1983, Harley and Rogers-Bennett 2004). Chitons are collected as bait for catching lobsters (Addessi 1994). In Orange County, Murray et al. (1999) found that poaching was rampant in protected rocky intertidal areas. At a rocky intertidal site in San Diego, Addessi (1994) found that over 19% of human visitors were collecting marine organisms. In addition to the obvious species such as abalones, mussels, large limpets, and sea urchins, our group has witnessed people collecting sea weeds and scrapping the anemones and small littorines off the rocks. Gooseneck barnacles are also prone to harvesting for consumption. *Lottia gigantea* has been commercially harvested in California for decades, but landings of all limpet species peaked in the 1980s due to a decline in demand (Harley and Rogers-Bennett 2004). I did not see a decrease in *L.*

*gigantea* abundances at either site, however this long-lived species was already decreased due to harvest at the time of the historical surveys (Zedler 1978, Harley and Rogers-Bennett 2004). The wide ranging and large scale effects of human harvesting in the intertidal have been described elsewhere (see reviews by Paine 1994 and Thompson et al 2002). Collection can lead not only to decline in certain species, but to landscape-level changes to the ecosystem.

Human trampling can also have profound direct effects on sessile invertebrate communities by crushing and removing individuals (Povey and Keough 1991, Brosnan and Crumrine 1994). Certain algae species are also extremely sensitive to damage by human trampling. For example, while Povey and Keough (1991) found that articulated coralline algal turf recovered from trampling disturbance after four months, the brown algae *Hormosira* had not recovered. Furthermore, Huff (2011) and Jarrell (personal communication) have described many consequences of the loss of algal turf from human trampling in San Diego, and it seems likely that this can reduce the settlement and recruitment of the exploited species. Much of Dike Rock is not prone to trampling due to more vertical orientation of the surface, so these effects may be stronger at Ocean Beach where the surface is more horizontal and easily disturbed by the weight of a foot, and may have caused the decreases in invertebrates and algal percent cover. The biological assemblages damaged by human trampling can take years to recover (Brosnan and Crumrine 1994) however, as visitation to these sites is not restricted in any way, there is likely very little, if any, recovery from this press disturbance (Bender et al. 1984, Keough and Quinn 1998).

Other forms of human activity in the intertidal can negatively affect the community. Even if visitors do not collect animals, many poke them and pick them up (Zedler 1978, Ghazanshahi et al. 1983, Murray et al. 1999, Kimura 2003). This can lead to reduced fitness and survival rate. Zedler (1978) found that experimentally jiggling *Lottia austrodigitalis* led to 12% mortality after one week, and completely removing and replacing individuals from the rock led to 38% mortality in *L. austrodigitalis* and 73% mortality in *L. scabra*. Photographs from the California Coastal Records Project show that an erosion prevention wall was built along the base of the cliff at Ocean Beach sometime between 1979 and 1987 (can be seen in Fig. 1C). Although such modifications to coastal environments can significantly affect communities, this wall is likely too far from the intertidal to have had any discernible impact on the community.

Perhaps the most important conclusion from this study is that by far the most serious perturbation impacting this habitat is related to human visitation and poaching. Most of the species show no major changes over the years, speaking to a remarkable resiliency of this benthic community: the majority of the species are still present, and in relatively the same ratios. The resilience of rocky intertidal communities in face of anthropogenic pressure has been documented by Van De Werfhorst and Pearse (2007) in California, and in fact seems to be the general pattern (Thompson et al. 2002).

The methods used by both historical surveys may have been inappropriate for determining community changes over long time scales, and certainly the 10x10 cm and 5x5cm quadrats and sampling methods used by Fager's class were insufficient. This size of quadrat is much too small to gain an accurate estimate of the larger and rarer species (e.g. Van De Werfhorst and Pearse 2007). Furthermore, both surveys sampled cross

shore, not stratified by tidal height. By being blind to the obvious zonation, the early ecologists lumped different habitats into each sample and did not adequately offer the precise tidal heights necessary to correct this problem with much precision. Quadrat size and transect orientation can greatly affect whether human impact is detected (Van De Werfhorst and Pearse 2007).

Overall, results from this study allow me to reject the null hypotheses. First, the hypotheses of no change in invertebrate species composition or, second, no changes in abundance or percent cover of flora and fauna at either site are both rejected as there were changes in composition, abundance, and percent cover. Third, the hypothesis that any changes would be consistent between the sites can be rejected as the changes were not in parallel. Invertebrate species compositions changed at both sites, with some changes that can be related to shifts in climate. Abundances of multiple invertebrate species at both site also changed and these changes were not similar, as the species at Dike Rock increased and the species at Ocean Beach decreased. This demonstrates how local factors determine how regional and global trends are manifested, as the substrate at each site likely played a large role in the changes observed. Human impacts can also affect the rocky intertidal in dramatic ways and may have contributed to the reductions seen at Ocean Beach. However, despite the stresses caused by climate change and human visitation, the biological communities at these sites seem to be remarkably resilient. It is important that measures be taken to ensure this resiliency. By comparing current observations to baseline data, this study documents multidecadal changes as well as consistency to rocky intertidal habitats in San Diego. The data presented here establishes yet another baseline to which future observations can be similarly compared.

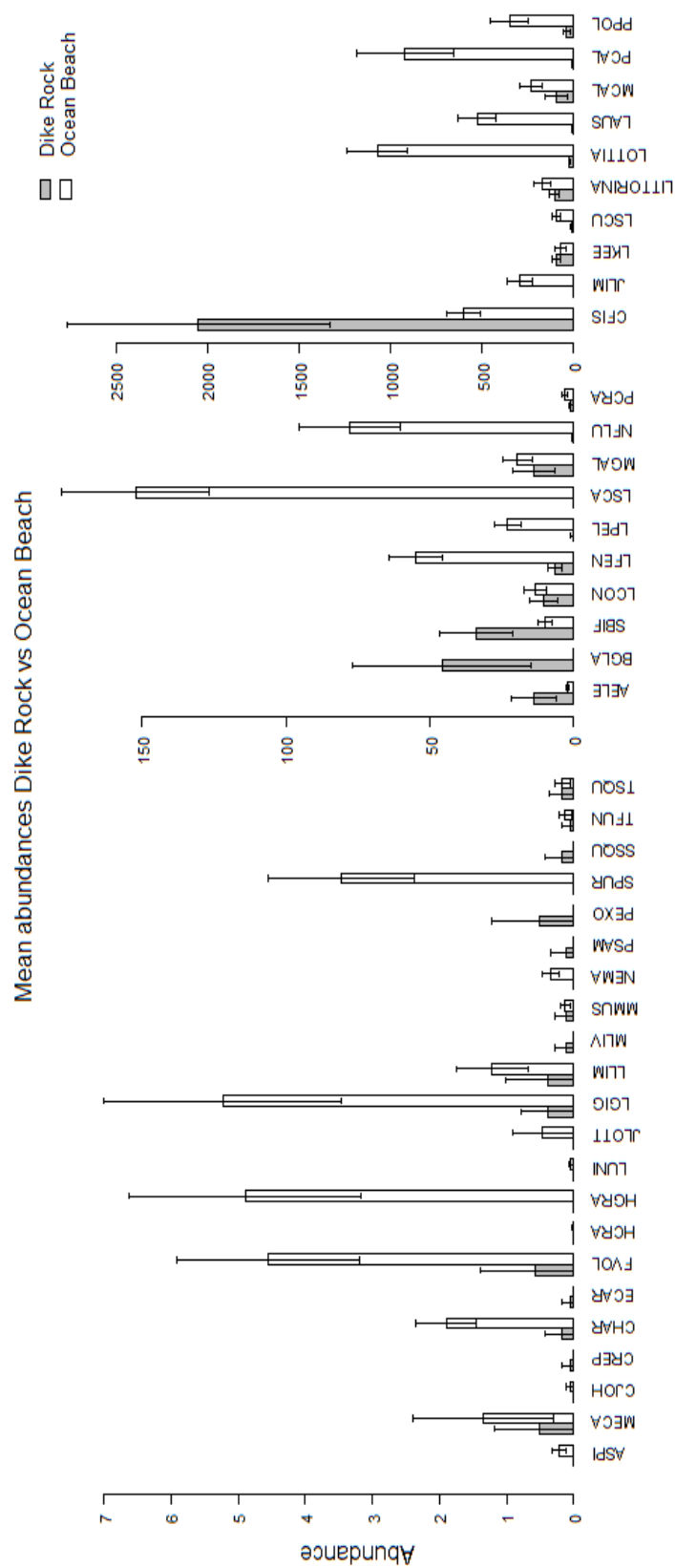


## Figures and Tables

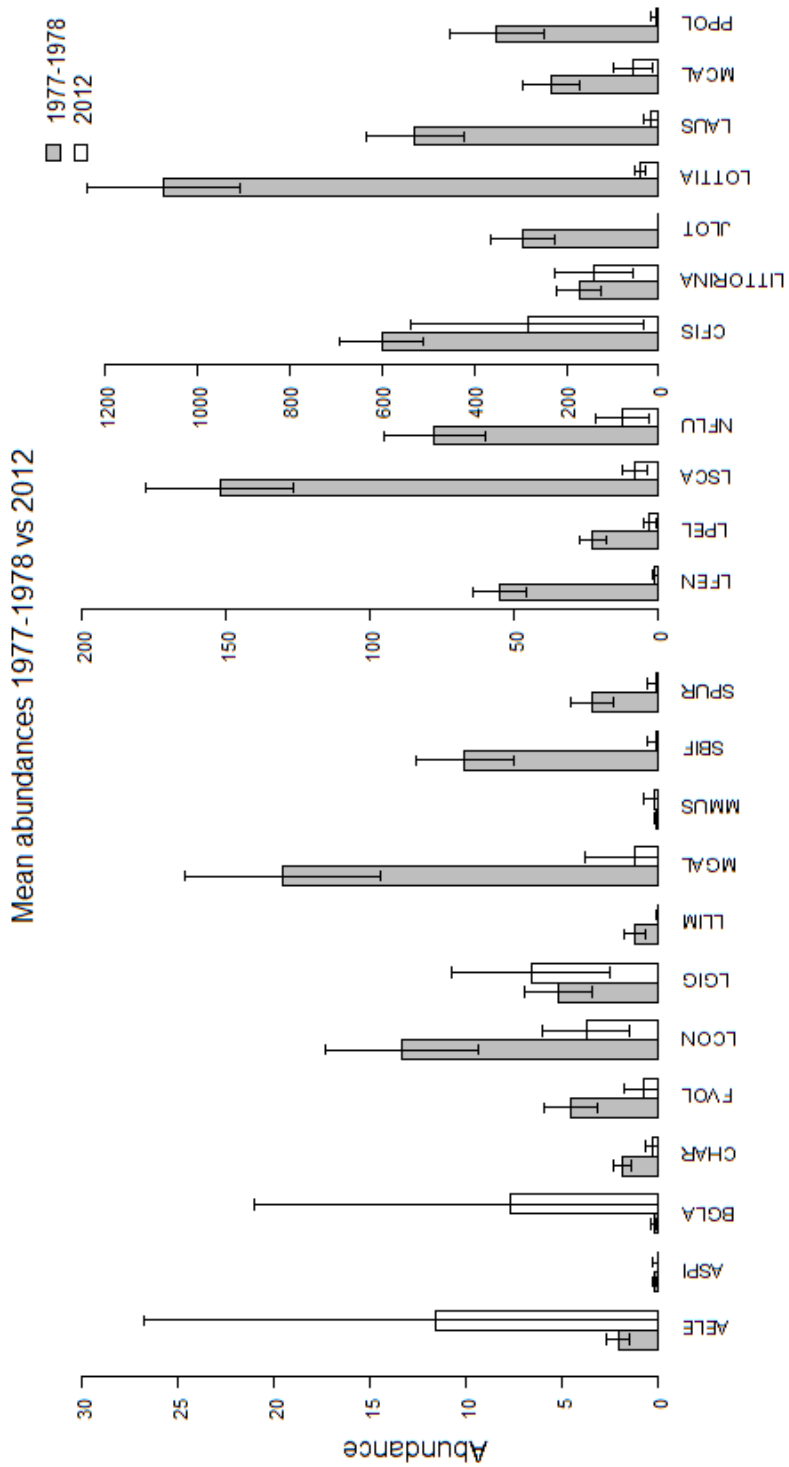


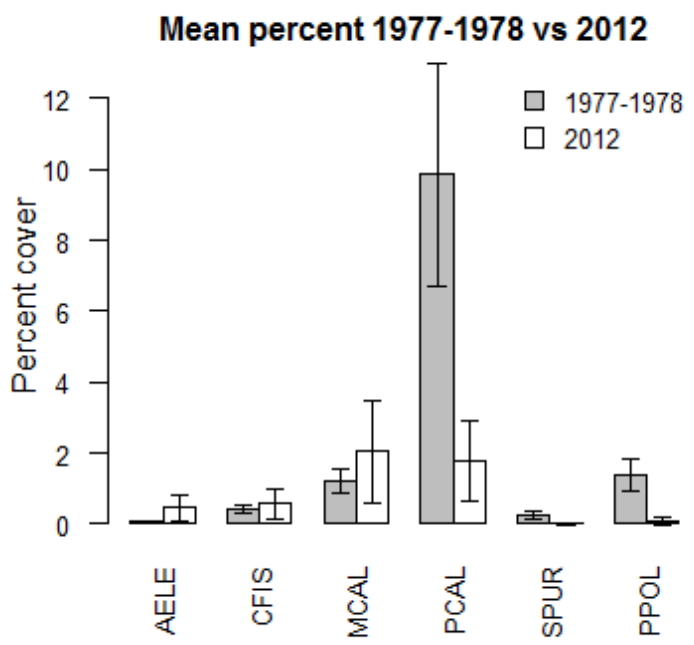
**Figure 1:** Map of (A) general location of sites and specific location of surveys at (B) Dike Rock and (C) Ocean Beach. Photos from Google Earth, and California Coastal Record Project (Copyright © 2002-2010 Kenneth & Gabrielle Adelman, California Coastal Records Project, [www.californiacoastline.org](http://www.californiacoastline.org)).

**Figure 2:** Barplot of mean abundances at Dike Rock and Ocean Beach with 95 % confidence intervals. ASPI = *Acanthinucella spirata*; AELE = *Anthropleura elegantissima*; BGLA = *Balanus glandula*; CJOH = *Cancer jordani*; CFIS = *Chthamalus fissus*; CHAR = *Cyanoplax hartwegii*; FVOL = *Fissurella volcano*; HCRA = *Haliotis cracherodii*; LKEE = *Littorina keeane*; LSCU = *Littorina scutulata*; LAUS = *Lottia austrodigitalis*; LCON = *Lottia conus*; LFEN = *Lottia fenestrata*; LGIG = *Lottia gigantia*; LLIM = *Lottia limatula*; LPEL = *Lottia pelta*; LSCA = *Lottia scabra*; MLIV = *Macron lividus*; MMUS = *Mopalia muscosa*; MCAL = *Mytilus californianus*; MGAL = *Mytilus galloprovincialis*; NEMA = *Nucella emarginata*; NFLU = *Nuttallina fluxa*; PCRA = *Pachygrapsus crassipes*; PSAM = *Pagurus samuelis*; PPOL = *Pollicipies polymerus*; SBIF = *Septifer bifurcates*; SSQU = *Serpulorbis squamigerus*; SPUR = *Strongylocentrotus purpuratus*; TFUN = *Tegula funebris*; TSQU = *Tetreclita squamosa*.

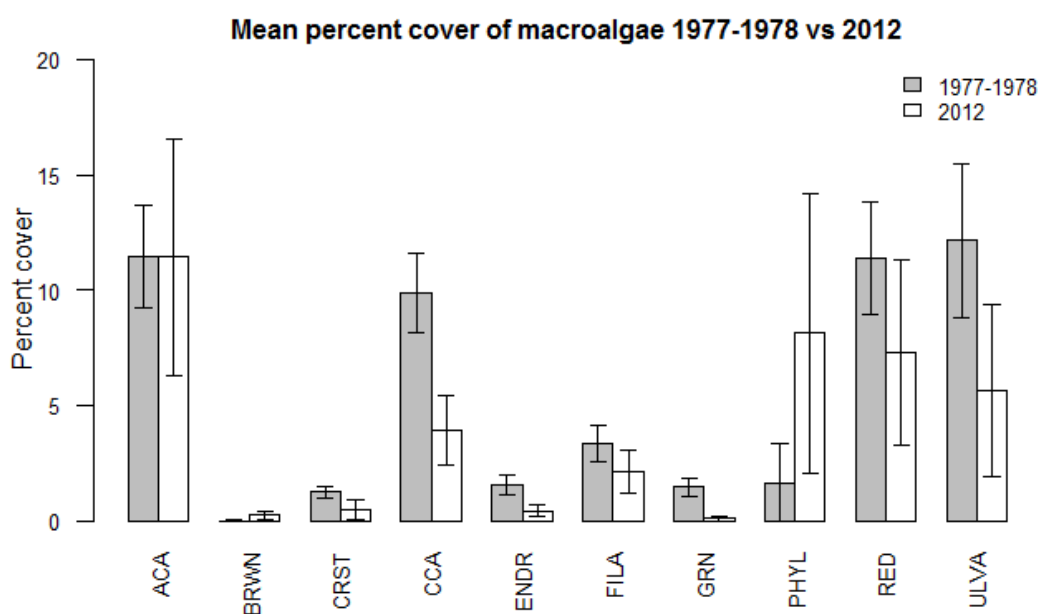


**Figure 3:** Mean abundance at Ocean Beach, 1977-1978 vs 2012. ASPI = *Acanthinucella spirata*; AELE = *Anthropleura elegantissima*; BGLA = *Balanus glandula*; CFIS = *Chthamalus fissus*; CHAR = *Cyanoplax hartwegii*; FVOL = *Fissurella volcano*; LAUS = *Lottia austrodigitalis*; LCON = *Lottia conus*; LFEN = *Lottia fenestrata*; LGIG = *Lottia gigantia*; LLIM = *Lottia limatula*; LPEL = *Lottia pelta*; LSCA = *Lottia scabra*; MMUS = *Mopalia muscosa*; MCAL = *Mytilus californianus*; MGAL = *Mytilus galloprovincialis*; NFLU = *Nuttallina fluxa*; PPOL = *Pollicipies polymerus*; SBIF = *Septifer bifurcates*; SPUR = *Strongylocentrotus purpuratus*; TSQU = *Tetrelita squamosa*;





**Figure 4:** Percent cover of pertinent sessile species at Ocean Beach, 1977-1978 vs. 2012. AELE = *Anthropleura elegantissima*; CFIS = *Chthamalus fissus*; MCAL = *Mytilus californianus*; PCAL = *Pollicipes californica*; SPUR = *Strongylocentrotus purpuratus*; PPOL = *Pollicipes polymerus*.



**Figure 5:** Percent cover of macroalgae at Ocean Beach, 1977-1978 vs. 2012. ACA = Articulated coralline algae; BRWN = Other brown algae; CRST = Non-coralline crustose algae; CCA = Crustose coralline algae; ENDR = Non-crustose *Scytosiphonaceae*; FILA = Filamentous algae; GRN = Other green algae; PHYL = *Phyllospadix*; RED = Fleshy red algae; ULVA = *Ulva* spp.

**Table 1:** Methods used by SIO class in 1961 and 1963 for surveying the Dike Rock community.

Transect	Direction	Year	Method
1	SSE-NNW (northmost), bisecting rock	1963	10x10 cm quadrats every 1 ft., 36 quadrats total. Species density recorded except: all species in quadrat 1 (East most); <i>Mytilus edulis</i> in quadrat 24; <i>Balanus glandula</i> in quadrats 25, 26, 31, 32, and 33; <i>Septifer bifurcatus</i> in quadrat 28; <i>Serpulorbis squamigerus</i> in quadrat 36; <i>Chthamalus fissus</i> in all quadrats.
2	SSE-NNW, bisecting rock	1961	1 10x10 cm quadrat every 10 cm, 129 quadrats total. Every 5th sample quantitatively analyzed with the presence/absence of species noted on all other samples.
3	SSE-NNW, bisecting rock	1963	Quadrats every 1 ft., 33 quadrats total. Quadrats 15-27 are 5x5cm, remainder are 10x10cm. Species density recorded except: <i>Chthamalus fissus</i> in quadrats 11 and 29; <i>Mytilus californianus</i> in quadrats 12, 31, and 32; <i>Mytilus edulis</i> in quadrat 24; <i>Balanus glandula</i> in quadrat 14; "Chitons" in quadrat 12; <i>Phragmatopoma californica</i> in quadrats 21 and 36; "Polycheates" in quadrats 28, 29, and 30.
4	SSE-NNW (southmost), bisecting rock	1961	1 10x10 cm quadrat every 10 cm, 33 quadrats in mid-intertidal. Every 5th sample quantitatively analyzed with the presence/absence of species noted on all other samples.
5	W-E, from MLLW to apex of rock	1963	3 groups of 3 10x10 cm quadrats located at 4, 6, and 8 feet above MLLW. At each tidal height, one quadrat is directly on the transect, with one quadrat 1 m perpendicular to each side. Did not include limpet species.
6	NE-SW, from MLLW to apex of rock	1963	4 groups of 3 10x10 cm quadrats located at 2, 4, 6, and 8 feet above MLLW. At each tidal height, one quadrat is directly on the transect, with one quadrat 1 m perpendicular to each side. Did not include limpet species.
7	ESE-WNW, from MLLW to apex of rock	1963	4 groups of 3 10x10 cm quadrats located at 2, 4, 6, and 8 feet above MLLW. At each tidal height, one quadrat is directly on the transect, with one quadrat 1 m perpendicular to each side. Did not include limpet species.
8	SSW-NNE, from MLLW to apex of rock	1963	4 groups of 3 10x10 cm quadrats located at 2, 4, 6, and 8 feet above MLLW. At each tidal height, one quadrat is directly on the transect, with one quadrat 1 m perpendicular to each side. Did not include limpet species.



**Table 2:** Presence (+) and absence (-) data for both sites and time periods.

	<b>Dike Rock</b>		<b>Ocean Beach</b>	
	<b>1961+1963</b>	<b>2012</b>	<b>1975-1978</b>	<b>2012</b>
<i>Acanthinucella spirata</i>	+	+	+	+
<i>Anthropleura elegantissima</i>	+	+	+	+
<i>Aplysia californica</i>	-	-	+	-
<i>Balanus glandula</i>	+	+	+	+
<i>Septifer bifurcatus</i>	+	+	+	+
<i>Cancer jordani</i>	-	-	+	-
<i>Chthamalus fissus</i>	+	+	+	+
<i>Cyanoplax hartwegii</i>	+	+	+	+
<i>Fissurella volcano</i>	+	+	+	+
<i>Haliotis cracherodii</i>	-	-	+	-
<i>Littorina keeane</i>	+	+	+	+
<i>Littorina scutulata</i>	+	+	+	+
<i>Lottia asmi</i>	+	+	-	+
<i>Lottia austrodigitalis</i>	+	+	+	+
<i>Lottia conus</i>	+	+	+	+
<i>Lottia fenestrata</i>	+	+	+	+
<i>Lottia gigantia</i>	+	+	+	+
<i>Lottia limatula</i>	+	+	+	+
<i>Lottia pelta</i>	+	+	+	+
<i>Lottia scabra</i>	-	+	+	+
<i>Megabalanus californicus</i>	+	-	+	-
<i>Macron lividus</i>	+	+	-	-
<i>Mexacanthina lugubris</i>	-	+	-	+
<i>Mopalia muscosa</i>	+	-	+	+
<i>Mytilus californianus</i>	+	+	+	+
<i>Mytilus galloprovincialis</i>	+	+	+	+

**Table 2:** Presence (+) and absence (-) data for both sites and time periods, Continued.

<i>Nucella emarginata</i>	-	-	+	-
<i>Nuttallina fluxa</i>	+	+	+	+
<i>Pachygrapsus crassipes</i>	+	+	+	+
<i>Pagarus hirsutiusculus</i>	-	-	+	-
<i>Pagurus samuelis</i>	+	-	-	-
<i>Phragmatopoma californica</i>	+	+	+	+
<i>Pisaster ochraceus</i>	-	+	-	-
<i>Pollicipies polymerus</i>	+	+	+	+
<i>Pugettia producta</i>	-	-	+	-
<i>Serpulorbis squamigerus</i>	+	+	-	-
<i>Strongylocentrotus purpuratus</i>	-	-	+	+
<i>Tegula eiseni</i>	-	+	-	-
<i>Tegula funebris</i>	+	-	+	-
<i>Tetrelita squamosa</i>	+	+	+	-
<i>White tube worm</i>	+	+	+	+
<b>Number of species recorded</b>	31	31	34	27

**Table 3:** Mean abundances ( $\pm$  standard error) for Dike Rock 1961 and 1963 vs. 2012, with p-values Significant differences are denoted by \*.

Species	1960s	2012	P value
<i>Anthropleura elegantissima</i>	13.89 $\pm$ 4.02	51.62 $\pm$ 20.89	0.006*
<i>Balanus glandula</i>	45.83 $\pm$ 15.74	52.92 $\pm$ 13.12	0.835
<i>Chthamalus fissus</i>	2049.26 $\pm$ 367.13	2736.60 $\pm$ 454.66	0.362
<i>Cyanoplax hartwegii</i>	0.17 $\pm$ 0.13	0.16 $\pm$ 0.09	1
<i>Fissurella volcano</i>	0.57 $\pm$ 0.42	1.14 $\pm$ 0.58	0.505
<i>L. conus + L. scabra</i>	10.56 $\pm$ 2.51	14.43 $\pm$ 2.98	0.44
<i>Littorina keeane</i>	95.17 $\pm$ 13.16	---	---
<i>Littorina scutulata</i>	10.34 $\pm$ 2.91	---	---
<i>Littorina spp</i>	104.97 $\pm$ 13.11	163.46 $\pm$ 36.94	0.077
<i>Lottia austrodigitalis</i>	5.47 $\pm$ 1.47	16.38 $\pm$ 3.82	0.0022*
<i>Lottia conus</i>	10.56 $\pm$ 2.51	10.49 $\pm$ 2.29	0.99
<i>Lottia fenestrata</i>	6.38 $\pm$ 1.25	20.11 $\pm$ 3.25	0.000027*
<i>Lottia gigantia</i>	0.39 $\pm$ 0.25	4.43 $\pm$ 0.831	0.000000009*
<i>Lottia limatula</i>	0.39 $\pm$ 0.32	0.11 $\pm$ 0.11	0.82
<i>Lottia pelta</i>	0.47 $\pm$ 0.35	3.08 $\pm$ 0.82	0.0018*
<i>Lottia scabra</i>	0	3.95 $\pm$ 0.99	---
<i>Lottia spp</i>	23.36 $\pm$ 3.43	59.24 $\pm$ 5.97	0.00000002*
<i>Mytilus californianus</i>	98.36 $\pm$ 31.19	235.41 $\pm$ 64.30	0.055
<i>Mytilus galloprovincialis</i>	13.99 $\pm$ 3.66	0.22 $\pm$ 0.22	0.067
<i>Nuttallina fluxa</i>	0.46 $\pm$ 0.18	1.14 $\pm$ 0.32	0.104
<i>Pollicipes polymerus</i>	41.37 $\pm$ 10.08	48.76 $\pm$ 17.31	0.76
<i>Septifer bifurcatus</i>	34.08 $\pm$ 6.51	114.11 $\pm$ 25.83	0.0001*
<i>Tetraclita squamosa</i>	0.17 $\pm$ 0.10	13.24 $\pm$ 6.32	0.000000016*

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