Rocky Intertidal Ecology in Response to a Purple Sea Urchin Population Collapse



Practicum Team Casey Crampton Joseph Curti Nichole Hawley Elizabeth Mazmanian Danielle Thoene Denita Toneva Tiffany Tran

Faculty Advisor

Dr. Rebecca Shipe

Client The Bay Foundation Client Advisors: Heather Burdick & Dr. Tom Ford

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Abstract

Along the Palos Verdes Peninsula, a population decline of the lower rocky intertidal grazer, *Strongylocentrotus purpuratus* (purple sea urchin), occurred in Fall 2015. The observed population collapse could be attributed to warmer waters that are characteristic of the warm phase of El Niño-Southern Oscillation (ENSO). This study investigates the relationships between changes in abiotic conditions following the third largest El Nino warming period, the decrease in population size of purple sea urchins and their effect on the intertidal community along the Palos Verdes coast. Transect surveys of species abundance were performed at two rocky intertidal sites, Honeymoon Cove and Underwater Arch, from February to May 2016. In addition, species abundances from 2013 to 2015 allowed us to better understand how these recent changes in community structure compare to historical population levels.

Anomalously warm annual fluctuations in sea surface temperature (SST) characterized the study region relative to the past eight years (2008-2015). Local temperature nutrient relationships indicate that nitrate concentrations were likely low (> 2 μ M) over the course of the study period. Despite the low nutrient levels and warm waters, a substantial increase in primary producer and grazer abundances occurred at both study sites during our four month study period. It is possible that macroalgae and other grazers have been able to proliferate due to the loss of grazing pressure by purple sea urchins. However, with the onset of the strong El Nino warm phase in 2015, higher trophic levels including secondary consumers including chitons at Honeymoon Cove have declined in abundance over our study period, while most primary producers and grazer abundances increased. From 2013 - 2014, decreasing abundance of purple sea urchins was coupled to an increasing abundance of primary producers; our study period was characterized by the greatest amount of primary producers and the presence of new grazer species.

Introduction

Rocky intertidal ecosystems support a vital and robust community of marine organisms and serve as a transition zone between terrestrial and marine environments. The rocky intertidal provides critical functions, such as stabilizing shorelines (Bos et al. 2007) and providing food such as kelp which supports adjacent ecosystems like dunes, sandy shores, and rocky subtidal kelp forests (Helmuth et al. 2006). The rocky intertidal is sensitive to changes in abiotic conditions, for example desiccation risk in response to temperature (Dayton 1971) as well as wave inundation (Thomas et al 1985), which can influence the distribution of rocky intertidal organisms. Similarly, this sensitive ecosystem is also highly impacted by anthropogenic stressors including trampling (Povey et al 1991; Brosnan et al 1994; Pinn and Rogers 2005) and water pollution (Gappa et al 1993; Cabral-Oliveira et al 2014). As a result, rocky intertidal ecosystems have recently become a target of conservation efforts.

<u>Characteristics of the Rocky Intertidal</u>

One of the most significant characteristics of the rocky intertidal ecosystem is its division into distinct zones. Each zone is inhabited by a unique assemblage of species that are adapted to the different abiotic and biotic challenges present in each zone. Generally, the upper regions of the rocky intertidal zone are subject to greater physical disturbances, while the lower regions are subject to greater herbivory, interspecies competition, and predation (Paine 1974).

The upper intertidal zone is only submerged during high tide; therefore, this zone is most frequently exposed to high wave energy, temperature extremes, and desiccation stress (Masselink et al. 1993). This zone is dominated by stress-tolerant shelled organisms such as barnacles, limpets, and chiton - which represent a mixture of grazers and secondary consumers (Anderson 2007). In addition, opportunistic or colonizing algae are able to withstand the physically stressful and variable conditions of the supra-littoral zone. Examples include thin, leafy algae such as the Ulva and Dictyota genera which are characterized by fast reproduction rates, short life-spans, and high dispersal abilities (Littler and Littler 1984). Algae in this zone have high photosynthetic capacity, but are susceptible to grazing.

The middle zone of the rocky intertidal is completely exposed to air during low tide, but completely submerged underwater during high tide. This zone is characterized by a shift from primarily stress-tolerant, shelled organisms to domination by mussels that have a competitive advantage over other invertebrates (Anderson 2007). The lower intertidal zone, which is only exposed to air during the lowest spring tide, tends to be comprised of a large diversity of macroalgae and invertebrates. Competition for space is an important limiting factor which significantly influences community structure in this zone (Paine 1974). In conclusion, organisms in the upper intertidal must be adapted to tolerate a range of abiotic stressors; whereas organisms in the lower intertidal must compete for space and are at greater risk of herbivory and predation.

El Niño-Southern Oscillation (ENSO) Effects on Rocky Intertidal

ENSO is a global climate phenomenon characterized by fluctuations in ocean-atmosphere conditions in the equatorial Pacific. ENSO is typically divided into two phases, the warm phase is commonly known as El Niño whereas the cold phase is known as La Niña (Philander 1985). The Multivariate ENSO Index (MEI) is a metric used to monitor the strength of ENSO events based on six variables including sea-level pressure, zonal and meridional surface wind, sea surface temperature, surface air temperature, and cloudiness (Wolter 2016). The 2015-2016 El Niño is the third strongest in recent history after the 1982-1983 and 1997-1998 events (Wolter 2016).

The response of intertidal communities to ENSO-induced temperature changes represents an area of active research as responses vary depending on geographic location and local conditions. A study of rocky intertidal communities in Central California found that southern ranging species were able to successfully expand northward, displacing the species that previously inhabited the area (Barry et al. 1995). In addition, a comprehensive study by Helmuth et al. (2006) found that on average intertidal communities have shifted 25 kilometers poleward every decade, far surpassing terrestrial northern range shifts. Other studies have found that thermally tolerant ecosystem engineers, such as mussels, were able to grow during warming events which could be attributed to a preference for warmer waters and greater food availability from phytoplankton blooms (Menge et al. 2008). These studies indicate that rising SST has driven range shifts and modified species assemblages in intertidal habitats. These changes may intensify in response to the effects of climate change. In particular, a warming ocean has been associated with acidification and coral bleaching (Hoegh-Guldberg 2007) and the introduction of invasive species (Stachowicz et al. 2002). Findings from ENSO-related studies can be used to enhance our understanding of global climate change and its associated impacts on marine life. For example, a study by Collins et al. (2003) combined historical oceanic and atmospheric data to model future ocean warming and found evidence that suggests ENSO warming conditions could become more frequent and intense in the future. However, recent research that empirically links climate change effects to changes in rocky intertidal community structure is limited.

Context of Population Decline of Strongylocentrotus purpuratus (Purple Sea Urchin)

Marine invertebrates are particularly vulnerable to a warming ocean (Dupont et al. 2010). Increased temperature has been shown to affect the activity level of poikilothermic (organisms that rely on their environment to maintain metabolic rates) marine invertebrates (Newell and Northcroft 1967). Further, larval stages of many marine invertebrates are sensitive to fluctuations in temperature, where growth and metamorphosis can be delayed or stunted in response to higher than normal temperatures (Thorson 1949).

Purple sea urchins depend on a narrow temperature range (12 - 21 °C) to maintain their metabolic rate and oxygen consumption (Ulbricht and Pritchard 1972). Further, when sea temperatures exceed 23.5 °C, or the maximum temperature that purple sea urchins are able to sustain in a laboratory setting, urchins can shift their range subtidally in order to meet these temperature requirements (Farmanfarmaian and Giese 1963). Two stages of urchin development, gastrulae and 4-arm plutei, showed this same pattern of strict temperature limits (in some cases a two degree range) that determined survivorship in offspring (Hammond and Hofmann 2010).

In future climate regimes with warming ocean temperatures, purple sea urchin populations can have a great effect on intertidal health. A study by Byrne et al. (2009) demonstrated that purple sea urchins could produce viable oocytes with up to a 4 °C change in ocean temperature. Further, the abundances of purple sea urchins within the rocky intertidal can have a dramatic affect on other trophic levels, specifically that overgrazing by urchins can lead to barren habitat with decreases in algal diversity and survivorship (Pearse et al. 2006). Urchin overpopulation has also been linked to declines in limpet and sea snail populations (Shears and Babcock 2003) and crustose coralline algae (Shears and Babcock 2003; O'leary and McClanahan 2010). Depending on the extent of ocean warming, the future of rocky intertidal communities may look very different from the present day.

<u>Research Questions</u>

Questions that we address in the study include:

- 1. How do the physical and biological conditions of the selected rocky intertidal sites change over the course of the study period (February May 2016)?
 - a. Physical parameters studied will include temperature and nitrate concentration; biological parameters studied will include species abundances, community diversity, and benthic cover.
- 2. How do current physical and biological conditions of the rocky intertidal sites compare to previous years (2013 2015) when urchin barrens persisted?
- 3. What is the relationship between changes in the physical environment and community composition and structure in our study sites?
- 4. What is the recommended management strategy for The Bay Foundation given the current state of the rocky intertidal sites?

Methods

Study Sites

Data collection in the lower rocky intertidal is only physically possible in low tide and low wave height conditions; therefore, site visit dates were chosen in accordance with these two variables. Dates with a low tide height of 0.1 feet or below were chosen since this threshold ensured that the transects in the study sites would be exposed and we could reliably collect data. Dates with a wave height of 3 feet or below were chosen to ensure safe field work conditions. Wave height and direction information were gathered online from "PV Cove Report"¹ and tidal height information was gathered from the U.S. Harbors website². Tidal height readings specific to Palos Verdes could not be found, therefore data for the Port of Los Angeles was used as a proxy. The site visit dates and conditions are summarized in Table 1.

¹ http://www.surfline.com/surf-report/pv-cove-southern-california_4936/

² http://ca.usharbors.com/monthly-tides/California-South%20Coast/Los%20Angeles/2016-03

Days Since First Visit	Date	Time	Low Tide Height (ft)
Honeymoon Cove			
0	2/6/2016	15:30	-0.9
14	2/20/2016	14:30	-0.9
33	3/10/2016	16:10	-0.3
40	3/17/2016	13:15	-0.2
57	4/3/2016	13:30	-0.3
65	4/11/2016	7:30	-0.7
93	5/9/2016	6:15	-1.2
Underwater Arch			
0	2/20/2016	15:43	-0.9
15	3/6/2016	14:12	-0.8
19	3/10/2016	17:38	-0.3
26	3/17/2016	14:45	-0.2
46	4/3/2016	14:40	-0.3
51	4/11/2016	8:53	-0.7
79	5/9/2016	7:34	-1.2

Table 1. Site visits were conducted whenever tides and waves permitted safe conditions.

At least three team members attended each site visit in order to complete the transect surveys and water quality measurements before high tide. The geographic focus of our study is southwestern coast of the Palos Verdes Peninsula and within this region we selected two sites: Honeymoon Cove and Underwater Arch. At each study site we established a 30 meter transect (Figures 1 and 2). In addition, we recorded the GPS coordinates of each endpoint using a Garmin eTrex 10 device (Table 2). A reference map of the study sites was created using ArcGIS (version 10.3.1) software (Figure 3).

Honeymoon Cove is more vulnerable to wave disturbances and inundation, as it remains exposed and unprotected to the open ocean. On the other hand, Underwater Arch is more protected from wave inundation due to its raised platform sedimentation with rocks that block the interior of the site from incoming waves.



Figure 1. Photo of the Honeymoon Cove study site, taken from the southern endpoint on February 6th, 2016. The red line indicates the path of the 30 meter sampling transect.



Figure 2. Photo of the Underwater Arch study site, taken from the southern endpoint on April 11th, 2016. The red line indicates the path of the 30 meter sampling transect.

Study Site	Northern Endpoint	Southern Endpoint
Honeymoon Cove	33.764933°N, -118.422183°W	33.764717°N, -118.42225°W
Underwater Arch	33.754167°N, -118.415717°W	33.754117°N, -118.4154°W

Table 2. The locations of each transect at the two study sites in Palos Verdes, CA, and GPS coordinates in decimal degrees.



Figure 3. The location of Honeymoon Cove and Underwater Arch along the Palos Verdes Peninsula in Southern California.

Transect Surveys

Species abundances were measured along each transect using two survey methods from the Cooperative Research and Assessment of Nearshore Ecosystems (CRANE) protocol (Vantuna Research Group). The Swath survey method allowed us to determine the population densities of individual invertebrates (larger than 2.5 cm) and macroalgae across a large area. Past data sheets for the Swath method list 51 organisms of interest that were specifically chosen due to their significant ecological impact on the rocky intertidal. Key macroalgae species include articulated erect coralline algae (*Corallina spp.*), brown algae (*Sargassum spp.*), and southern sea palm (*Eisenia arborea*); key invertebrate species include black sea hares (*Aplysia vaccaria*), aggregating anemone (*Anthopleura elegantissima*), and purple sea urchins (*Strongylocentrotus purpuratus*) (Algae Swath (CRANE Based Survey)). Organisms were counted in 10 meter increments which included the area of one meter on either side of the 30 meter transect. Organisms with more than half of their body inside the Swath area were counted. If 30 individuals of a species were counted within a 10 meter increment, we recorded the distance on the transect tape where the thirtieth individual was reached, and ceased counting that species until the next tenth meter increment.

This varied from our protocol of extrapolating species density from the meter mark where a particular organism reached 30 counts. Assuming an evenness of coverage throughout that 10 meter increment, we extrapolated abundances. We found our extrapolated abundance by using the following formula:

$$AC/MM = XC/10$$

Where AC is the actual count, MM is the meter mark where we stopped counting species, XC is the extrapolated count, and 10 represents the full 10 meter transect since we conducted our counts on one square foot to either side of the transect. Our modified protocol kept 30 as the maximum AC and we made note of the MM. For most species, AC was under 30 and MM was noted as the count for the full 10 meters so that AC was equivalent to XC.

Only algal species that were consistently identified in 70% (or 5 out of 7) of field visits were included in our final Swath survey data in order to reduce the likelihood that species richness and abundance were influenced by our becoming more familiarized and adept at identifying species. Further, we inspected data to evaluate the effect of variability in visibility; therefore, on site visits with high waves and reduced sunlight, we may expect to see species diversity and density to be lower than normal. In particular, on March 10th the transect surveys were conducted in the late afternoon as the sun was setting. On March 10th, March 17th, and April 3rd, the low tide was -0.3 ft or higher, making it difficult to identify organisms closer to the reef floor due to the depth of the water.

In order to understand how organism diversity at both of our sites varied during our study period, we used organism counts from Swath surveys to calculate the Shannon-Wiener Index. We calculated the proportion of each intertidal species to the total counts for that species for each site and sampling date (p_i) and used the following summation to find Shannon-Wiener's Diversity Index:

$$H = -\sum p_i x \ln(p_i)$$

We measured species richness (E) by taking the natural log of the total number of different species for each date and location sampled. We estimated species evenness by dividing species diversity (H) by species richness.

The Uniform Point Contact (UPC) method provides another measure of species abundances and substrate topography, which gives insight into settlement and recruitment patterns (Santa Monica Baykeeper). We recorded substrate type, substrate relief, and benthic cover at each meter mark along the established 30 meter transects. Substrate type is defined as bedrock, boulder, cobble, or sand. Substrate relief is defined as the difference between the highest elevation and the lowest elevation of the substrate within a meter on either side of the transect tape. It is categorized into the following intervals: <10 cm, 10 cm-1 m, 1-2 m and >2 m. Benthic cover can be classified by either taxonomic group, if an organism lies beneath the meter mark, or by abiotic cover (rock, sand, shell debris, mud or sediment).

We used the UPC data to calculate percent coverage for substrate, relief, and taxa. Each survey includes 31 data points for each of the three factors that we measured representing what was under the transect tape at each meter mark (including zero). For percent cover, we divided the number of each taxa by 31 which shows how abundant that specific taxa is along the transect. We then did the same calculation for substrate and relief so that we can look at the changes in percent cover over the span of the study period.

Historical Data Collection

The Bay Foundation collected data using UPC and Swath surveys from 2013 - 2015. These data contain total species counts and benthic cover for our study sites at Honeymoon Cove and Underwater Arch. Through a collaboration with Vantuna Research Group (VRG) at Occidental College, they were able to calculate percent cover and mean density. The Bay Foundation provided us with the results calculated by VRG for both study sites for the years 2013 and 2014. Using these same protocols we were able to calculate percent cover and mean density for 2015 - 2016.

Sampling protocols varied between our study and the 2013 - 2015 data taken by The Bay Foundation. The Bay Foundation collected exact counts of each species observed per 10 meter increment of the transects and from an area of one meter on either side of the transect resulting in a total area of 60 square meters. Mean density was derived by summing the total count of the species over the entire transect and divided by 60 square meters. The final unit derived from this calculation is organisms per square meter.

Weekly water temperature and nitrate concentration measurements from the Santa Monica Pier were obtained for the period of June 2008 through May 2016 from the Southern California Coastal Ocean Observing System (SCCOOS) website, which is a pier-based monitoring network funded by the National Oceanographic and Atmospheric Administration (NOAA). Since we were unable to determine nitrate concentrations at our Palos Verdes study sites, the relationship between temperature and nitrate concentrations during the period of February to May of 2008-2015 was used to estimate the nitrate concentrations at the two sites during the study period using Long Beach SST, as below.

<u>Abiotic Conditions</u>

Measurements of temperature and dissolved oxygen were taken at Honeymoon Cove and Underwater Arch during site visits. Due to gaps in our temperature readings, we used local SST values from the nearby Long Beach monitoring station $(33^{\circ}43'12.9"N, 118^{\circ}16'21.0"W)$, about 18 km south of the study sites, to serve as a replacement for our measurements. The Long Beach measurement is made at mean lower low water height, which is the average height of the lowest tide recorded each day. This is the closest local SST data that is taken daily, which is why it was chosen as a proxy for our Palos Verdes sites. Temperature measurements recorded by the Southern California Coastal Ocean Observing System (SCCOOS) at the Santa Monica pier, about 28 km north were used as a context for on-site measurements from the years 2008-2016. Nitrate concentrations from that monitoring station were used to establish a temperature-nitrate relationship for the region. Using that relationship we were able to extrapolate Nitrate levels for our study sites. The formula y = -0.7685x + 13.922 was used to calculate the results.

Results

Abiotic Conditions

Sea surface temperature (SST) data from the Santa Monica pier between 2008-2016 shows annual cycles of summer highs ranging from 20 to 25°C and winter lows ranging from 12 to 15°C for the years between 2008-2015. In comparison, the lowest SST for 2016 was 16.2°C which is above the range of lows for the past eight years indicating an unusually warm winter (Figure 4). The Long Beach temperature data, which we used a proxy for temperature at our sites, was slightly warmer than the Santa Monica pier data.



Figure 4. Sea surface temperature (°C) at Santa Monica Pier between November-June ranges from 12-22°C. Long Beach data during our study in February to May 2016 is slightly higher than the annual cycle at Santa Monica Pier.



Figure 5. MEI index for the last decade showing positive anomalies and a warm El Niño event during 2015-2016 immediately prior to the study period.

Our current study period (February - May 2016) is marked by the persistence of El Niño conditions, or positive anomalies of the Multivariate ENSO Index (MEI) (Figure 5). During the El Niño phase, there is a warming of the eastern boundary current of the North Pacific Gyre associated with the positive El Niño-Southern Oscillation (ENSO) environmental phenomenon which began in March - April 2015. Throughout spring, MEI was approximately +2.0 which establishes this warming event as the third strongest El Niño since 1950. The peak MEI anomaly of +2.53 occurred August-September 2015 (Earth System Research Laboratory 2016).

Using Santa Monica Pier temperature and nitrate data from the past eight years, a linear regression analysis was performed in order to determine the correlation between the two variables (Figure 6). Using that inverse correlation estimated nitrate concentrations at our two Palos Verdes sites over the course of the study period by using SST from Long Beach. Based on the observed temperature range of approximately 15 - 17°C, the estimated nitrate concentrations during our study period approximately 2 μ M. Nitrate concentrations around 1 - 2 μ M have been shown to limit primary productivity and vary with seasonal patterns of upwelling (Pennington and Chavez 2000).

At both Honeymoon Cove and Underwater Arch, temperatures fluctuated between 15.2 - 16°C from mid-March to mid-April. After mid-April, temperatures rose again slightly to 17.5°C at both sites. Dissolved oxygen concentrations were between 9 and 12 mg/L at Honeymoon Cove and between 9 and 15 mg/L at Underwater Arch, which are saturated dissolved oxygen conditions at the observed temperatures, typical of coastal waters in a surf and swash zone.



Figure 6. Relationship between nitrate and temperature at the Santa Monica pier during February to May in the years 2008 - 2015. (n = 126, $r^2 = 0.25$ was a statistically significant negative relationship at the -0.05 level)



Figure 7. Temperature, dissolved oxygen and nitrate over time at Honeymoon Cove study sites: Estimated nitrate concentrations from temperature readings at nearby Long Beach station, based on the statistically significant negative correlation between nitrate and temperature in local waters in Figure 5.



Figure 8. Temperature, dissolved oxygen and nitrate over time at Underwater Arch: Estimated nitrate concentrations from temperature readings at nearby Long Beach station, based on the statistically significant negative correlation between nitrate and temperature in local waters in Figure 5.

Biotic Conditions

Organism Abundance (2016)

The Swath transect survey allowed us to track changes in species abundance over the course of the study period at Honeymoon Cove (Figure 9) and Underwater Arch (Figure 10). Since transect surveys began in February 6th for Honeymoon Cove, and not until February 20th for Underwater Arch, we analyzed changes in species abundance by "days since first site visit". Most of the same organisms were present at both sites; however, feather boa, sea palm, rockweed, and Dictyota were only observed at Honeymoon Cove and turban snails and california sea hares were only observed at Underwater Arch. At Honeymoon Cove, abundance of *Gelidium spp.*, Articulated Red Algae, and Sea Palm increased with time, while Chiton and *Dictyota spp.* decreased (Figure 9). At Underwater Arch, abundance of *Gelidium spp.*, Anemone,

and *Sargassum* increased over the sampling period, while we observed decreases in *crustose red algae* (Figure 10). Underwater Arch generally had higher organism abundance with some species exceeding 100 counts/m², while Honeymoon Cove showed higher organism richness (n = 16) when compared to Underwater Arch (n = 14).



Figure 9. Abundances of organisms identified at Honeymoon Cove during February - May 2016 using the Swath survey method.

Underwater Arch



Figure 10. Abundances of organisms identified at Underwater Arch during February - May 2016 using the Swath survey method.

There was a general increase in total organism abundance (organisms m²) at both sites with maxima at both sites on April 11. The relative proportions of the three trophic levels seemed to be constant over time at Honeymoon Cove with primary producers being the dominant trophic level. On average, primary producers made up the largest proportion of species abundance at both sites, with 50.4% at Underwater Arch and 66.7% at Honeymoon Cove. Grazers represented another large proportion of the total organism abundance, with 21.8% at Underwater Arch and 18% at Honeymoon Cove. Lastly, secondary consumers made up 27.8% of the organism abundance at Underwater Arch and 15.3% at Honeymoon Cove. At Underwater Arch secondary consumers increased dramatically from April - May, primarily as a result of an increase in both acorn and buckshot barnacles.

Scientific name	Common name	Trophic Group
Corallina spp.	Erect Coralline Algae	Primary Producer
Corallina spp.	Articulated Coralline Algae	Primary Producer
Lithophyllum spp.	Crustose Coralline Algae	Primary Producer
Sargassum spp.	Gulfweed	Primary Producer
Eisenia arborea	Southern Sea Palm	Primary Producer
Egregia menziesii	Feather Boa Kelp	Primary Producer
Codium fragile	Dead Man's Fingers	Primary Producer
Fucus distichus	Rockweed	Primary Producer
Colpomenia peregrina	Bladderweed	Primary Producer
Endocladia muricata	Scouring Pad Red Algae	Primary Producer
Gelidium spp.	Branching Red Algae	Primary Producer
Macrocystic pyrifera	Giant Kelp	Primary Producer
Dictyota spp.	Forkweed	Primary Producer
Strongylocentrotus purpuratus	Purple Sea Urchin	Grazer
Pagurus spp.	Hermit Crabs	Grazer
Aplysia vaccaria	Black Sea Hare	Grazer
Aplysia californica	California Sea Hare	Grazer
Pachygrapsus crassipes	Shore Crab	Grazer
Nuttallina spp.	Chitons	Grazer
Chlorostoma funebralis	Black Turban Snail	Grazer
Megathura crenulata	Giant Keyhole Limpet	Grazer

Table 3. List of all organisms found at each study site, grouped by trophic level.

Lottia spp.	Limpets	Grazer
Anthopleura spp.	Anemones	Secondary Consumer
Chthamalus spp.	Buckshot Barnacle	Secondary Consumer
Balanus spp.	Acorn Barnacle	Secondary Consumer
Pollicipes polymerus	Gooseneck Barnacle	Secondary Consumer

Honeymoon Cove

200 Secondary Organism Abundance per m² Consumer Grazer 150 Primary Producer 100 50 0 2/22/16 3/07/16 3/21/16 4/04/16 4/18/16 5/02/16 Time

Figure 11. Organism abundance per square meter at Honeymoon Cove over the course of the study period. Stacked data indicates organisms categorized as primary producers, grazers or primary consumers and secondary consumers.



Figure 12. Organism abundance per square meter at Underwater Arch over the course of the study period. Stacked data indicates organisms categorized as primary producers, grazers or primary consumers and secondary consumers.

Two survey methods were used to assess the contribution of different organisms to the intertidal community; the Swath method, which estimates abundances of organisms per area and the UPC method which estimates area cover. These two methods produced slightly varying results. For example, the Swath data indicated less of a contribution of primary producers to total organism abundances at Underwater Arch from April - May, while this change was not observed in the UPC data. Further, measurements of abundance using Swath indicate a higher percentage of secondary consumers than grazers at Underwater Arch and a higher percentage of grazers than secondary consumers at Honeymoon Cove. This trend is only reflected in percentage cover for Underwater Arch, while percent cover at Honeymoon Cove indicates a higher percentage of secondary consumers than grazers. However, similarities between the two data sets include relatively stable levels of each trophic level over the course of our study period.

Percent Cover (2016)

UPC survey data provided information on percent benthic cover of each study site. The percent cover of living taxa at Honeymoon Cove stayed constant throughout the study period, ranging from 84% to 97% cover, with an average of 88.5% cover (Figure 13). However, living

taxa covered 71% to 87% percent of the substrate at Underwater Arch, where there was a trend of increasing percent cover over the study period (average 78% cover).



Figure 13. The percent cover of living taxa over the course of the study period (February - May 2016) at Honeymoon Cove and Underwater Arch.

The percent cover for each trophic level is mostly stable through time at both sites. Primary producers are the main organisms that inhabited both intertidal sites, covering 52% to 90% of the substrate during the study period (Figure 14 and Figure 15). Primary producers include the observed types of coralline, red, brown, and green algae and cover an area 4-8 times greater than grazers and secondary consumers. Grazers mostly consisted of molluscs such as chitons, limpets, and sea hares, whereas secondary consumers included barnacles, sea anemones, and tube worms. At Honeymoon Cove, the percent cover of secondary consumers is slightly greater than that of grazers during the first half of our study, but both drop down to zero for the rest of the study period. Primary producers are much more abundant at Honeymoon Cove compared to Underwater Arch where we see a persisting cover of both grazers and secondary consumers throughout the study. At Underwater Arch, secondary consumers (10 to 19% cover) inhabit slightly more area than grazers (0 to 3% cover).



Figure 14. The average percent cover of living taxa, grouped by trophic level over the course of the study period (February - May 2016) at Honeymoon Cove.



Figure 15. The average percent cover of living taxa, grouped by trophic level over the course of the study period (February - May 2016) at Underwater Arch.

Percent Cover by Taxa (2016)

The main primary producer that inhabits the intertidal at both sites is coralline algae. Throughout the study period, coralline algae (ranging from 32 to 81% cover) covers a larger area than any other primary producer, invertebrate, or substrate. At Honeymoon Cove, however, the area covered by coralline algae decreased through time (from 78% down to 32%) while other primary producers including brown and red algae increased in percent cover over time. In contrast to this decrease, the percent cover of coralline algae at Underwater Arch was relatively stable during the study with one slight dip to 39% cover. Unlike Honeymoon Cove, the percent cover of brown algae was relatively low compared to substrates and other taxa, and there was no red algae recorded. In terms of invertebrates, Underwater Arch had a higher percent cover than Honeymoon Cove where invertebrate cover dropped to zero in the second half of the study period. Overall, the percent cover at Honeymoon Cove is strongly skewed toward coralline algae, while percent cover of algae, substrates, and invertebrates is less divided and less variable at Underwater Arch.



Figure 16. The average percent cover of living taxa and substrates over the course of the study period (February - May 2016) at Honeymoon Cove.



Figure 17. The average percent cover of living taxa and substrates over the course of the study period (February - May 2016) at Underwater Arch.

Diversity by Trophic Level (2016)

At Underwater Arch we observed a weak decrease over time in Shannon's Diversity Index of primary producers and both grazers and secondary consumers. Specifically, as primary producers decreased (r-squared = 0.6046) over our sampling period, there was an increase in the diversity of both grazers (r-squared = 0.0038) and secondary consumers (r-squared = 0.1842). At Honeymoon Cove, we observed an increase in both primary producers (r-squared = 0.7837) and grazers (r-squared = 0.8335) while we saw a decrease in secondary consumers (r-squared = 0.8869). Using Pearson's Correlation Coefficient Test, at a significance level (alpha) = 0.05 and 5 degrees of freedom, the critical value is 0.755.



Figure 18. Scatterplot with linear regression of Shannon's Diversity Index for Honeymoon Cove by trophic level



Figure 19. Scatterplot with linear regression of Shannon's Diversity Index for Underwater Arch by trophic level

Comparison to Historical Data (2013 - 2016)

Primary producers have historically been the main species to cover the intertidal. The percent cover of coralline algae, which is the dominant primary producer, dramatically increased in 2014 at both sites. At Honeymoon Cove, percent cover increased from 9.0 to 47.6% and at Underwater Arch it increased from 15.1 to 40.3%. This led to a decrease in red and brown algae and no records of any green algae after 2013. Coralline algae continued to slowly increase between 2014-2016 to a current average percent cover of 54% at Honeymoon Cove and 61% at Underwater Arch. The change in percent cover of invertebrates and substrates, on the other hand, differs between the two sites. Substrates cover about the same area throughout the four-year period at Honeymoon Cove ranging from 14 to 26%. However, substrate percent cover greatly increases in 2014 at Underwater Arch from 10 to 40% and then drops down to 22% in 2016. Invertebrate cover similarly shows opposing trends between the two sites, where it decreases over time at Honeymoon Cove (from 20 to 3%) and increases over time at Underwater Arch (from 1 to 17%). In general, coralline algae increased between 2013-2016 leaving less area for other primary producers and invertebrates.



Figure 20. The average percent cover of living taxa and substrates from 2013-2016 at Honeymoon Cove. The 2013-2015 data is based on annual surveys from the Bay Foundation. The 2016 data is the averages from our survey data.



Figure 21. The average percent cover of living taxa and substrates from 2013-2016 at Underwater Arch. The 2013-2015 data is based on annual surveys from the Bay Foundation. The 2016 data is the averages from our survey data.

From 2013 - 2014, grazers made up the largest percentage of organism abundance at both Honeymoon Cove (78-96%) and Underwater Arch (55-75%). When grazers are separated into different genera, purple sea urchins make up the majority of the grazer abundance at Honeymoon Cove (51-74%) and at Underwater Arch (76-95%). Secondary consumers represented the second largest organism abundance between 2013 - 2014 at Underwater Arch (19-38%) and Honeymoon Cove (4-17%). Finally, primary producers during this period made up the least percentage of organism abundance at Underwater Arch (6-8%) and Honeymoon Cove (0-5%).

In 2015 there was a dramatic decrease in purple sea urchin at Underwater Arch (22%) and Honeymoon Cove (2%). This was coupled with a decrease in primary productivity at Underwater Arch (9%) and Honeymoon Cove (57%). Further, secondary consumers followed the increase in organism abundance at Underwater Arch (69%) and Honeymoon Cove (40.3%).

During our study period in 2016 primary producers were at their greatest abundance in since 2013 at Underwater Arch (50.4%) and Honeymoon Cove (67%). There was a decrease of purple sea urchins at Underwater Arch (2%) and an increase at Honeymoon Cove (8%). Following the decrease in purple sea urchins there was also a return of other grazer genera at Honeymoon Cove (12%) and Underwater Arch (20%). Secondary consumers decreased between 2015 - 2016 at Underwater Arch (28%) and Honeymoon Cove (15%)



Figure 22. The abundance by trophic level from 2013-2016 at Honeymoon Cove showing the percentage of grazers made up of purple sea urchins. The 2013-2015 data is based on annual surveys from the Bay Foundation. The 2016 data is from our survey data.

Underwater Arch



Figure 23. The abundance by trophic level from 2013-2016 at Underwater Arch showing the percentage of grazers made up of purple sea urchins. The 2013-2015 data is based on annual surveys from the Bay Foundation. The 2016 data is from our survey data.

Honeymoon Cove

Discussion

Community Structure Changes (2016)

In this study, observed changes in community structure are used to make inferences about trophic interactions and ecosystem wide stability. Community structure is determined by the relative proportion of different functional groups, which include primary producers, grazers, and secondary consumers. Primary producers are photosynthetic organisms such as macroalgae that provide food to support the growth and proliferation of higher trophic levels. Grazers feed on primary producers and include non-sessile invertebrates such as limpets, chitons, sea urchins and sea hares. Grazer abundance is highly dependent on both bottom up control from nutrient levels that supplement primary production and top down control from secondary consumers. Secondary consumers include both predators such as sea stars and anemones, as well as filter feeders like barnacles and mussels which do not distinguish between consumption of phytoplankton and zooplankton. Community structure provides information on abiotic conditions such as nutrient availability as well as information on relationships between different intertidal organisms. By analyzing an ecosystem-wide metric such as community structure, we can simplify analyses and reduce the impact of confounding variables.

The percent cover of different trophic levels stayed constant on average at both sites with secondary consumers covering more area at Underwater Arch compared to Honeymoon Cove. There was a small increase in secondary consumers from April - May at Underwater Arch (Figure 15). This peak was also seen in data collected using the Swath survey. The increase in secondary consumers is largely attributable to an increase in barnacles at both of our study sites. Given the onset of the warm El Niño phase of 2015, these results are supported by findings from Farell et al (1991) who found the largest barnacle recruitments followed warm water upwelling events and the introduction of new species of zooplankton.

Primary producers represented the largest proportion of total species abundance and cover at our sites. In particular, coralline and crustose algae covered the largest expanse of the rocky intertidal which can be attributed to their rigidity and structural strength which aids in resistance to predation and physical abrasion (Littler and Littler 1984). However, during our study period coralline algae decreased and other primary producers such as brown and red algae increased in percent cover at Honeymoon Cove. The abundance of coralline algae is largely tied to the abundance of purple sea urchins which can cause large decreases in algal abundance (Shears and Babcock 2003; O'leary and McClanahan 2010). It is possible that the decrease in coralline algae at Honeymoon Cove could correspond with the increase in purple sea urchins over our study period. Our results point to a possible successional progression of an intertidal community that was formerly dominated by a single alga and few grazers to one with a greater diversity of algal species. The increase in brown and red algae could indicate that the

Honeymoon Cove community is recovering and a healthy level of grazers is allowing for more different types of algae rather than just coralline algae.

We observed several bleaching events of coralline algae during our study period which could explain some of the decrease in coralline algae at Honeymoon Cove. Bleaching is a common effect of increased water temperatures that can occur at warming events as small as a few degrees (McCoy and Kamenos 2015). Following the greatest bleaching event on May 9, 2016, we observed an increased in turf red algae (*Endocladia muricata*) as well as the presence of previously less common brown algae (*Colpomenia peregrina, Fucus distichus, Sargassum spp.*, and *Dictyota spp.*) growing above the bleached coralline algae (Figure 24). During our study period we observed a change in ocean temperature from 15.6 - 17.8°C. While the average temperature at our study site was around this upper limit of 17.8°C, the observed differences in algae still indicate a shift in community structure over the course of our study period.

The same decrease in coralline algae was not seen at Underwater Arch where percent cover of each type of algae was relatively constant over our study period. This could be attributed to the fact that there is less water exchange due to deeper channelization at Underwater Arch which may take longer to respond to SST changes because of the lower exposure to constant water flow compared to Honeymoon Cove. A relatively constant abundance and cover of coralline algae conflict with the increase in purple sea urchins we observed. One study by Lauzon-Guay and Scheibling (2007) found that wave height and temperatures over 17°C limited green sea urchin (Strongylocentrotus droebachiensis) aggregating and grazing. Considering that urchins were less abundance at Underwater Arch (average 20 per m²) than at Honeymoon Cove (average 35 per m²) and we often observed high wave heights of around 5 meters, this could explain this pattern of increasing urchins, albeit at low levels, and coralline algae.



Figure 24. Left: healthy coralline algae from site visit on 4/11/2016. Right: bleached coralline algae from site visit on 5/9/16.

We observed two general patterns in Shannon's diversity measure at our sites; at Honeymoon Cove, as primary producers and grazers increased in diversity secondary consumers decreased in diversity, while at Underwater Arch both grazers and secondary consumers increased in diversity during our sampling period while primary producers showed a decrease. A study by Duffy et al. (2003) showed that an increase in primary producer diversity can be tied to an increase in grazer diversity by a more complete resource utilization. They also noted that increased grazer diversity resulted in enhanced secondary production. These findings agree with the increase in both primary producer and grazer diversity at Honeymoon Cove and the increase in both grazer and secondary consumers at Underwater Arch. These results point to a complicated relationship between food web dynamics of grazers and other trophic levels in the rocky intertidal.

Change in the Rocky Intertidal at Palos Verdes (2013 - 2016)

In 2013, the grazer community at Honeymoon Cove and Underwater Arch was largely dominated by purple sea urchins. In addition to a practically homogeneous grazer community, primary productivity was dominated by brown algae at both sites. Following the decrease in purple sea urchins in 2014, the primary producer community grew in overall abundance relative to other trophic levels as well as in diversity with an increase in abundance of green, red, and coralline algal species. In 2015 we observed the greatest warming period since 2008 as well as the highest abundance of primary producers since 2013 that were largely dominated by coralline species. During our study period in 2016, purple sea urchins were at the lowest abundance since 2013 while primary producers, and specifically coralline algae, were at the highest abundance during the past four years. Further, grazer diversity increased in 2016 with the introduction of species including black sea hare and california sea hare.

These findings agree with a study by Duffy and Hay (2000) that found a dominance of certain algal types based on the differential feeding preferences of grazers. Specifically, they found dominance of brown algae when fish grazing pressure was highest, the introduction of red and green algae when amphipod grazers but not not fish were present, and the dominance of a colonizer algal species when grazing pressure was absent. Our grazer community did not include fish, however purple sea urchins are known to preferentially graze brown algae (Vadas 1977) while california sea hares and black sea hares (that made up the largest proportion of new grazers in 2016) have been shown to prefer red algal species (Kupfermann and Carew 1974). When both of these grazers persisted in similar numbers in 2016, we saw the dominance of coralline algae which is highly resistant to grazing, coupled with the near absence of red algae and brown algae.

Climate Change Effects

Rocky intertidal zones are unique habitats that are exposed to dramatic environmental conditions due to climate change. Due to the fact that intertidal species occupy very narrow niches in the areas between low and high tide they have low tolerance for environmental stressors (Tomanek and Helmuth 2002). Their niches are characterized by zonation patterns that are defined by highly specific biotic and abiotic factors, so the smallest changes could have drastic impacts. For this reason, our study of the impacts of climate change and ENSO conditions are important for future management and restoration efforts.

The data we collected seems to be the result of multiple climate-related events that took place before our study period. One was the El Nino warming event that began in 2015 and resulted in an unusually warm winter compared to previous years right before we started collecting data in February 2016 (Figure 4). Another was the dramatic drop in local temperatures after they peaked at 25°C in September 2015 and then came down to a low of 12.8°C in February 2016. This was the largest difference in temperatures between summer and winter for the past 8 years which may reflect increased variability (Figure 4). Climate change not only results in long term gradual global warming, but creates more severe weather patterns including larger fluctuations in temperature. We cannot distinguish whether our results are due to the El Nino warming or the severe weather patterns of climate change. Despite this uncertainty, our results still serve as a valuable indicator for what could happen to rocky intertidal habitats under conditions of gradual warming and/or extreme weather associated with anthropogenic climate change.

Management Recommendations

Research on the resilience of rocky intertidal habitats to anthropogenic and environmental stressors can provide us with better insight and tools for efficient habitat preservation and management. In order to improve the study design, we suggest increasing the number of replicate sites and increasing the length of the study period. It would be ideal to monitor multiple rocky intertidal sites in Palos Verdes more than once per year. If logistically and financially possible, we recommend that the Bay Foundation conduct surveys once per season in order to see how the community changes in accordance with seasonal environmental fluctuations. In the short term we can expect mild variation due to localized changes in weather patterns and seasonal temperature fluctuations.

In the long term, SST is expected return to its normal pattern of seasonal oscillation as the El Niño phase passes, therefore it is possible that the purple sea urchin population may dominate the rocky intertidal once again. If this occurs, culling urchins may prove to be the most viable option for restoring this habitat (Tracey et al 2015). By maintaining urchin abundances at (2 per m^2 /current levels) the Bay Foundation can track the potential changes in trophic structure as the urchin population increases.

We recommend continuing to use trophic structure as an indicator of ecosystem function and stability since it captures both the biological and physical characteristics of an area (Rombouts et al. 2012). Since our research project primarily focused on "descriptive" indicators such as species composition and abundance, our analysis could have been improved by collecting information on "functional" indicators such as productivity and nutrient cycling which provide greater insight on ecosystem processes and activity (Rombouts et al. 2012).

Given that the Bay Foundation conducted transect surveys on November 23, 2015 after the peak of the warm El Niño phase in August, the timing of their surveys may have conveniently captured the ecological effects of that event. For this reason, it is recommended that the Bay Foundation continue to monitor annual temperature trends in order to analyze their data in a broader context.

Conclusion

The need for widespread habitat conservation, on both land and sea, is more crucial than ever as global climate change and its related effects threaten to imbalance and destabilize a wide range of habitats (Russell et al. 2012). Due to rapidly shifting habitat ranges and weather patterns, detecting and prioritizing areas that require protection has proven especially challenging. Another area of concern involves weighing the costs and benefits of preventative versus restorative conservation strategies. The magnitude of anthropogenic stress on the environment is not clearly known, which raises the concern as to whether preventative measures are being implemented too late. Contrarily, some scientists also warn against human intervention in restoring the environment as the consequences of artificial maintenance of habitats remains controversial. Although opinions on this issue remain divided within the scientific community; more informal conservation strategies are also at our disposal. We must not underestimate the importance of education and individual efforts in combating ecosystem degradation.

Literature Cited

Algae Swath (CRANE Based Survey). N.p.: Santa Monica Baykeeper, n.d. PPT

Anderson, Genevieve, Biological Sciences Department, Santa Barbara City College. "Tidepools (California)". Marine Science. 2007. Web. <u>http://www.marinebio.net/marinescience/03ecology/tptre.htm</u>

- Barry, J. P., Baxter, C. H., Sagarin, R. D., & Gilman, S. E. (1995). Climate-Related, Long-Term Faunal Changes in a California Rocky Intertidal Community. *Science*, *267*(5198), 672–675.
- Blanchette, C. A., Melissa Miner, C., Raimondi, P. T., Lohse, D., Heady, K. E. K., & Broitman, B. R. (2008). Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America. *Journal of Biogeography*, 35(9), 1593–1607. http://doi.org/10.1111/j.1365-2699.2008.01913.x
- Bos, A. R., Bouma, T. J., Kort, G. L. J. de, & Katwijk, M. M. van. (2007). Ecosystem Engineering by Annual Intertidal Seagrass Beds: Sediment Accretion and Modification. *Estuarine, Coastal and Shelf Science*, 74, 344–348.
- Byrne, M., Ho, M., Selvakumaraswamy, P., Nguyen, H. D., Dworjanyn, S. A., & Davis, A. R. (2009). Temperature, but not pH, compromises sea urchin fertilization and early development under near-future climate change scenarios. *The Royal Society*, 276, 1883–1888.
- Collins, M. (2005). El Niño- or La Niña-like climate change? *Climate Dynamics*, 89-104(24), 89-104.
- Duffy, J. E., & Hay, M. E. (2000). Strong Impacts of Grazing Amphipods on the Organization of a Benthic Community. *Ecological Monographs*, 70(2), 237–263.
- Duffy, J. E., Richardson, J. P., & Canuel, E. A. (2003). Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters*, *6*, 637–645.
- Dupont, S., Dorey, N., & Thorndyke, M. (2010). What meta-analysis can tell us about vulnerability of marine biodiversity to ocean acidification? *Estuarine, Coastal and Shelf Science*. http://doi.org/10.1016/j.ecss.2010.06.013
- Farmanfarmaian, A., & Giese, A. C. (1963). Thermal Tolerance and Acclimation in the Western Purple Sea Urchin, Strongylocentrotus purpuratus. *Physiological Zoology*, 36(3), 237–243.
- Hammond, L. M., & Hofmann, G. E. (2010). Thermal tolerance of Strongylocentrotus purpuratus early life history stages: mortality, stress-induced gene expression and biogeographic patterns. *Marine Biology*, 157, 2677–2687.
- Helmuth, B., Mieszkowska, N., Moore, P., & Hawkins, S. J. (2006). Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. Annual Review of Ecology, Evolution, and Systematics, 37, 373–404.

- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... Hatziolos, M. E. (2007). Coral Reefs Under Rapid Climate Change and Ocean Acidification. *Science*, *318*, 1737–1742.
- Kupfermann, I., & Carew, T. J. (1974). Behavior Patterns of Aplysia californica in its Natural Environment. *Behavioral Biology*, *12*, 317–337.

Laguna Ocean Foundation. "Tidepool Ecology and Common Organisms". 2007. Web. <u>http://www.lagunaoceanfoundation.org/tidepool_ecology.html</u>

- Larkum, Anthony WD, Edward A. Drew, and P. J. R. (2006). Photosynthesis and metabolism in seagrasses at the cellular level. *Springer*, 323–345.
- Lauzon-Guay, J. S., & Scheibling, R. E. (2007). Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (Strongylocentrotus droebachiensis) in relation to wave action and sea temperature. *Marine Biology*. http://doi.org/10.1007/s00227-007-0668-2
- Littler, M. M., & Littler, D. S. (1984). Relationships Between Macroalgal Functional Form Groups and Substrata Stability in a Subtropical Rocky-Intertidal System. *Marine Biology*, *74*, 13–34.

Masselink, Gerhard, and Andrew D. Short. "The effect of tide range on beach morphodynamics and morphology: a conceptual beach model." *Journal of Coastal Research* (1993): 785-800.

- McCoy, S. J., & Kamenos, N. A. (2015). Coralline Algar (Rhodophyta) in a Changing World: Integrating Ecological, Physiological, and Geochemical Responses to Global Change. *Journal of Phycology*, 51, 6–24.
- Menge, B. A., Chan, F., & Lubchenco, J. (2008). Response of a Rocky Intertidal Ecosystem Engineer and Community Dominant to Climate Change. *Ecology Letters*, 11, 151–162.
- Newell, R. C., & Northcroft, H. R. (1967). A re-interpretation of the effect of temperature on the metabolism of certain marine invertebrates, *151*, 277–298.
- O'Leary, J. K., & Mcclanahan, T. R. (2010). Trophic cascades result in large-scale coralline algae loss through differential grazer effects. *Ecology*. http://doi.org/10.1890/09-2059.1
- Paine, R. T. (1974). Experimental Studies on the Relationship between a Dominant Competitor and Its Principal Predator. *Oecologia*, 15, 93–120.
- Pearse, J. S. (2006). Ecological Role of Purple Sea Urchins. Science, 314, 940–941.
- Rombouts, I., Beaugrand, G., Artigas, L. F., Dauvin, J., Gevaert, F., Goberville, E., ... Kirby, R.
 R. (2013). Evaluating marine ecosystem health: Case studies of indicators using direct observations and modelling methods. *Ecological Indicators*, 24, 353–365.
- Russell, B. D., & Connell, S. D. (2012). Origins and consequences of global and local stressors: Incorporating climatic and non-climatic phenomena that buffer or accelerate ecological change. *Marine Biology*. http://doi.org/10.1007/s00227-011-1863-8

- S.G. H Philander. (1985). El Nino and La Nina. *Journal of the Atmospheric Science*, 42(23), 2652–2662.
- Shears, N. T., & Babcock, R. C. (2003). Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series*. http://doi.org/10.3354/meps246001
- Stachowicz, J. J., Terwin, J. R., Whitlatch, R. B., & Osman, R. W. (2002). Linking Climate Change and Biological Invasions: Ocean Warming Facilitates Nonindigenous Species Invasions. *Ecology*, 99(24), 15497–15500.
- Thorson, G. (1949). Reproductive and Larval Ecology of Marine Bottom Invertebrates, 1–45.
- Timothy Pennington, J., & Chavez, F. P. (2000). Seasonal fluctuations of temperature, salinity, nitrate, chlorophyll and primary production at station H3/M1 over 1989-1996 in Monterey Bay, California. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 47(5), 947–973. http://doi.org/10.1016/S0967-0645(99)00132-0
- Tomanek, Lars and Helmuth, B. (2002). Physiological Ecology of Rocky Intertidal Organisms-A Synergy of Concepts. *Integrative and Comparative Biology*, *42*(4), 771–775.
- Tracey, S. R., Baulch, T., Hartmann, K., Ling, S. D., Lucieer, V., Marzloff, M. P., & Mundy, C. (2015). Systematic culling controls a climate driven, habitat modifying invader. *Biological Invasions*, 17, 1885–1896.
- Ulbright, R. J., & Pritchard, A. W. (1972). Effect of Temperature on the Metabolic Rate of Sea Urchins, *142*, 178–185.
- UPC Uniform Point Contact (CRANE Based Survey). N.p.: Santa Monica Baykeeper, n.d. PPT
- Vadas, R. L. (1977). Preferential Feeding: An Optimization Strategy in Sea Urchins. *Ecological Monographs*, 47(4), 337–371.

Vantuna Research Group (VRG) Sampling Method; Occidental College, 2014 (Crane Protocol)

Wolter, Klaus. "Multivariate ENSO Index (MEI)." *Earth System Research Laboratory*. National Oceanic and Atmospheric Administration, 6 May 2016. Web.