

EVALUATING RECRUITMENT SEASONALITY OF RED ABALONE (*HALIOTIS*
RUFESCENS) TO INFORM FISHERIES MANAGEMENT AND CONSERVATION
POLICY

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ABSTRACT

Evaluating Recruitment Seasonality of Red Abalone (*Haliotis rufescens*) to Inform Fisheries Management and Conservation Policy

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Recruitment, the addition of new individuals to a population, must be understood to make predictions about population growth of marine invertebrates. Red abalone (*Haliotis rufescens*) represent a former important commercial fishery in California, and until recently, supported a major recreational fishery. However, there have been statewide declines since the 1960s due to overfishing, disease, and climatic factors. Thus, understanding population dynamics to inform management and population restoration is critical. Recruitment dynamics of red abalone are poorly understood, with no prior knowledge of seasonal trends. To address this knowledge gap, I assessed monthly (July 2016-June 2017) and annual (2012-2016) settlement rates of red abalone in the Monterey Bay, which has low density abalone populations due to sea otter predation. I evaluated associations between abalone recruitment and oceanographic factors (temperature, wave forces, and upwelling index) and food availability (kelp density) to understand potential predictors of recruitment. Abalone recruitment occurred year round, with generally higher recruitment in late summer to early fall (July-October) and peaks in August and October. This is the first demonstration of year-round abalone recruitment in the field. On a monthly basis, there were no statistically significant relationships between recruitment and oceanographic factors or food availability. Annual abalone recruitment was consistent in all years, with the exception of 2015 when recruitment majorly decreased during the second year of the North Pacific marine heatwave (i.e., warm blob and El Niño

Southern Oscillation (ENSO) events). The failure of recruitment during only the second year of warm temperature suggests that prolonged extreme temperatures lead to reproductive failure. The consistent annual recruitment in the Monterey Bay contrasts with sporadic recruitment observed in Sonoma and Mendocino Counties in northern California. This finding was unexpected because red abalone in northern California were twice as dense as those in Monterey Bay at the time of the study. Possible hypotheses behind the observed consistent recruitment in Monterey Bay despite low densities include that: sheltered embayments retain larvae and promote recruitment, predation by sea otters aggregates abalone in crevices and promotes fertilization success, and the perennially present *Macrocystis pyrifera* kelp forests better support abalone growth and fecundity than northern California forests dominated by annual *Nereocystis leutkeana*.

Keywords: red abalone, larval recruitment, settlement, population dynamics, coastal oceanography, broadcast spawning

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1. INTRODUCTION

Population growth cannot be predicted without understanding recruitment: the addition of new individuals to a population. Furthermore, recruitment can fluctuate due to both environmental (density independent) and population (density dependent) factors (Connell 1985; Ebert & Russell 1988; Broitman et al. 2008). Most marine species undergo broadcast spawning events, where individuals release their eggs and sperm into the surrounding seawater for fertilization (Roughgarden et al. 1988; Levitan and Sewell 1998; Baker and Tyler 2001). Broadcast spawning can increase variability in recruitment due to mortality and transport during the larval phase. For marine invertebrate species, most studies measure recruitment on timescales of weeks, months, or years after settlement due to the difficulty of finding new settlers (Wing et al. 1995; Soria et al. 2013; Wasson et al. 2016). Understanding the processes affecting the arrival of recruits (i.e., settlement) is critical and the focus on my thesis.

1.1 California abalone population and management history

To provide context to my work, I summarized the history of abalone management and declines in California. The seven species of abalone in California supported a recreational and commercial fishery prior to the 1960s (Rogers-Bennett et al. 2002). Rapid declines occurred in the abalone fisheries from the 1960s to 1990s, most severely in southern California (e.g., south of Santa Barbara), as a result of overharvesting and disease (Rogers-Bennett et al. 2002). Overharvesting caused abalone catches to drop from a peak of 24,000 tons in the late 1960s to 115 tons by 1995 (Figure 1, Karpov et al. 2000; Micheli et al. 2008). The fisheries were managed from density dependent data only and all abalone landings were grouped together, irrespective of the species. This grouping

masked significant depletions of certain species (Karpov et al. 2000). In addition to fishing induced declines, a chronic wasting disease, withering syndrome, reduced black abalone (*Haliotis cracherodii*) populations (Altstatt et al. 1996), and impacted farmed red abalone between 1985 and 1998 (Moore et al. 2000). Following sharp decreases in populations, the commercial and recreational fishery for all abalone species closed south of San Francisco in 1997 (Rogers-Bennett et al. 2002). Currently, pink (*Haliotis corrugata*), green (*Haliotis fulgens*), and pinto (*Haliotis kamtschatkana*) abalone are species of concern, and white (*Haliotis sorenseni*) and black (*Haliotis cracherodii*) abalone are endangered species. Southern California red abalone populations remain very low (0-0.18/m²; CDFG 2012; Karpov et al. 2000, CDFG 2005).

Commercial fishing was prohibited north of Point Lobos (San Francisco County) in 1949. Since 1953, only recreational-free dive fishing of red abalone has been permitted in northern California (north of San Francisco) in an attempt to protect the remaining population (Haaker et al. 1996; Karpov et al. 2000; CDFG 2004). Across northern California, red abalone populations were thought to be sustainably managed with average densities of 0.53 individuals/m² as of 2010 (CDFG 2010). However, several sites have shown signs of decline in abundance since 2008 (CDFG 2010). In 2018, the California's Fish and Game Commission announced a red abalone fishery closure for the northern California recreational fishery due to ongoing environmental conditions that caused population declines to 0.15 individuals/m² (Rogers-Bennett pers. comm. 2018). The decision came shortly after the North Pacific marine heatwave from 2014-2016 (warm blob of 2014 and El Niño Southern Oscillation (ENSO) of 2015), which caused abnormally high water temperatures (Di Lorenzo & Mantua 2016; Gentemann et al.

2017), kelp die offs, and abalone starvation (Rogers-Bennet et al. 2016). Existing data on juveniles indicates that there are large temporal gaps in red abalone recruitment in northern California of up to 10 years (CDFG 2010; Rogers-Bennett et al. 2016).

In the Monterey Bay in central California, my study region, population densities have been stable from 1972 to 2004 at 0.20 individuals/m² (Micheli et al. 2008; Rogers-Bennett et al. 2013). However, in 2017 one survey at Otter Point in Monterey Bay found 0.13 individuals/m² (Rogers-Bennett pers. comm. 2018). These populations are at the threshold of the Allee effect (Allee 1931), where reproduction dramatically reduces because individuals are too far apart for successful broadcast spawning. Population increases are unlikely in this region due to sea otter predation (Hines & Pearse 1982; Leet et al. 2001).

1.2 Prior knowledge of red abalone recruitment

Since there is a history of abalone fishery collapses in southern California and recent major declines in northern California, understanding population replenishment through recruitment is critically important. In 2007, the California Department of Fish and Wildlife (CDFW) adopted methods to assess early abalone settlement by collecting recruits from cobbles (~15 cm diameter) covered with crustose coralline algae (CCA), a benthic substrate that provides a critical chemical settlement cue for abalone (Morse et al. 1979; Roberts et al. 2004; Waal et al. 2012; Rogers-Bennett et al. 2011). This method allows for the enumeration of abalone settlers from settlement to three months old, and has been previously practiced in Japan (Tanaka et al. 1986; Takami et al. 2006; Horii et al. 2006), New Zealand (Aguirre and McNaught 2011), Australia (Nash 1992, 1995; Keesing et al. 1995), and Mexico (Rosetto et al. 2013). Using this method, CDFW found

that settlement in northern California is sporadic, with boom and bust, non-synchronous settlement across multiple sites (Figure 2; Rogers-Bennett et al. 2016). The factors contributing to these recruitment fluctuations are unknown. CDFW has also performed abalone larval tows in northern California from 2007-2015, and found abalone larval concentrations to be widely variable in space and time (Rogers-Bennett et al. 2016). There have been no prior field evaluations of seasonality in red abalone recruitment (e.g. monthly settlement trends) or potential correlations with physical oceanographic factors.

1.3 Oceanographic influences on early recruitment

For the production of a strong year class for marine invertebrates with a bipartite life cycle, adults in a population must be healthy enough to produce gametes and spawn eggs and sperm in synchrony. Larvae must survive the pelagic transport period before settlement on the benthic habitat, and new settlers must be able to metamorphose and survive (Rogers-Bennett et al. 2016). Differences in the number of early recruits on monthly scales can be affected by reproductive output, reproductive timing, larval transport, settlement success, or survival after settlement, all of which may correspond to changes in environmental conditions. Physical and biological variability along the California Current is largely driven by seasonal coastal upwelling, whereby alongshore equatorward winds drive the transport of cold, nutrient rich waters from depth to the surface (Parrish et al. 1981). Upwelling leads to strong seasonal changes in water temperature and water movement (Pennington and Chavez 2000; Garcia-Reyes and Largier 2012; Walter et al. 2018). To generate hypotheses about what might drive the timing of abalone recruitment seasonally, I reviewed the literature to understand what is

known about the effects of temperature and wave forces on reproduction, transport, settlement, and post-settlement survival/growth.

Previous field and laboratory studies have shown that warm temperatures have a negative effect on reproduction and development of larvae (Table 1). Two studies found that temperature increases of 2.5-5 °C above ambient were detrimental to gonad development and fecundity (Table 1). Furthermore, two studies found that cooler temperatures, 2.5-4 °C below ambient promote higher gonadal development and fertilization (Table 1). Thus, generally, warm temperatures appear to have a detrimental effect on red abalone reproduction. There are contradicting results on how wave forces influence reproduction (Table 2); limited wave forces enhance reproduction for some abalone species, however, increased wave forces serve as a trigger for spawning for other abalone species (Table 2).

Previous studies have investigated the role and timing of upwelling and relaxation cycles on larval transport. Larvae are transported offshore during strong upwelling and are transported back to shore during relaxations (Roughgarden et al. 1991, Le Fevre & Bourget 1992). Upwelling in coastal embayments can affect larval transport through the formation, propagation, and modulation of upwelling fronts that tend to accumulate larvae (Woodson et al. 2009; Ryan et al. 2014). However, for California red abalone, larval transport processes are thought to play a minor role in recruitment dynamics. California red abalone are nonfeeding lecithotrophic larvae that spend approximately 6-7 days as pelagic larvae before they settle on a benthic habitat (Morse et al. 1979, Ebert & Houk 1984, Rogers-Bennett et al. 2016). With a short larval duration and reproduction in

kelp forests that limits transport (Gaylord et al. 2007), red abalone are thought to settle near parental populations (McShane and Smith 1991).

Temperature fluctuations appear to have mixed effects on larval development negatively or positively depending on the magnitude of the temperature change (Table 1). For red abalone, the most rapid growth and survival of larvae has been found to occur with a 1°C temperature increase above ambient temperature (Table 1; Leighton 1974). However, another study showed that a 2°C temperature increase above ambient temperature caused decreases in larval competency (Table 1; Searcy-Bernal 1999). Furthermore, extended larval competency periods of red abalone have been seen at an ambient temperature of 14°C (Table 1; McCormick et al. 2012).

There are contrasting results of the effects of temperature on abalone settlement, with cases where increased temperatures were associated with both increased and decreased numbers of settlers (Table 1). For red abalone, there is only one prior study, where high temperatures associated with an ENSO event decreased the abundance of small size classes (Table 1; Tegner et al. 2001). Wave forces for other species seem to have differing effects on settlement (Table 2). One study found that high wave forces from typhoons enhanced the abundance of new settlers, but another found that areas with high wave action had lower numbers of settlers (Table 2). For red abalone, a laboratory study found that settlement is more likely under small scale flows (Table 2; Boxshall 2000), but there were no publications on the effects of wave forces.

Most studies do not distinguish between settlement and post-settlement survival, so it is difficult to find studies focusing only on the post-settlement stage. For red abalone, a small temperature increase of 0.5 °C increased growth for red abalone (Table

1, Searcy-Bernal et al. 2007). Studies on other abalone showed mixed effects on growth at higher temperatures ranging from 4-18 °C above ambient (Table 1). However, survival always decreased at increased temperatures ranging from 3-18 °C above ambient. Wave exposure caused more post-settlement mortality in the rainbow and variously colored abalone species (Table 2; *H. iris*, Naylor & McShane 2001, *H. diversicolor*, Onitsuka 2010), however this has not been evaluated for red abalone.

In summary, reproduction, larval transport, settlement, and post-settlement survival appear to be negatively influenced by temperatures ranging from 2-18 °C above ambient, though a slight increase in temperature (less than 1°C) may positively influence post-settlement growth rates. High wave exposure seems to have negative effects on post-settlement survival, but may have both positive or negative effects on reproduction. Since most of these studies were conducted in the laboratory and on non-California species, a key need is to evaluate whether these factors correlate with monthly and annual recruitment patterns for red abalone in field settings in California.

1.4 Study system and questions

I evaluated red abalone recruitment in central California at two temporal scales (monthly and annually) to understand recruitment dynamics and their association with environmental conditions (temperature, waves, and upwelling) and food availability (kelp). I asked the following questions: 1) How does annual recruitment in central California (Monterey Bay) where abalone population densities are low compare with recruitment in northern California where abalone densities are relatively high 2) Are there seasonal patterns in red abalone recruitment? 3) Are there oceanographic factors that correlate with annual and seasonal recruitment trends? I hypothesized that red abalone

recruitment at my study site in central California would be lower than the recruitment found in the last decade in northern California due to lower adult densities (~half of those of northern California). Further, I hypothesized that recruitment will occur during cooler upwelling periods (April-June), before seawater temperatures warm during upwelling relaxation (months).

2. MATERIALS & METHODS

2.1 Sampling newly settled abalone

Newly settled abalone were collected from crustose coralline algae (CCA)-covered cobbles at Hopkins Marine Life Refuge (HMLR) 36°37'12.44"N, 121°54'8.28"W in Pacific Grove, CA. In order to investigate yearly recruitment trends, I used data collected in the fall months (September-November) by Dr. Jennifer O'Leary (California Sea Grant, California Polytechnic State University) from 2012-2015 (unpublished data), and I collected cobbles in 2016. In addition, in 2012, Dr. O'Leary collected cobbles at three sites in Monterey Bay (HMLR, Lover's Point, and Point Pinos) to investigate any differences in abalone abundance between the sites (unpublished data). To investigate seasonality in recruitment, I collected cobbles monthly using SCUBA for a one-year period from July 2016 to June 2017 (with the exception of March, when it was not possible due to weather conditions). I targeted cobbles that had 50% coverage or more of CCA, and were approximately 4-6 cm in diameter. Each month, I collected 30-37 cobbles equally stratified across three depths (3, 6, and 9 m), representing the depth range of the kelp forest at HMLR, and bagged each cobble at the site of collection in two ziplock bags. Cobbles were then transported to shore and stored in running seawater from waters near the collection site. Once cobbles were measured onshore, they were processed within 3 hours to remove all settlers. To process the cobbles, each cobble was placed in an individual 5-gallon (18.9 liters) bucket with enough seawater to cover the top of the cobble (8-11 liters) and a 120 ml of 95% ethanol for 10 minutes to anesthetize all the mobile invertebrate settlers. To ensure that all settlers were removed from the cobble, I used soft brushes to gently scrub each surface of the cobble and then the cobble was

rinsed with seawater over the bucket. The contents of the bucket (rinsed material) were poured through an 80- μm mesh sieve and then the sieve contents were rinsed into a sample jar fixed with 43 ml of 95% ethanol. The samples were stored into a $-18\text{ }^{\circ}\text{C}$ freezer for 1-3 months before samples were sorted microscopically to count abalone recruits and determine the abundance. Samples were individually placed in a black s-tray and newly settled abalone were identified and counted under an Olympus SZ61 dissecting microscope with 3x magnification (see Section 2.2 below). Following the CDFW protocol (Rogers-Bennett et al. 2016), abalone recruit abundance is reported as the average number of recruits per cobble.

2.2 Species identification

Morphological identifications were based on an extension of the radial lamellae underneath the spire (Figure 3). However, for abalone $<360\text{ }\mu\text{m}$, the radial lamellae extension had not developed and identification is difficult. Because these small abalone could be confused with other species, I counted two size classes separately: $<360\text{ }\mu\text{m}$ (potential abalone) and $>360\text{ }\mu\text{m}$ (identifiable abalone). I photographed each individual and measured lengths of a subset of samples using ImageJ. Each abalone was stored in its own strip tube vial with 95% pure ethanol in a -18°C freezer to allow for genetic confirmation of identity. To confirm species identity, I collaborated with Dr. Peter Shum, a postdoctoral researcher at Stanford University. Dr. Shum sequenced 22 abalone $>360\text{ }\mu\text{m}$ and 55 specimens, $<360\text{ }\mu\text{m}$ in length. All samples were pulse centrifuged to collect specimens to the bottom of the tube. Ethanol was removed leaving the early settlers inside the tubes and the remaining ethanol was evaporated in a fume hood. DNA was extracted using a commercial kit NucleoSpin 96 (Macherey-Nagel GmbH & Co. KG,

Düren, Germany). An approximately 650 base pair (bp) fragment of the coding mitochondrial cytochrome oxidase 1 was amplified using degenerate Folmer primers (Folmer et al. 1994); LCO1490: 5'-TAA ACT TCA GGG TGA CCA AA-3' AND HCO2198: 5'-GGT CTA CTA ATC ACA AAG AYA THG G-3'). Reactions were carried out in 20 µl volumes containing 1× PCR buffer, 2 mM MgCl₂, 4 mM dNTPs, 0.5 µM of each primer, 0.05 units Taq DNA polymerase, with 2 µl of DNA template. Amplifications were performed in an Eppendorf Vapo Protect Thermocycler (Hamburg Germany) using the following temperature profiles: 94 °C (2 min), 35 cycles of [94 °C (30 s), 50 °C (30 s), 72 °C (60 s)], followed by 7 min at 72 °C. A positive and negative control was included in all reactions, however if the positive control failed to amplify or there was a visible band in the negative control the PCR was re-run. PCR products were subjected to electrophoresis through a 1% Sodium-Borate acid (1X SB) gel stained with GelRed for visualisation via a UV-transilluminator. PCR products were purified using magnetic beads (0.5x) to remove unincorporated primers and deoxynucleotides in preparation to sequencing. Purified products were sequenced by ELIM BIOPHARM (ELIM BIOPHARM, USA; <https://www.elimbio.com>). Resulting sequences were manually checked for quality, edited and trimmed using Chromas Lite 2.1.1 (http://technelysium.com.au/?page_id=13).

2.3 *Macrocystis pyrifera* surveys

To determine food resources available to abalone over the course of the study, I used kelp data collected by Dr. James Watanabe in July each year within 30 m of my collection site (at 36°37'12.69"N, 121°54'7.86"W). Kelp data was collected on SCUBA. Divers counted *Macrocystis pyrifera* plants with four or more fronds (i.e., adult kelp) in

circular plots with an area of 7.26 m², or in 10 x 2 m² transects. Data were collected annually from 2012-2016. Circular plots and transects were chosen using random compass bearings and fin kicks. All data were normalized per 10 m².

2.4 Temperature, wave, and upwelling index data

I obtained seawater temperature (°C) data from the Monterey Bay Aquarium's intake pipe, located in 17 m of water (at 36°37'8.42"N, 121°54'4.67"W) and in close proximity (155 m) to my collection site. Temperature data were recorded every 5 minutes from an RTD temperature sensor. Calculations were made for yearly temperature averages, standard deviations, and minimum/maximum temperatures from 2012-2016, as well as monthly from July 2016-June 2017.

I obtained wave data from the Cabrillo Point National Data Buoy Center (NDBC) wave buoy were obtained. This is NDBC buoy 46240 (36°37'35"N, 121°54'25"W), and it is adjacent (0.8 km) to my collection site. Wave statistics were reported every 30 minutes. I calculate monthly averages and standard deviations of the significant wave height annually from 2012-2016 and monthly from July 2016-June 2017.

Continuous wind vector data were not available from Monterey-area buoys (e.g. NDBC 46042, 46092) over the entire time series. Therefore, I used the Bakun Upwelling Index, which provides estimates of offshore Ekman transport (Bakun 1975). Data for the index were collected for the grid point just offshore of Monterey Bay (at 36 °N, 122 °W) <https://www.pfeg.noaa.gov/products/PFELData/upwell/daily/p10dayac.all>), which is 72 km from my collection site. These data represent wind-driven cross-shelf transport per 100 meters of coastline. I calculated annual averages and standard deviations of the upwelling index from 2012-2016 and monthly from July 2016-June 2017.

2.5 Data analysis

Based on the size of the abalone included in this study's recruitment estimates (from 360-1303 μm), and growth rates based on a range of laboratory studies (mean of 27 μm /day, Table 3), the sampled abalone were determined to be 2 weeks to 2 months old (with a mean of 1 month old). Oceanographic factors can influence recruitment during pre-settlement phases (reproduction) as well as settlement and post-settlement survival. Therefore, simply looking at the oceanographic conditions around the time of sample collection could miss prior periods of influence. I summarized the oceanographic data in four 30-day periods back-dated from each monthly date of collection (0-30, 30-60, 60-90, and 90-120 days back). For each oceanographic parameter, I independently used a Granger causality test to evaluate whether there was an association between that parameter and recruitment at any of the four time lags. For significant wave height and the Bakun index, I used the mean values in each of the 30-day periods. For temperature, I independently evaluated the mean, standard deviation, minimum, and maximum values for the 30-day periods.

3. RESULTS

3.1 Species identification and sizes

In my monthly samples (2016-2017), I collected a total of 49 abalone >360 μm and 92 potential abalone <360 μm . Of the 22 samples sequenced that were >360 μm , 17 were successfully sequenced and all were red abalone (*H. rufescens*, >99% similarity). For the potential newly settled abalone, <360 μm , only five of the 55 were successfully sequenced because most (44) did not amplify and some (6) were contaminated with human DNA. Of the five sequenced, only one was a red abalone (>99% similarity *H. rufescens*; Figure 4), one was a flat abalone (>99% similarity *H. walallensis*), one was an opalescent nudibranch (>99% similarity *Hermisenda crassicornis*), and two were brown turban snails (>99% similarity *Tegula brunnea*). Given that there were only five non-contaminated and successful sequenced samples, and only one of these was a red abalone, the potential abalone (<360 μm) were not included in my recruitment estimates.

Confirmed newly settled abalone ranged in size from 300-1303 μm , with an average size of 790 μm (Figure 4). Based on a range of laboratory studies conducted on red abalone growth rates (Table 3), using a mean growth rate of 27 $\mu\text{m}/\text{day}$, I estimated that abalone in my samples were between 2 weeks and 2 months old (mean of 1 month old).

3.2 Annual recruitment patterns

Collected cobbles were measured onshore, and ranged in size from 40-4,353 cm^3 (Figure 5). Though cobbles with a high CCA cover were targeted, sometimes cobbles meeting this criteria were not found. As a result, cobbles ranged from 0-97% cover based

on visual estimates. Recruit density estimates show no patterns in relation to cobble size or CCA percent cover (Figures 6 and 7).

The average number of newly settled abalone found per cobble at HMLR ranged from 0.36-0.48 abalone/cobble for all years except 2015 (Figure 8). In 2015, the average abalone/cobble decreased to 0.08 (Figure 8). Though in my thesis, I only sampled at one site in the Monterey Bay, in 2012, O'Leary sampled three sites in southern Monterey Bay during the same fall month and found similar recruitment levels: 0.38 abalone/cobble at Lover's Point (36°37'30.30"N, 121°54'56.07 W) and Point Pinos (36°38'16.99"N, 121°56'2.04"W), and 0.49 abalone per cobble at HMLR.

The average number of newly settled abalone found per cobble was fairly consistent at the HMLR in the Monterey Bay across years (2012-2016) with the exception of 2015. Fall recruitment in 2012-2014, and 2016 ranged from 0.36-0.49 abalone/cobble but dropped to 0.08 in 2015. CDFW sampled one site in northern California consistently across the same time period, Van Damme in Mendocino County (Rogers-Bennett et al. 2016). In contrast with annually present recruits in the Monterey Bay, recruitment at Van Damme was sporadic with boom and bust years (Figure 8). From 2012 to 2016, the only year that Van Damme had abalone recruits was 2013, with an average of 1.05 red abalone/cobble. In 2013, Van Damme had recruitment 2.5 times higher than recruitment in that year in the Monterey Bay. However, all other years had no recruitment at Van Damme. CDFW sampled three sites per year from 2007-2015 and found similar boom and bust recruitment across sites in northern California.

3.3 Annual patterns of environmental conditions

Kelp density consistently ranged between 1.0 and 3.4 plants per 10m² at HMLR from 2012-2016, with no clear temporal trends (Figure 9D). Annual mean temperatures ranged from 11.7-12.6°C, with the exception of 2014 and 2015, when there was both an ENSO event and the North Pacific marine heatwave. During 2014-2015, annual mean temperatures increased to 13.2°C both years (Figure 9C). In the fall (September-November) when abalone recruits were collected annually, mean temperatures ranged from 12.4 to 13.4°C in 2012, 2013, and 2016, and increased to 14.5°C in 2014-2015. Red abalone recruitment did not show any apparent change during the first year of high temperature (2014) with 0.45 abalone/cobble in that year. However, recruitment decreased to 0.08 abalone/cobble in 2015, the second year of anomalously high temperatures.

The Bakun upwelling index shows a strong and persistent seasonal pattern every year, following the well-established upwelling seasonality in central California, whereby upwelling increases during the early spring and persists until the so-called relaxation season in fall months (Figure 9A, e.g., Pennington and Chavez 2000; Garcia-Reyes and Largier 2012; Walter et al. 2018). Surface gravity waves consistently came from the north or northwest (Figure 10). On an annual scale, there was a distinct seasonal pattern of strong waves in the winter months (November-February) and weaker waves during the remaining seasons, however, there was no apparent change in pattern between years (Figure 9B).

3.4 Monthly recruitment patterns

Newly settled abalone at HMLR were found throughout the year, with the exception of May, when no recruits were found (Figure 11). The average recruitment from July 2016 to June 2017 during which monthly samples were collected was 0.13 ± 0.04 abalone/cobble. The late summer and early fall showed the highest recruitment from 0.29 ± 0.10 abalone/cobble in August to the annual maximum of 0.36 ± 0.12 abalone/cobble in October. Recruitment significantly decreased in November through January with an average of 0.10 ± 0.07 to 0.03 ± 0.03 abalone/cobble. There appears to be another relatively small increase in recruitment in February with an average of 0.19 ± 0.11 abalone/cobble.

3.5 Monthly environmental conditions

During 2016 and 2017, the period in which I collected monthly samples, HMLR experienced colder temperatures during the transition to upwelling in early spring that persists throughout the summer as expected in the region (Figures 12A and 12C, Pennington and Chavez 2000; Booth et al. 2012; Garcia-Reyes and Largier 2012; Walter et al. 2018). During the fall, a large-scale relaxation of the upwelling favorable winds resulted in an expected increase in temperatures (Figure 12C). The fall relaxation had strong temperature fluctuations, which are associated with 1-2 week period upwelling/relaxation cycles, as well as higher-frequency fluctuations associated with strong internal wave and nearshore bore activity documented at this location (Figure 12B; Booth et al. 2012; Walter et al. 2012; Walter et al. 2014; Walter and Phelan 2016). Also as expected in the region, the winter had minimal temperature variability (Figure 12C),

because the offshore thermocline deepens and results in minimal internal wave and bore activity in the nearshore (Booth et al. 2012; Walter and Phelan 2016).

Red abalone recruitment was generally high in the late summer/fall (August-October), when temperatures were relatively warmer (13.4°C) and variable ($\sigma = 1.05^\circ\text{C}$, where σ denotes the standard deviation over the time period of interest; Figure 12C). However, there was also an increase in abalone recruitment in February when temperatures were lower (mean temperature of 12.8°C) and much less variable ($\sigma = 0.23^\circ\text{C}$; Figure 12C). The lowest recruitment occurred in months of warmer and highly variable temperature (e.g. November, mean = 13.7°C, $\sigma = 0.96$), and also in months with colder and less variable temperature (e.g. December-January, mean = 12.1°C and 12.8°C, $\sigma = 0.24^\circ\text{C}$ and 0.23°C respectively), and when temperatures were moderate and variable (e.g. May, mean = 10.9°C, $\sigma = 1.01^\circ\text{C}$; Figure 12C). Based on the Granger causality test, the mean, standard deviation, minimum, and maximum temperatures were not associated with monthly red abalone recruitment at any of the tested time lags (Table 4).

The annual wave cycle from 2016-2017 shows larger waves in the winter as expected for the region, however red abalone recruitment does not appear to correspond to the significant wave height (Figure 12B). The Granger causality test did not find any associations between the significant wave height and monthly abalone recruitment during any of the tested time lags (Table 4).

The annual upwelling index from 2016-2017 demonstrates an expected increase in upwelling during the spring and summer months, followed by declines in the late fall and winter (Figure 12A). The Granger causality test did not find an association between the upwelling index and abalone recruitment for any of the time lags tested (Table 4).

4. DISCUSSION

This is the first study to assess red abalone recruitment in the field throughout an entire annual cycle. This study shows that red abalone are capable of both reproducing and spawning throughout the year in the field. Within the 2016-2017 monthly sampling period, there was no statistically significant relationships between abalone recruitment and temperature, surface waves, or wind-driven coastal upwelling. In contrast, on an annual scale from 2012-2016, it appears that large temperature anomalies, such as those observed during the North Pacific marine heat wave, can decrease abalone recruitment. Recruitment was maintained during the first year of abnormally warm temperatures (2014), but decreased by 82% during the second year of abnormally warm temperatures.

Consistent annual recruitment in Monterey Bay is in stark contrast with boom and bust recruitment in northern California populations during the same time period. This is surprising, because at the time of the study, northern California abalone population densities were ~2.7 time greater than those in central California with 0.53 abalone/m² across 8 sites in northern California versus 0.13-0.2 abalone/m² in the southern Monterey Bay (CDFG 2010; Rogers-Bennett pers. comm. 2018; Micheli et al. 2008). The factors leading to the moderate, but consistent, recruitment observed in central California are not entirely clear. One possibility is that since abalone in Monterey Bay are aggregated in cracks and crevices due to sea otter predation (Lowry and Pearse 1973; Hines and Pearse 1982), the abalone have localized areas of high density that helps overcome the Allee effect and increases fertilization success. Thus, though densities are higher in northern California, it is possible that individual abalone are more dispersed in the absence of otter predation, and fertilization success varies widely. Another possible reason for different

annual recruitment patterns in central and northern California may be differences in regional oceanography and coastline features. Coastal embayments, such as Monterey Bay, often have increased retention times due to shielding from strong regional upwelling, and less surface wave forcing (Graham and Largier 1997, Walter et al. 2018). In these upwelling shadow systems, convergent fronts and enhanced residence times allow for the accumulation of buoyant organisms (Graham and Largier 1997, Ryan et al. 2014). The sites CDFW surveyed in northern California, including Van Damme, represent a much more open coastline. Thus, it is possible that the sheltered embayment of Monterey Bay provides a region where recruitment might be more consistent than an open coastline in northern California that experiences stronger upwelling. If this is the case, sheltered embayments along California's coast may provide recruitment hotspots, and this should be further evaluated.

A third possibility explaining more consistent annual recruitment in central California is that food resources are less limiting. Central California kelp forests are dominated by *Macrocystis pyrifera*, which is perennially present and continually releases large blades which can be consumed by abalone. In contrast, in northern California, kelp forests are dominated by *Nereocystis leutkeana*, which typically dies back annually. Lack of food for red abalone can negatively affect sperm and egg production (Rogers-Bennett et al. 2010), and it is suggested that in northern California reproduction failure may have occurred recently as a result of poor food resources as kelp died back due to high temperatures (Rogers-Bennett et al. 2016). However, there were recruitment failures in previous years when kelp densities were normal (Rogers-Bennett et al. 2016). Thus, the role of food limitation on long-term recruitment dynamics remains unclear in northern

California. At my study site in the Monterey Bay, though there were two years of elevated temperatures, there was no indication of reduced kelp (*Macrocystis pyrifera*) density, and does not appear that the 2015 recruitment crash was due to food limitation.

During the warm temperature anomaly from 2014-2015, red abalone recruitment was normal in the first year of warming, but dramatically declined during the second year of warming (2015) in the southern Monterey Bay. This suggests that an increase in water temperature may be impacting reproduction rather than settlement and survival. Increased sea surface temperatures began in late summer and early fall of 2014 (Leising et al. 2015). Thus, though recruits collected in October of 2014 would have been affected by the warming, adult abalone had been exposed to warmer temperatures for a relatively short period of time. There was no evidence of increased post-settlement mortality due to the warming in 2014. However, as the warming trend continued through October in 2015, prolonged heat stress may have caused abalone to reallocate energy resources from gamete production to survival, leading to the low recruitment observed in the fall of 2015. Thus, for red abalone, reproduction may be more susceptible to the negative effects of warming than survival of recruits post-settlement.

California red abalone populations collapsed in southern California in the 1990s largely due to poor fisheries management that grouped multiple species and used only fisheries dependent data (Karpov et al. 2000). In northern California, abalone were fished recreationally and was previously thought to be persistent. However in 2018, the fishery was closed due to population declines attributed to warming-induced food limitation. Thus, statewide, red abalone have been subjected to heavy fishing pressure, and have shown high susceptibility to changing environmental conditions, particularly increased

temperature. Further, though populations in central California have been persistent over time at low densities, they face high predation from sea otters and are at maximum density for the region (Lowry and Pearse 1973; Hines and Pearse 1982). Given the low abundance of abalone in southern California, and declining stocks in northern California, red abalone may be at risk statewide. When a fished resource like abalone is subject to both human and environmental impacts, it is critical to understand population replenishment through recruitment. This study demonstrates that even low density populations of abalone can persist through constant, moderate recruitment, and suggests that certain locations (e.g. coastal embayments) could be recruitment hotspots for this species. To better understand the complex spatial and temporal patterns of recruitment statewide, recruitment samples should be collected at numerous locations at finer temporal scales. However, it is extremely labor intensive processing recruit samples and identifying new settlers using microscopy. Sorting each cobble sample takes between 1 and 4 hours (dependent on the abundance of settlers), limiting the ability to collect and process daily samples. At a monthly scale, I found no association between recruitment and temperature, upwelling conditions, or wave forces. However, daily samples might reveal associations with temperature, upwelling, or waves that I did not find in my study. In the future, new techniques like metagenomics might allow rapid processing of samples of mixed settlers to determine if abalone DNA is present. Since most cobbles contained 0-3 abalone, presence or absence of abalone DNA from numerous field samples through metagenomics would allow mapping of temporal and spatial patterns in recruitment. This could provide information not just on abalone, but dozens of new settlers found on CCA covered cobbles or other collection devices.

One limitation of my study was the lack of confidence in identifying abalone <1 month old (<360 μ m), which I therefore did not include in my recruitment estimates. Based on the five sequenced specimens in this size range, it is possible that up to 20% of the 92 specimens I found in this size range were abalone. Using this estimate, average monthly recruitment for 2016-2017 would have increased only marginally from an average of 0.13 ± 0.04 abalone/cobble to 0.18 ± 0.04 abalone/cobble. Thus, even though I likely underestimated recruitment by missing abalone <2 weeks old, the data appear to be robust. Evaluating recruitment at this stage on a monthly scale has never been done before for red abalone. Though the annual and monthly recruitment samples I evaluated came from only one site in the Monterey Bay, in 2012, samples were collected from three sites in the fall (O'Leary unpublished data) and recruitment was broadly similar across sites. Thus, it seems likely that the results described here represent broader conditions of the southern Monterey Bay.

This study has implications for management of the red abalone fishery and for recovery efforts. This study shows that red abalone have the capacity to spawn and recruit year round in the field, with a general increase in recruitment from August to October and in February. CDFW has traditionally closed the northern California fishery for the month of July each year to allow for spawning and recruitment. It does not appear that July is a peak recruitment period, and the CDFW might want to re-evaluate this closure month in the future when abalone fishing is reopened in northern California. However, the month-long closure during the middle of the open season in northern California still acts to alleviate overall fishing pressure, and may be kept in place for that reason. The time period CDFW (Rogers-Bennett et al. 2016) has been using for its annual

sampling in northern California (August-October) seems to be an appropriate to evaluate trends. While I found no clear environmental cues which predict monthly recruitment peaks, prolonged warming events are detrimental to abalone recruitment due to reproductive failure, as shown in our annual time series.

In coral research, people are searching for climate refugia, locations where either temperature does not fluctuate as much or where organisms are better adapted to temperature fluctuations (Lesser et al. 2009, Bongaerts et al. 2010, Langlais et al. 2017). If warming events increase in frequency along the California coastline, identifying resistant abalone populations and areas with less variable temperature may be critical to ensure adequate abalone reproduction. Further, my study indicates that embayments (such as the Monterey Bay) may have more consistent red abalone recruitment than open shorelines (such as Van Damme in northern California). If this is borne out through further research, embayments may represent recruitment hotspots that should be protected, and could be used as locations for restorative outplanting to maximize population reestablishment.

5. TABLES

Table 1: Literature review on the effects of temperature on abalone reproduction, transport, settlement, and post-settlement survival/growth. Because there were few publications on red abalone, the review includes multiple species globally. The “Temperature Change” column represents the change in temperature from the average ambient temperature. In the “Recruitment Stage” column, R = recruitment, LD = larval development, S = settlement, and PS = post-settlement. In the “Study Type” column, L = laboratory, F = field, and M = model.

Recruitment Stage	Reference	Species	Location	Study Type	Average Ambient Temperature	Temperature Change	Factor Evaluated	Effect: Temperature Increase	Comments
R	Vilchis et al. 2005	<i>Haliotis fulgens</i>	southern California	L	16	+2.5	gonad development	-	reproduction was more strongly influenced by abundance in food resources
R	Boch et al. 2017	<i>Haliotis rufescens</i>	central California	L	13	-4	fertilization rates	+	fertilization rates decreased during colder upwelling periods
R	Rogers-Bennet et al. 2010	<i>Haliotis rufescens</i>	northern California	L	11	+5	sperm production/ fecundity	-	reproductive failure in males and diminished fecundity in females
R	Vilchis et al. 2005	<i>Haliotis rufescens</i>	southern California	L	16	-2.5	gonad development	-	cooler temperature promotes higher gonad development
LD	Leighton 1974	<i>Haliotis rufescens</i>	southern California	L	15	+1	survival, growth	+	
LD	Searcy-Bernal 1999	<i>Haliotis rufescens</i>	northern California	L	14	+2	survival	-	larval competency decreased
LD	McCormick et al. 2012	<i>Haliotis rufescens</i>	southern California	L	14	0	survival	+	larval competency periods were extended at 14°C in comparison to previous transport period estimations
LD	Leighton 1972	<i>Haliotis sorenseni</i>	southern California	L	16	+4	larval development	+	individuals did not survive once they settled at warmer temperature
LD	McCormick et al. 2016	<i>Haliotis sorenseni</i>	southern California	L	12	±3	survival	-	
S	Rodriguez-Valencia et al. 2004	<i>Haliotis corrugata</i> , <i>Haliotis fulgens</i>	Mexico	F	19	+2	settlement	-	warm temperatures caused by ENSO conditions
S	Lu et al. 2004	<i>Haliotis diversicolor</i>	China	L	NA	+	survival	+	ambient temperature was not indicated
S	Guzman del Proo et al. 2013	<i>Haliotis fulgens</i>	Mexico	M	21	±2	settlement	-	
S	Tegner et al. 2001	<i>Haliotis rufescens</i>	southern California	F	16	+3	settlement	-	warm temperatures caused by ENSO conditions
S	Shepherd et al. 1985	<i>Haliotis scalaris</i>	Australia	F	NA	+	settlement	+	ambient temperature was not indicated
S	Forster et al. 1982	<i>Haliotis tuberculata</i>	England	F	NA	+	settlement	+	ambient temperature was not indicated
PS	Searle et al. 2006	<i>Haliotis iris</i>	New Zealand	L	8	+4-18	growth/survival	+/-	growth was higher, however survival decreased (abalone were larger than in this study: 10-60 mm)
PS	Britz et al. 1997	<i>Haliotis midae</i>	South Africa	L	16	+5	growth	-	juvenile abalone tested were larger than in this study: 17.5 mm
PS	Steinarsson & Imsland 2003	<i>Haliotis rufescens</i>	central California	L	15	+5	survival	-	mortality increased at 20°C (abalone were larger than in this study: 15.6-95.3 mm)
PS	Searcy-Bernal et al. 2007	<i>Haliotis rufescens</i>	Mexico	L	NA	+0.5	growth	+	ambient temperature was not indicated
PS	McCormick et al. 2016	<i>Haliotis sorenseni</i>	southern California	L	12	+3	survival	-	

Table 2: Literature review on the effects of wave forces/water movement on abalone reproduction, transport, settlement, and post-settlement survival/growth. Because there were few publications on red abalone, the review includes multiple species globally. In the “Recruitment Stage” column, R = recruitment, and PS = post-settlement. In the “Study Type” column, L = laboratory, F = field, and R = review paper.

Recruitment Stage	Reference	Species	Location	Study Type	Wave action	Factor Evaluated	Result: Increased Waves	Comments
R	Sasaki 1985	<i>Haliotis discus hannai</i>	Japan		increase	spawning	+	storms are cue for spawning
R	Onitsuka et al. 2007	<i>Haliotis diversicolor</i>	Japan	F/L	increase	gonad development	+	typhoons trigger spawning
R	Campbell et al. 2003	<i>Haliotis kamtschatkana</i>	Canada	L	decrease	gonad development/ fecundity	-	higher fecundity found in abalone sheltered from wave action
R	Zimmer & Riffell 2011	<i>Haliotis rufescens</i>	NA	L	decrease	sperm motility, gamete encounter rate	-	spawning abalone aggregated where water motion decreased
S	Onitsuka et al. 2007	<i>Haliotis diversicolor</i>	Japan	F/L	increase	settlement	+	higher abundance of new settlers following typhoons
S	Roberts et al. 1999	<i>Haliotis iris</i>	New Zealand	F	increase	recruitment	-	low recruitment found on coasts with high wave exposure
S	Boxshall 2000	<i>Haliotis rufescens</i>	NA	L	decrease	settlement	-	larvae were more likely to settle when small-scale flows were mild
PS	Onitsuka et al. 2010	<i>Haliotis diversicolor</i>	Japan	R	increase	survival	-	higher mortality occurred with storm induced waves
PS	Naylor & McShane 2001	<i>Haliotis iris</i>	New Zealand	F	increase	survival	-	recruit survival decreased in a bay exposed to ocean swells

Table 3: Literature review of laboratory studies on red abalone (*Haliotis rufescens*) post-settlement growth per day.

Reference	Location	Temperature (°C)	Study Duration (Days)	Abalone Growth (µm/day)	Influential Factors
Searcy-Bernal et al. 2007	Baja California, MX	14.3-15	100	37 - 63	temperature/light intensity
Gabriel Correa-Reyes et al. 2009	Baja California, MX	18	50	18.5 - 34.2	diet
Rogers-Bennett et al. 2010	Mendocino/Sonoma, CA	14	NA	7.14	NA
Munoz et al. 2012	Chile	13	30	16.8 - 21.2	diet
Anguiano-Beltran et al. 2012	Baja California, MX	16-18	10	4.1 - 11.2	diet
Anguiano-Beltran & Searcy-Bernal 2013	Baja California, MX	17.5	63	44.6 - 61.6	water flow

Table 4: Granger causality test results for oceanographic parameters. Non-significant p-values indicate that there was no correlation between the parameter and recruitment at any of the time periods evaluated (0-30, 30-60, 60-90, and 90-120 days back from the date of collection).

Predictor	F Statistic	Numerator df	Denominator df	p-value
Temperature Mean	1.895249	4	6	0.2306326
Temperature Standard Deviation	2.276225	4	6	0.1760146
Temperature Minimum	1.523069	4	6	0.3067987
Temperature Maximum	2.184267	4	6	0.1875189
Significant Wave Height	1.978149	4	6	0.2170654
Upwelling Index	1.005436	4	6	0.4729517

6. FIGURES

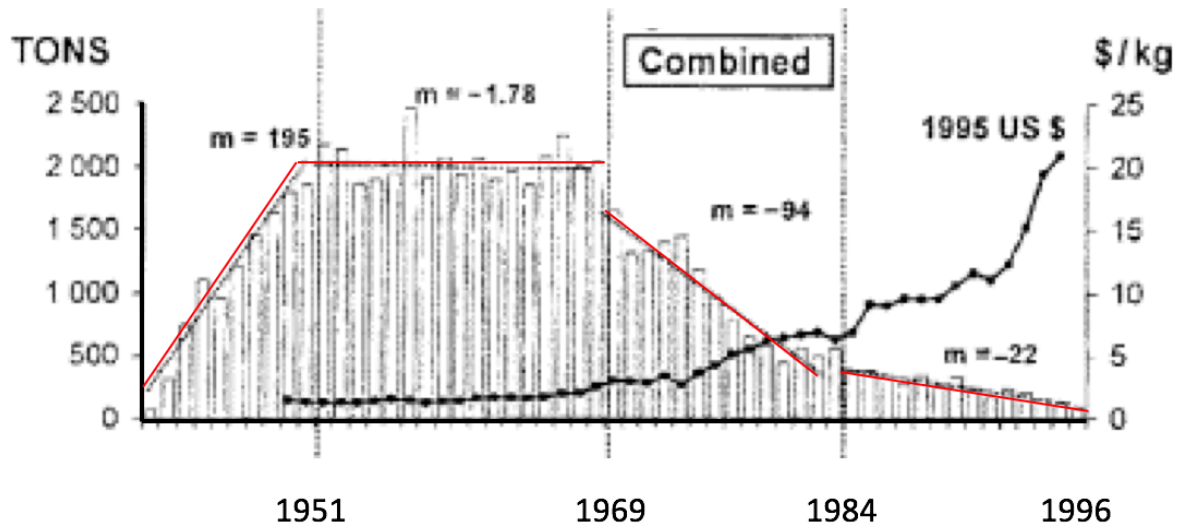


Figure 1: Time series of commercial landings highlighting the decline of abalone (red, pink, green, black, and white abalone combined). Bars represent the commercial landings (metric tons) of the California abalone fishery. Regression lines for each divided period are represented by solid red lines (figure from Karpov et al. 2000).

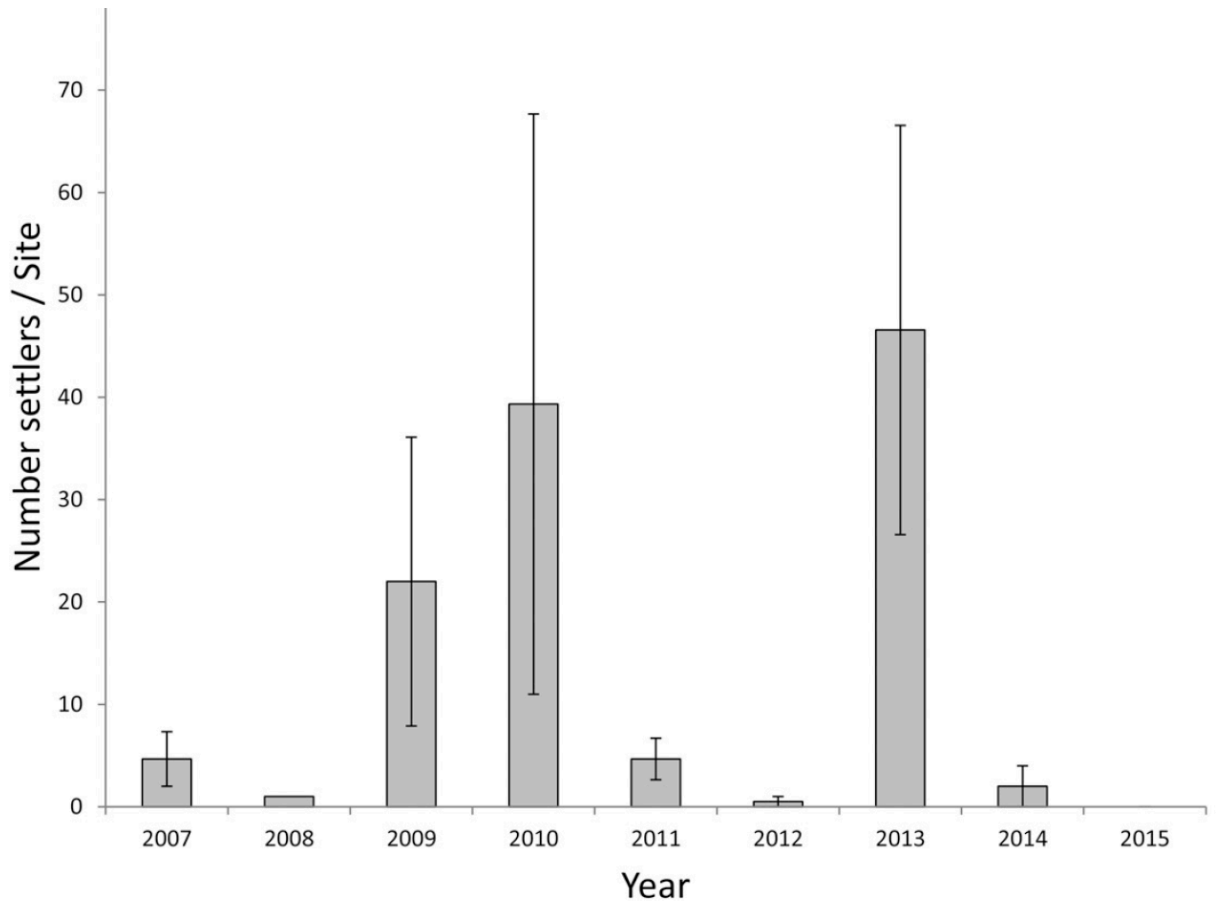


Figure 2: The number of newly settled abalone captured from cobbles (\pm SE) northern California (Mendocino and Sonoma Counties) from 2007 to 2015 (figure from Rogers-Bennett et al. 2016). In any given year, three sites were surveyed, but as the sites surveyed varied, a total of eight sites are represented. One site, Van Damme, in Mendocino County, was surveyed every year as one of the three sites.

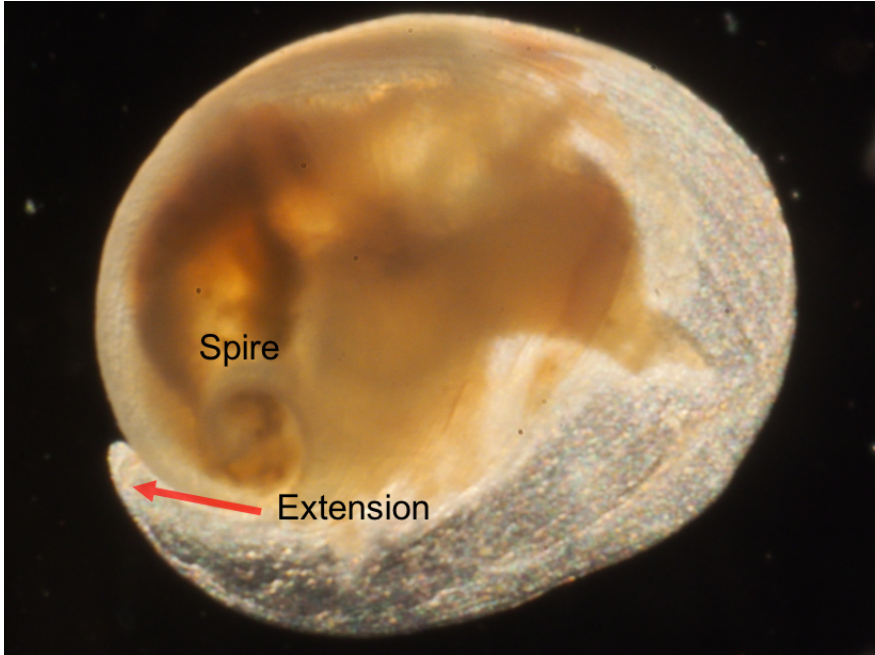


Figure 3: The extension of the abalone shell under the spire was characteristic of a newly settled abalone using morphological identification.

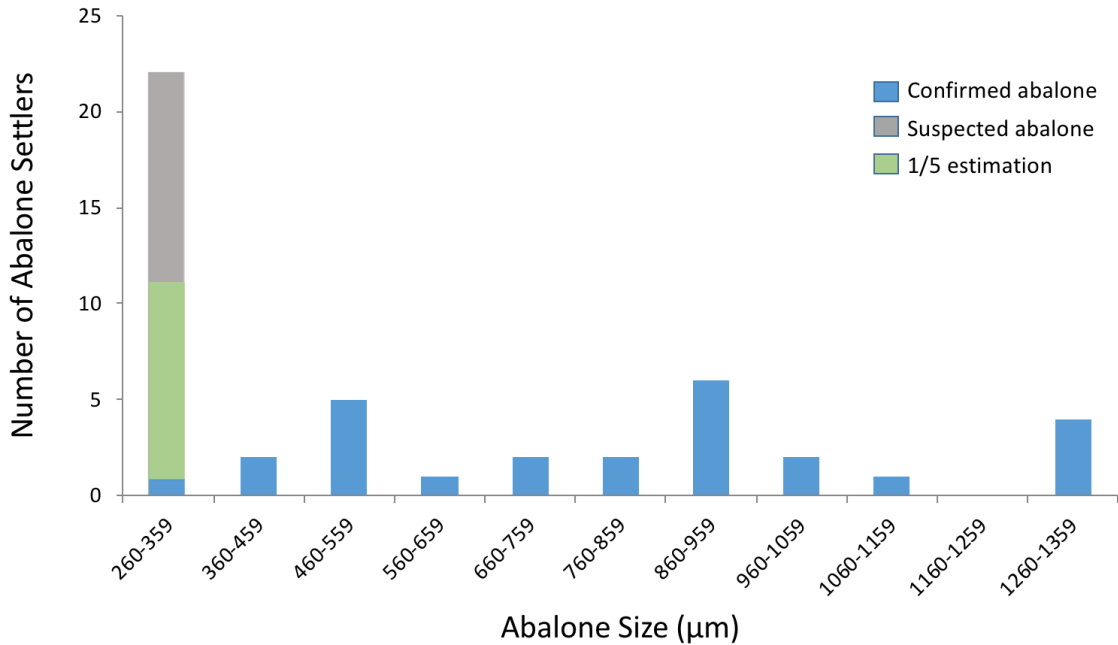


Figure 4: The size frequency distribution of newly settled abalone found on crustose coralline covered cobbles at HMLR. The blue bars indicate the genetically or morphologically confirmed abalone (>360 µm). The gray bar, in the smallest size class (<360 µm), indicates the total number of “suspected” newly settled abalone counted. However, since only five of these sequenced, and only one of the five of was an abalone, the green bar is my estimate of how many abalone would have been in this size class if 1/5 is a good estimate. However, due to uncertainty in identifications of these small specimens, I only included sizes >360 µm in my analyses.

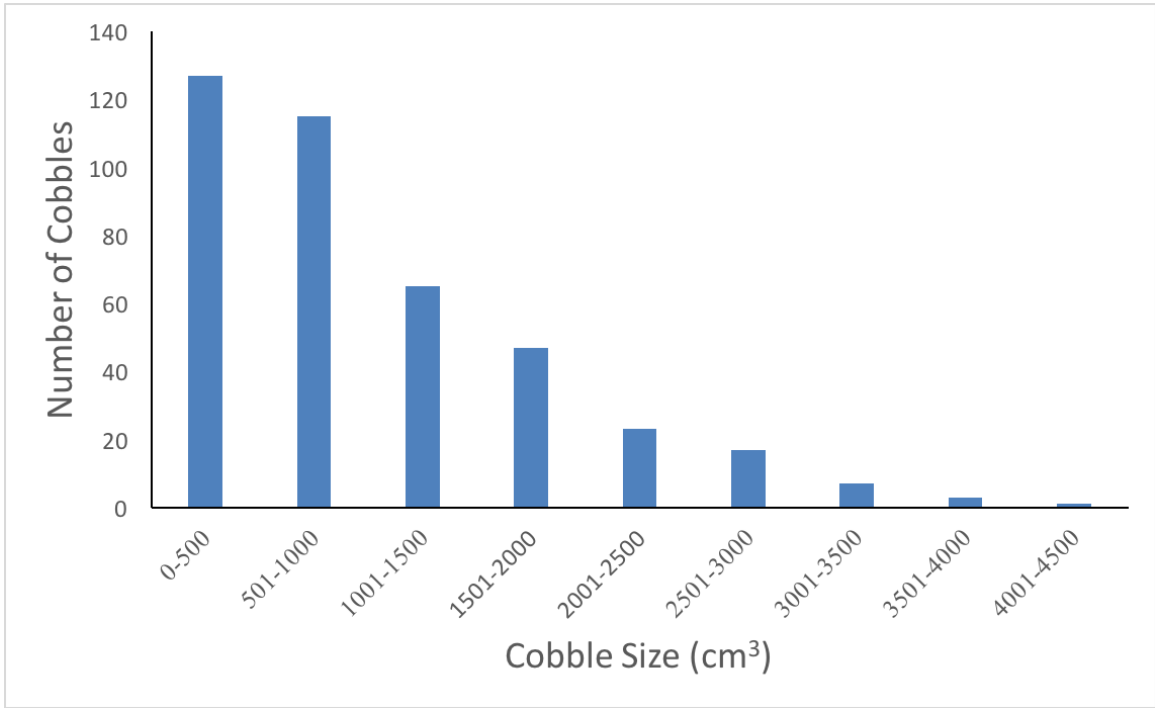


Figure 5: The size frequency distribution of cobbles (cm³) collected at HMLR.

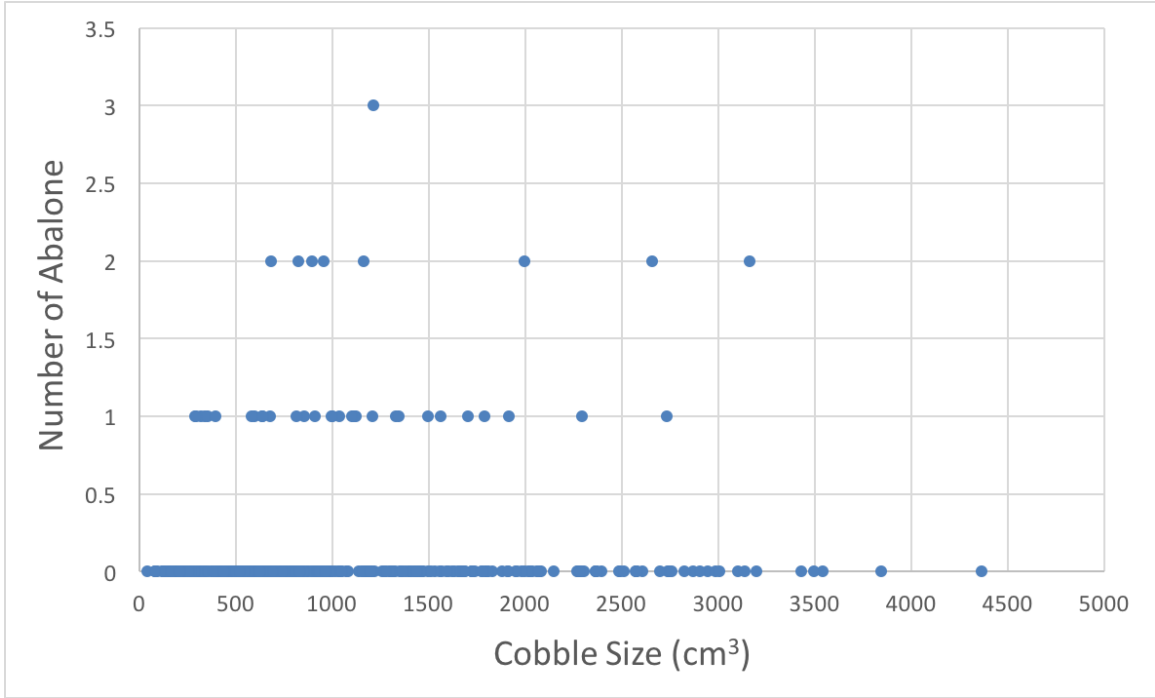


Figure 6: The number of newly settled abalone found per cobble as a function of the cobble size at HMLR.

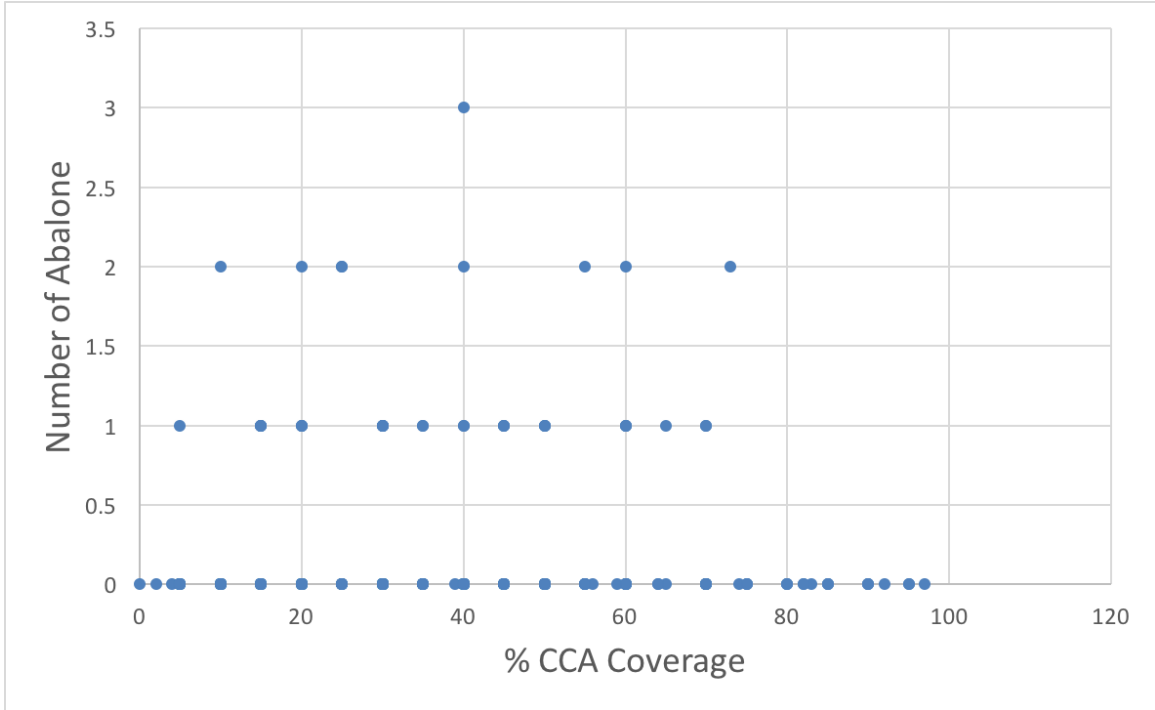


Figure 7: The number of newly settled abalone found per cobble as a function of the crustose coralline algae on the cobble at HMLR.

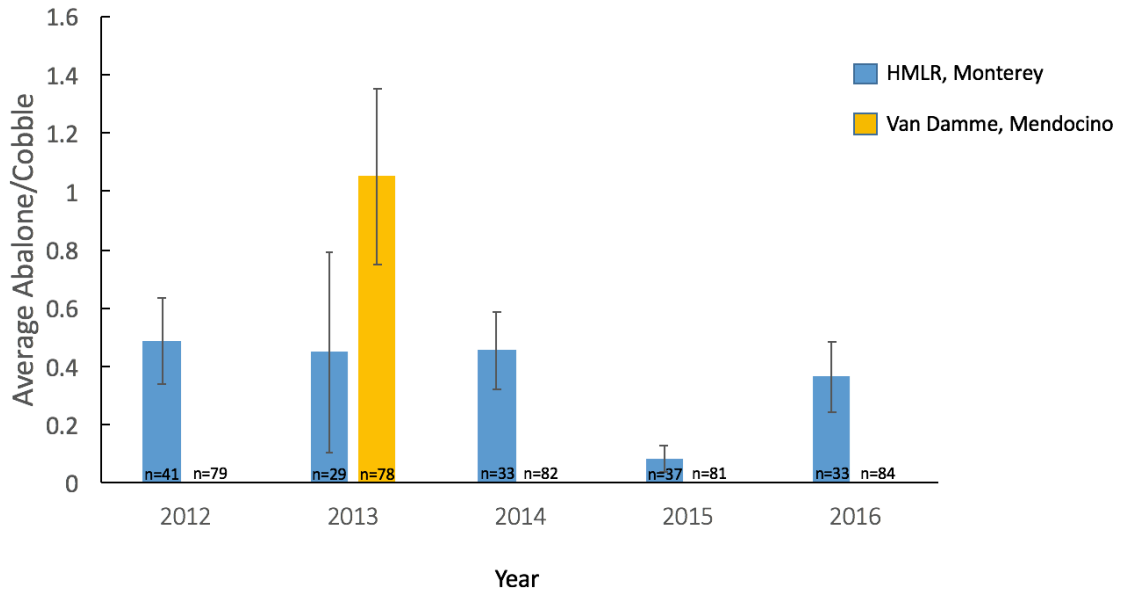


Figure 8: The average number of newly settled abalone (\pm SE) per crustose coralline-covered cobble collected annually at Hopkins Marine Life Refuge in central California (blue) and Van Damme State Park in northern California (yellow) from 2012 to 2016. Van Damme was the only site that was consistently surveyed in northern California across this time period. The number of cobbles sampled at each site during each year is shown at the bottom of the bars.

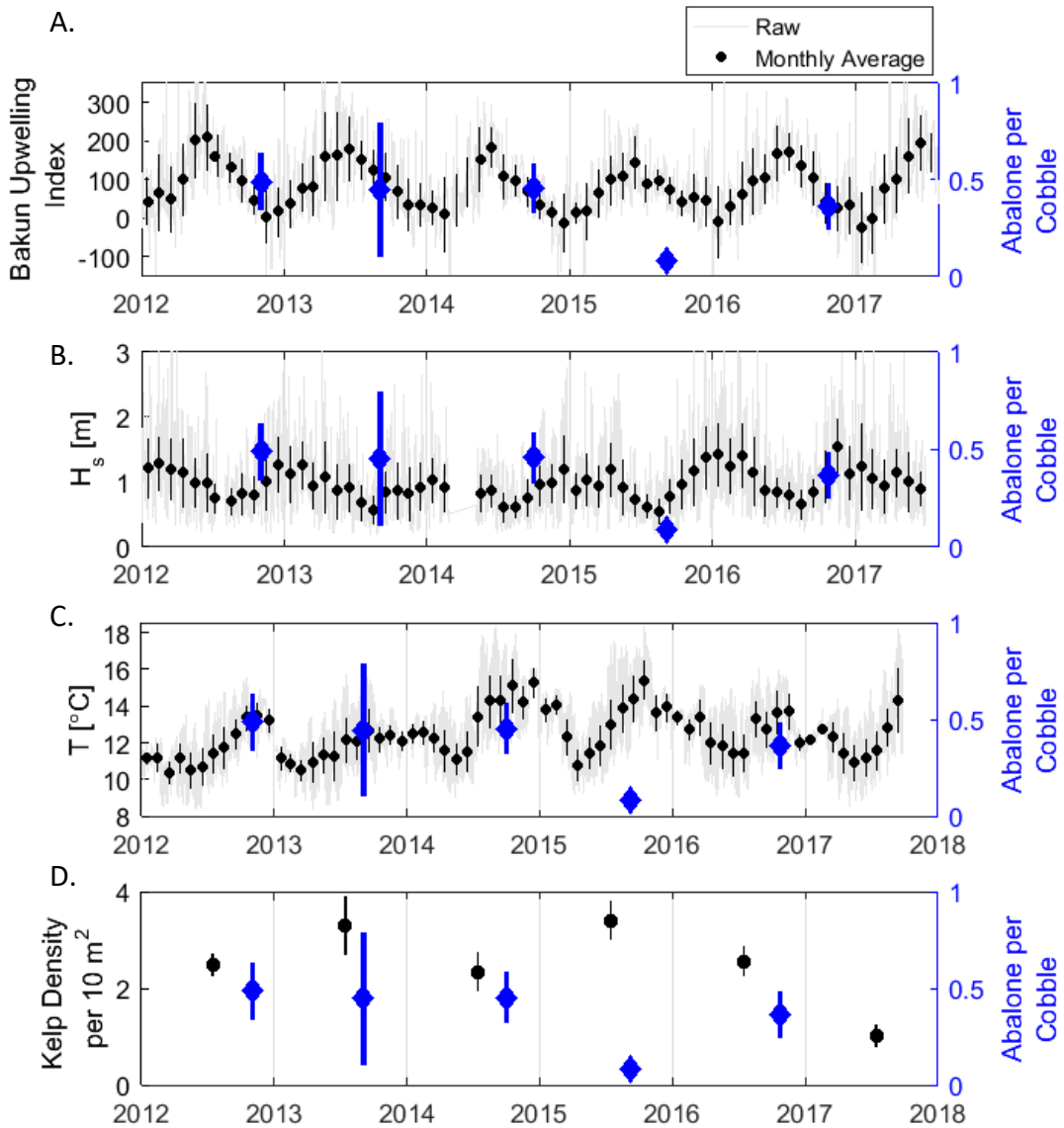


Figure 9: Time series of environmental conditions (left y-axis) and annual abalone recruitment (right y-axis) at HMLR from 2012-2017. For environmental conditions, gray lines denote the raw data, while black dots and error bars represent the monthly mean and standard deviation, respectively. For abalone recruitment, blue dots and error bars represent the mean and standard deviation, respectively. (A) Bakun upwelling index (m^3/s per 100 m of coastline) (B) Significant wave height (C) Temperature, and (D) mean kelp (*Macrocystis pyrifera*) density.

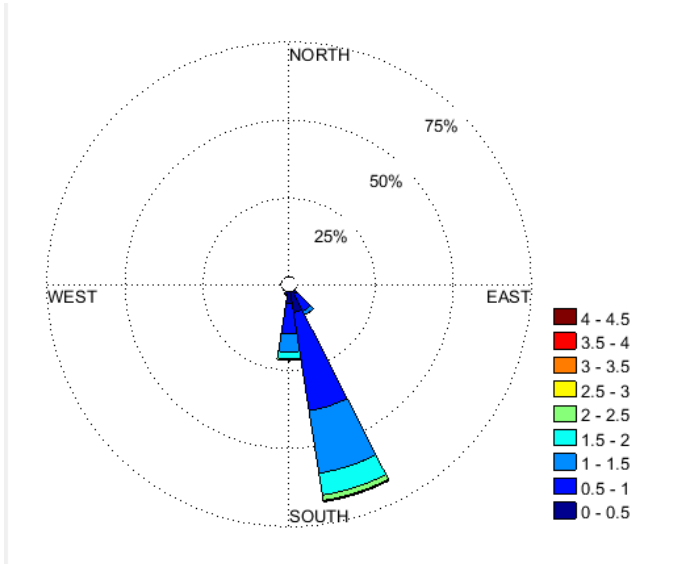


Figure 10: Directional wave rose showing the distribution of significant wave height as a function of the dominant wave direction.

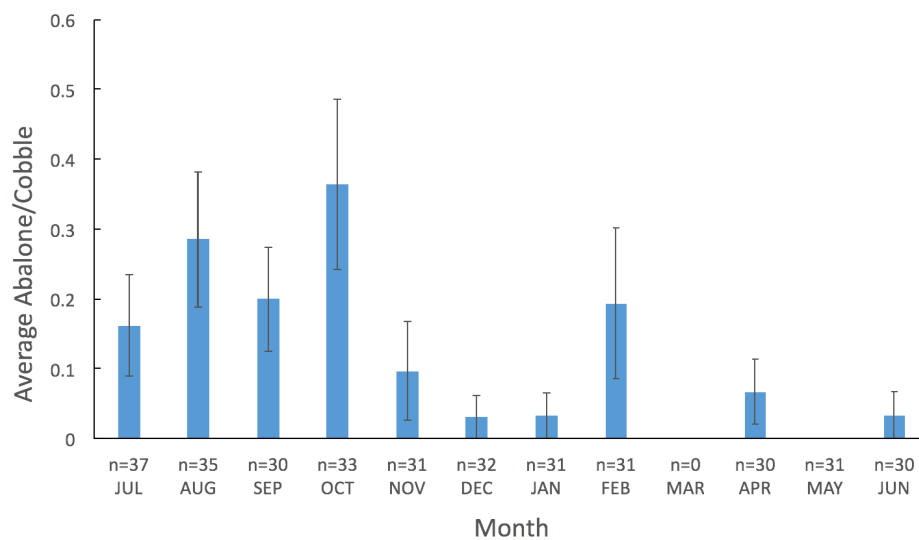


Figure 11: The average number of newly settled abalone (\pm SE) per crustose coralline-covered cobble collected monthly at HMLR in central California from July 2016 to June 2017. The number of cobbles sampled at each site during each year is also shown at the bottom of the bars.

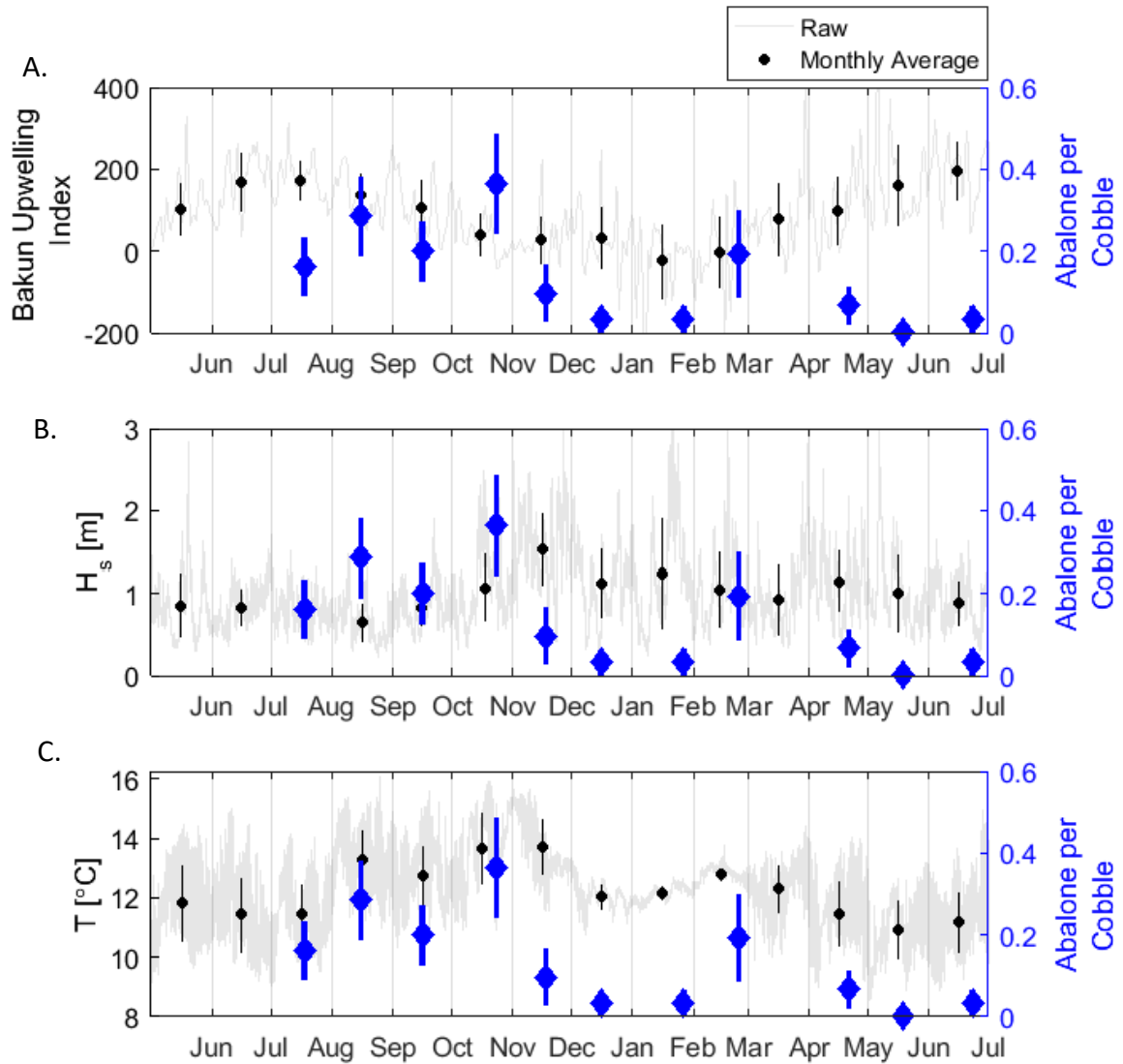


Figure 12: Time series of environmental conditions (left y-axis) and monthly abalone recruitment (right x-axis) at HMLR from July 2016-June 2017. For environmental conditions, gray lines denote the raw data, while black dots and error bars represent the monthly mean and standard deviation, respectively. For abalone recruitment, blue dots and error bars represent the mean and standard deviation, respectively. (A) Bakun upwelling index (m^3/s per 100 m of coastline) (B) Significant wave height, and (C) Temperature.

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