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Bird, Amanda C

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DETERMINING POPULATION STRUCTURE, REPRODUCTIVE POTENTIAL,
AND HABITAT ASSOCIATIONS OF PINTO ABALONE (*HALIOTIS*
KAMTSCHATKANA) IN SOUTHERN CALIFORNIA

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Faculty of

California State University, Fullerton

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

in

Biology

By

Amanda Cathleen Bird

Thesis Committee Approval:

Danielle C. Zacherl, Department of Biological Science, Chair

Paul Stapp, Department of Biological Science

Douglas J. Eernisse, Department of Biological Science

Melissa J. Neuman, NOAA National Marine Fisheries Service

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ABSTRACT

This study provides the first assessment of demographic and habitat information for pinto abalone (*Haliotis kamtschatkana*) in San Diego, California, two decades after the closure of all abalone fisheries in southern California. SCUBA surveys conducted from June 2014 to December 2016 indicate that current low densities (0-0.03 individuals/m²) were far below critical thresholds identified for other abalone species (0.15-0.30 abalone/m²) for successful spawning and recruitment. A broad range of sizes were represented (13-146 mm), however, only 95 individuals were found. Some sites showed significant aggregation of adult (> 50 mm) pinto abalone, 30% of adults had a nearest-neighbor within a critical spawning distance of 2 m, and 65% had a neighbor within 5 m, indicating that at least a small proportion of individuals may be capable of reproducing successfully. Pinto abalone showed a significant preference for boulder habitat at a lower relief (< 10 cm) relative to available habitat— a preference that may influence aggregation around habitat features and enhance reproduction. The frequency, timing, and broad spatial distribution of these surveys was not sufficient to measure patterns in recruitment or changes in abundance, particularly over a strong El Niño event that occurred during the study period. There is a critical need for consistent long-term monitoring in southern California to better understand demographic and environmental processes affecting recovery and persistence of populations, particularly at the southern edge of the broad range of pinto abalone.

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CHAPTER 1

INTRODUCTION

Conservation research is often focused on two central and interconnected questions: 1) what allows historically overexploited populations to recover from a severely depleted state; and 2) at what point is human intervention necessary to prevent extinction? Our ability to measure recovery is complicated by a lack of important historic information on population abundances prior to exploitation, and a lack of understanding of the demographic and environmental processes that drive natural population fluctuations in the *absence* of exploitation (Jackson et al. 2001). Other factors such as disease (Burge et al. 2014), environmental disturbances (e.g., El Niño events, Dayton et al. 1999), global climate change (Vilchis et al. 2005), anthropogenic and environmental stressors (Dayton et al. 1999; Tegner & Dayton 2000), and density-dependent reproductive failure (Allee 1931) may negatively impact depleted populations and limit recovery. However, some coastal ecosystems and associated species show signs of resilience in the face of numerous stressors (O’Leary et al. 2017). Effective recovery and management requires a better understanding of the demographic and environmental processes that affect depleted populations, which can only be captured through long-term monitoring and incorporation of available historic data to measure success of conservation efforts.

Historically, seven species of abalone, large marine gastropods in the family Haliotidae (genus *Haliotis* Linnaeus, 1758), were abundant along the west coast of North America (Geiger 1999) and supported viable subsistence fisheries for centuries (Cox 1962). However, modern commercial fishing pressure (which peaked during the mid-1900s), disease, and environmental conditions led to precipitous declines in abalone abundance (Tegner et al. 2001) over the span of only a couple of decades prompting the closures of most fisheries (CDFW 2005). In California, all fisheries south of San Francisco were closed in 1997 (Karpov et al. 2000). Most abalone populations have not since recovered (Rogers-Bennett et al. 2002). A free-dive only red abalone (*Haliotis rufescens*) (Swainson, 1822) fishery north of San Francisco remains, but is currently (2018) closed due to high mortality of red abalone likely resulting from widespread decline of kelp forest habitat following a recent El Niño event (CDFW 2018).

A host of environmental factors may have played a role in continued declines, or lack of recovery, since fishery closures (Tegner et al. 2001). These include: 1) disease, such as withering syndrome, (Altstatt et al. 1996; Friedman et al. 2000; VanBlaricom et al. 2009; Neuman et al. 2010; Ben-Horin et al. 2013); 2) competitive interactions and predation, particularly within the range of sea otters (*Enhydra lutris*; Hines & Pearse 1982; Fanshawe et al. 2003; Neuman et al. 2010; Chadés et al. 2012); 3) differential susceptibility to mortality among various life stages (Shepherd & Breen 1992); 4) climate change (Rogers-Bennett 2007) and El Niño events causing warmer than average sea temperatures which affect food abundance/quality and reproduction (Tegner et al. 2001; Vilchis et al. 2005); and 5) reproductive failure at low adult densities (Prince et al. 1988; Shepherd & Brown 1993; Hobday et al. 2001; Dowling et al. 2004).

For broadcast-spawning marine invertebrates, successful reproduction and recruitment may be reduced at low population densities as distances between potential mates increase and the probability of gamete fertilization diminishes (Levitan et al. 1992; Levitan & Young 1995). An *in situ* study of fertilization success in an Australian abalone species, *Haliotis laevis*, demonstrated that fertilization of female abalone eggs decreased dramatically from 48% at a distance of 2 m to 2.8% at 16 m downstream of a sperm source (Babcock & Keesing 1999). Recruitment failure was observed in *H. laevis* populations at densities of 0.15/m² (Shepherd & Partington 1995) and 0.30/m² (Shepherd & Brown 1993). Average distance between adults (hereafter, nearest-neighbor distances) for these populations was 1-2 m. Such an occurrence where reproductive success declines below a critical density threshold is referred to as an Allee effect (Allee 1931). It has been suggested that below a critical density of 0.15 – 0.30/m², abalone populations are susceptible to Allee effects (Babcock & Keesing 1999).

Due to continued population declines following fishery closure, in 2001, the white abalone (*H. sorenseni* Bartsch, 1940) became the first marine invertebrate listed as Endangered under the U.S. Endangered Species Act (ESA) (66 FR 29046) followed shortly thereafter by the black abalone in 2009 (74 FR 1937). Three other species, the pinto (*H. kamtschatica* Jonas, 1845), green (*H. fulgens* Philippi, 1845) and pink (*H. corrugata* Gray, 1828) abalones, are currently identified as Species of Concern (69 FR 19975) by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS). Species of Concern are recognized as those potentially at risk that may require proactive conservation actions, but for which not enough is known to develop comprehensive management plans (NMFS 2009).

In 2005, the California Department of Fish and Wildlife (CDFW; formerly the California Department of Fish and Game) released the Abalone Recovery and Management Plan (ARMP) to: 1) guide recovery efforts for the seven abalone species in southern California that have severely reduced populations, 2) manage current and future fisheries, and 3) prevent future population declines for all species throughout California with the ultimate goal of reestablishing sustainable fisheries. Recovery, paraphrased here, is defined as rebuilding populations throughout a species' historic range to self-sustaining levels. Two criteria are used in the ARMP to evaluate whether recovery goals are being met: 1) evidence of a broad size distribution with 25% of individuals in the population larger than the legal size limit for each species, and 2) densities above 0.2 animals/m² (2,000 animals/ha), which is based on reports of recruitment failure in other abalone species at densities of 0.15-0.30 abalone/m² (Tegner et al. 1989; Shepherd & Brown 1993; Shepherd & Partington 1995; Karpov et al. 1998; CDFW 2005).

In 2013, NMFS was petitioned to list the pinto abalone as threatened or endangered in response to evidence of continued declines in abundance despite fishery closures, primarily in areas throughout the northern range of the species. In 2014, a review of the status of the species was conducted and it was concluded that listing was not warranted; the review panel emphasized that the lack of baseline data increased the uncertainty of their assessment and pointed to a significant need for improved monitoring of this species throughout its range, particularly in southern California where basic ecological data were lacking (70 FR 11998; NMFS 2014).

The pinto abalone has the broadest geographic distribution of the seven abalone species native to the west coast of North America. It ranges from Salisbury Sound in

Sitka, Alaska to Bahía Tortugas, in Baja California, Mexico and is associated with macroalgal communities (Geiger 2000). In the northern extent of its range, pinto abalone are most common in intertidal to shallow subtidal kelp forest habitats (0-20 m depth; Sloan & Breen 1988). Conversely, in the southern portion of its range, pinto abalone are strictly subtidal, occurring up to 40 m but are most common between 20-30 m (Geiger & Owen 2012). Two other abalone species, the flat (*H. walallensis* Stearns, 1898) and the red abalone, found as far north as Washington and Oregon, respectively (Geiger 2000), are also found deeper in the southern portion of their range, which may be related to cooler water temperature with increasing depth (Cox 1962). In addition to exhibiting a trend towards occupying increasingly deeper habitat from the northern to southern extent of its range, the pinto abalone also shows a distinct shift in shell morphological features; adult southern pintos have slightly more convex, rounder and heavier shells (McLean 1966; Geiger & Owen 2012). Likely these morphological and distributional distinctions contributed to modifications in the species designation over the years.¹

¹Prior to NOAA initiating a Status Review, the pinto abalone was subdivided into two subspecies as recognized by McLean (1966): *Haliotis kamtschatkana kamtschatkana* (the “northern” abalone), occurring from Sitka, AK to Point Conception, CA and *Haliotis kamtschatkana assimilis* (the “threaded” abalone), found from Monterey, CA to Bahía Tortugas, Baja California, Mexico. Originally, these were identified as two distinct species, *H. kamtschatkana* Jonas, 1845 and *H. assimilis* Dall, 1878. However, McLean (1966) and Geiger (2000) are among those who have regarded them as a single species but with geographically adjacent subspecies characterized size and shell feature distinctions. As McLean (1966) and others have noted, a transition zone occurs in central California where there is an overlap of shell features. Although not studied experimentally, the geographic transition observed could be related to differences in habitat characteristics and environmental conditions throughout the range of the species, rather than any pronounced reproductive isolation that could warrant subspecies designations. In the status review, NMFS (2014) cited two pieces of evidence in support of recognizing only a single species, the pinto abalone (*Haliotis kamtschatkana*). First, three separate studies found no genetic differentiation between abalone sampled north and south of the putative transition zone, each with shell characteristics representative for the subspecies, using 1) sequenced portions of the mitochondrial genes COI and Cyt b as well as VERL (vitelline envelope receptor for lysin; Gruenthal & Burton 2005); 2) sperm lysin and VERL (Supernault et al. 2010); and 3) COI and lysin (Straus 2010). Second, they noted the lack of consistent morphological separation. Owen & Raffety (2017) compared even more extensive collections of shells and provide evidence of an even broader transition zone; they found the “northern” morphology represented between Alaska and Baja California and the “southern” morphology found as far north as Monterey, California. This

Very little information exists on pinto abalone populations prior to modern commercial fisheries and thus current abundance estimates have little or no pre-fishery basis for comparison. British Columbia in Canada and Alaska and Washington in the United States (Geiger 2000), the northern range of pinto abalone, historically supported the largest commercial fisheries. Currently, all fisheries are closed except for a small subsistence and personal-use fishery in southeastern Alaska (NMFS 2014). At sites in the Haida Gwaii area of British Columbia, average densities of 16 abalone/m² (ranging from 0-28/m²) were reported in 1978 during the fishery (Breen & Adkins 1979; Sloan & Breen 1988). In 2007, densities of large adult and mature abalone in Haida Gwaii declined to 0.03-0.15 abalone/m² (Hankewich et al. 2008; NMFS 2014), levels at or below critical density thresholds and just one example of an area within the range of pinto abalone that experienced dramatic declines in abundance. In British Columbia, the pinto abalone was listed as “endangered” both under the Canadian Species at Risk Act in 2009 and on the IUCN Red List in 2006. In Washington, historical abundances are not well known but the best current available information suggests that pinto abalone abundances continue to decline and are experiencing recruitment failure (Rogers-Bennett 2007; Rogers-Bennett et al. 2011; Rothaus et al. 2008; Bouma et al. 2012). However, there is recent evidence of increasing densities above critical thresholds and recruitment at some long-term monitoring sites in southeast Alaska (average adult densities = 0.17-0.29/m²; Donnellan

overlap is quite a bit larger than Monterey to Point Conception (McLean 1966). Here, the pinto abalone is regarded as a single widespread species based on lack of evidence for genetic separation and new evidence of a much larger geographic range overlap for both morphological types. As also listed in MolluscaBase (2018), only *Haliotis kamtschatkana* is currently recognized, with *H. assimilis* as a synonym.

& Hebert 2017) and British Columbia (adult densities above short-term recovery objective of $0.32/\text{m}^2$; Lessard, personal communication, cited in Neuman et al. in prep).

In the southern portion of its range— California and the Channel islands to Baja California Sur, Mexico – pinto abalone represented a far more modest proportion of the abalone fishery than that of their northern counterparts (NMFS 2014), perhaps due to the greater abundance of other abalone species. In northern California, Rogers-Bennett et al. (2002) estimated a ten-fold decline in pinto abalone abundance from 156,000 to 18,000 based on a comparison between historic fishery-independent abundance data (1971-1975) and modern density estimates (1999-2001), respectively. Recent (2007-2013) surveys indicate adult densities at CDFW monitoring sites in Sonoma and Mendocino Counties ($0.65/\text{m}^2$ and $1.75/\text{m}^2$, respectively) above critical density thresholds (Rogers-Bennett unpublished data, cited in NMFS 2014). In southern California, the highest fishery landings of pinto abalone were reported from Point Conception in Santa Barbara County and Point Loma in San Diego County between 1950 and 1997 and the peak of the pinto abalone fishery occurred over the span of a decade from 1971 to 1980, during which time, an estimated 99.6% (~21,000 individuals) of the pinto abalone population in southern California was harvested (Rogers-Bennett et al. 2002).

Current population trends in southern California are less clear due primarily to the lack of targeted surveys. From 1980 to 1999 there were few reports of pinto abalone in southern California (NMFS 2014), but beginning in the early 2000s, observations occurred more frequently among the northern Channel Islands and along the mainland in San Diego, California (NMFS 2014). Most recently, white abalone surveys conducted between 2010 and 2013 also revealed areas where pinto abalone were common and there

was limited evidence of recruitment with the presence of several juveniles (< 50-mm shell length; Hagey, personal communication; Witting, personal communication).

However, consistent surveys focused specifically on pinto abalone in southern California have never been conducted and are needed to assess baseline population demographics for this species in the region (NMFS 2014).

Of the other potential factors that may hinder or prevent recovery of pinto abalone populations, current low adult densities and reproductive failure are of the greatest concern (NMFS 2014). However, abalone aggregate, or group together, during spawning seasons (Shepherd 1986; Seamone & Boulding 2011) and spawning events (Breen & Adkins 1980; Stekoll & Shirley 1993). Pinto abalone populations aggregate in British Columbia, Canada at reported densities of 0.12-0.64/m², which are near or above a 0.15-0.30/m² critical spawning density (Seamone & Boulding 2011). A positive relationship between degree of aggregation and fertilization success has been identified in other broadcast-spawning marine invertebrate species (Levitan et al. 1992; Levitan & Young 1995). Aggregative behavior in abalone populations may increase reproductive success, even at low densities (Seamone & Boulding 2011; Coates et al. 2013).

Traditional approaches have relied on density estimates to provide measures of abalone recovery (e.g., CDFW 2005). However, several studies have incorporated measures of aggregation in assessing reproductive (and recovery) potential of depleted populations (Dowling et al. 2002; Button 2008; Seamone & Boulding 2011; Stierhoff et al. 2012; Catton & Rogers-Bennett 2013). Measures of aggregation may be more appropriate for describing low-density populations for species known to actively aggregate. Spatial dispersion measures can be incorporated into density surveys if

abalone locations are known and distances between nearest neighbors can be attained by mapping locations (Button 2008; Seamone & Boulding 2011).

Irrespective of sex or spawning condition, abalone may aggregate around habitat features such as crevice habitat (Shepherd 1986a). In British Columbia, Canada, Seamone and Boulding (2011) found that pinto abalone abundance increased with the abundance of boulder and bedrock containing crevices, and this habitat association may have facilitated reproductive aggregation. Understanding habitat associations/preferences may provide insight on small-scale spatial distribution patterns, which may have further implications for assessing reproductive potential. Further, known habitat preferences can inform construction of habitat models and refine methods for locating appropriate habitat (Okano 2009; Ostrowski 2016). Habitat preferences for pinto abalone in southern California have not been defined.

Here, I evaluate the current status of pinto abalone and their potential for long-term population sustainability in southern California two decades after the closure of fisheries. I conducted SCUBA-based transect surveys in subtidal kelp forest habitat at numerous sites throughout San Diego, California to determine where pinto abalone are present and to quantify size and density distributions in order to evaluate these two demographic measures against criteria defined in the ARMP for self-sustaining abalone populations (CDFW 2005). I evaluated whether recruitment was occurring, determined nearest-neighbor distances, determined whether pinto abalone are significantly aggregated, and tested whether individual pinto abalone show preferences for substratum type and positioning on substrata relative to the seafloor, all to inform future management of this imperiled species.

CHAPTER 2

METHODS

Study Area

I conducted my research from June 2014 to December 2016 in San Diego, California, in one of the largest and best-studied giant kelp forests on the west coast of North America (Schiel & Foster 2015). Giant kelp (*Macrocystis pyrifera*) covers roughly 10 km² of nearshore underwater rocky habitat (Parnell 2015) divided into two major forests, La Jolla to the north and Point Loma in the south, which are separated by a large expanse of mostly sandy bottom in the vicinity of Mission Bay (Figure 1). Dominant macroalgal species include canopy-forming *Macrocystis pyrifera* and *Pelagophycus porra* and understory macroalgae including *Laminaria farlowii*, *Pterygophora californica*, *Eisenia arborea* and *Agarum fimbriatum* (Schiel & Foster 2015). These forests sit atop extensive hard bottom seafloor sloping gently offshore and covering a range of depths (Parnell 2015) that support several species of abalone, including pinto abalone (Witting, personal communication; Hagey, personal communication). This area historically supported a large proportion of commercial and recreational abalone fisheries in southern California (CDFW 2005).

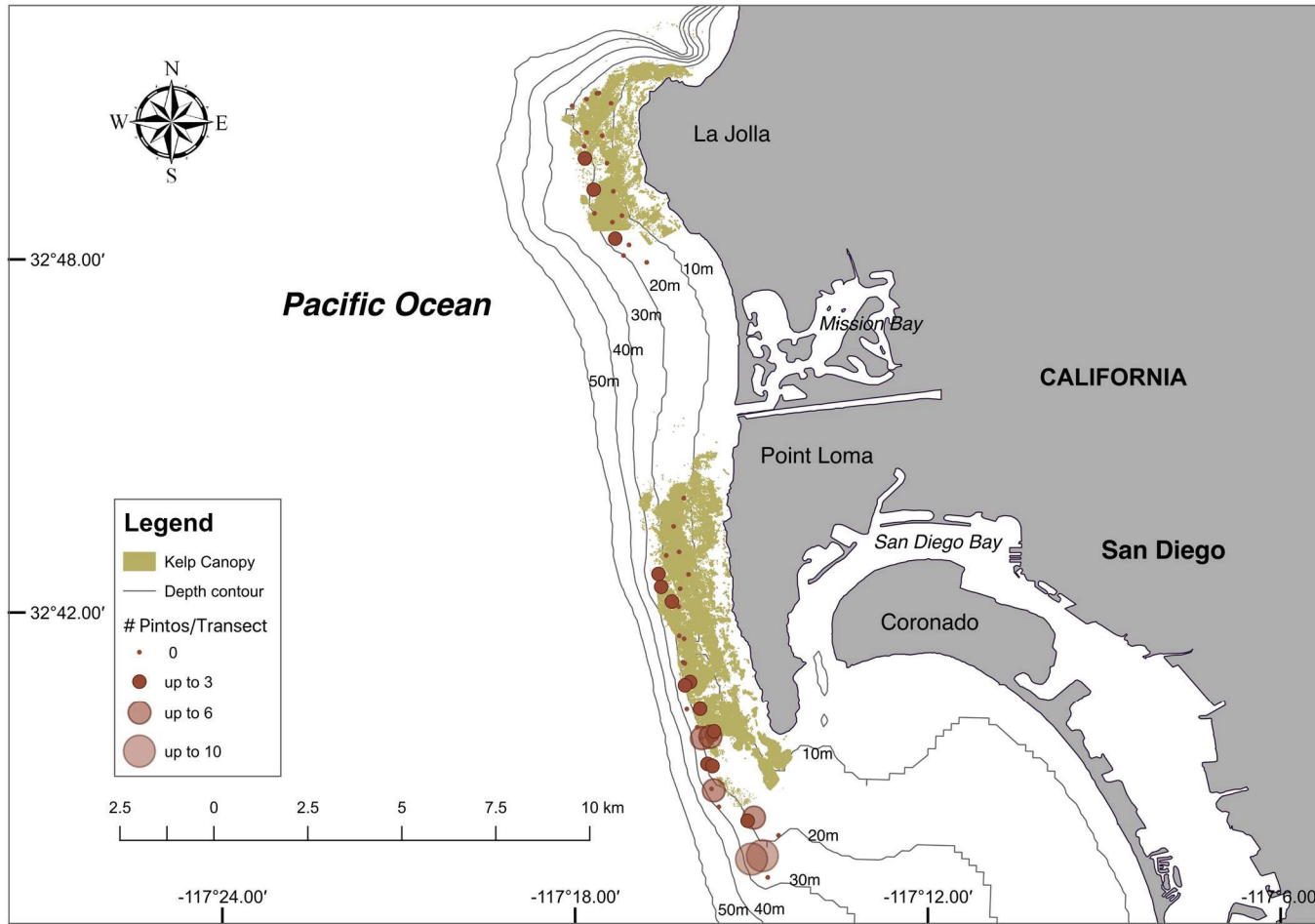


Figure 1. Counts of pinto abalone observed on transects at survey sites ($N = 55$) in La Jolla and Point Loma kelp forests in San Diego, CA, between June 2014 and December 2016. Features include bathymetric contours (10-m intervals; solid lines) between 10 and 50 m depth and *Macrocystis pyrifera* canopy cover from data collected in 2011 by CDFW (2014; green areas on top of bathymetric contours).

Survey Design

I used two sources of information specific to pinto abalone to constrain my study area prior to initiation of surveys: 1) the known historic depth range of pinto abalone in southern California of 12-40 m (Geiger & Owen 2012), and 2) association with macroalgae and rock substratum. I used ArcMap (version 10.2.2; ESRI 2014) to determine the spatial extent of potential habitat based on existing spatial data for bathymetry (CDFW 2009) and *Macrocystis pyrifera* surface canopy aerial cover (CDFW 2014; Table 1). I calculated the total kelp canopy area by forest and proportions among the two kelp forests, La Jolla and Point Loma (Figure 1; Table 1).

Once I constrained available seafloor habitat in San Diego by depth and kelp canopy cover, I further divided these areas into two depth strata: shallow (10-20 m) and deep (21-30 m) to evenly distribute survey locations among depths. In ArcMap, I generated random points within each kelp forest in proportion to the estimated amount of available habitat (Table 1) and evenly among the two depth strata within each forest. Each random point corresponded to discrete GPS coordinates I used to identify potential survey sites. In the field, I selected a starting point randomly but final site locations were determined by identifying appropriate depth within a predetermined stratum (shallow or deep) and presence of canopy or understory macroalgal cover using a Fishfinder 160 Blue (GARMIN, Olathe, KS). Final locations were < 100 m from the initial random GPS point.

Table 1. Giant Kelp (*Macrocystis pyrifera*) Surface Canopy Cover in 2011 in La Jolla and Point Loma Kelp Forests in San Diego, CA (CDFW 2014)

Forest	Aerial Canopy Cover		Proportion of total
	m ²	km ²	
Point Loma	6,036,626	6.04	0.72
La Jolla	2,302,656	2.30	0.28

Abalone Abundance, Size, and Nearest-Neighbor Distance

At each survey site, dive teams enumerated all abalone species found within a 400-m² transect area and measured the size, maximum shell length (mm) along the longest axis of the shell, of each abalone found (Figure 2). The location of each abalone in the transect area was recorded to the nearest 0.1 m using x and y coordinates (Figure 2B) so that locations could be mapped for nearest-neighbor distance calculations. Divers searched around each abalone for conspecifics within a 5-m extended search radius (including outside of the transect area; Figure 2B). For abalone found outside of the transect area, I recorded size and location but did not include these abalone in density calculations. To determine nearest-neighbor distances for individual abalone on transects, I used x and y locations and calculated the linear distance between adult (> 50 mm shell length) conspecifics (Figure 2C). Animals on transects with no nearest-neighbor within 5 m were assigned a nearest-neighbor distance value of > 5 m (Figure 2C).

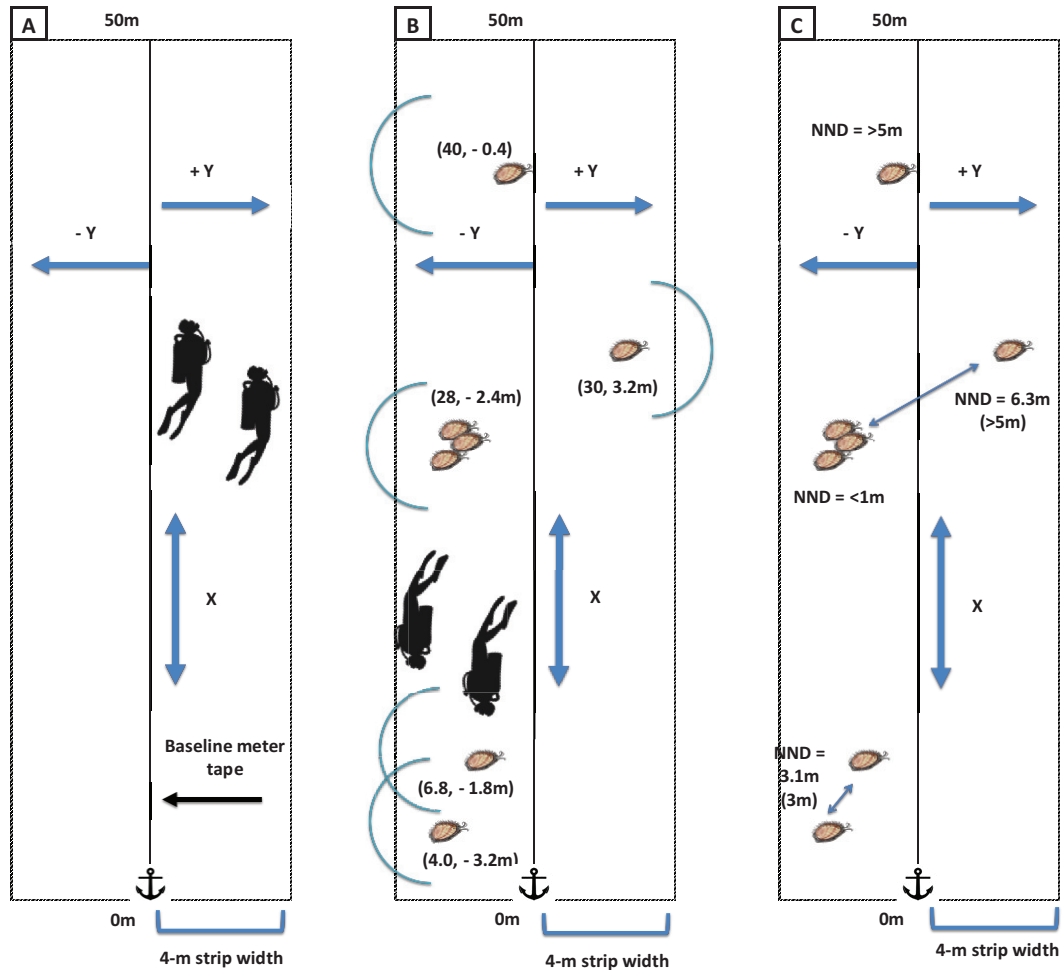


Figure 2. Pinto abalone site survey design within a standard transect area (50 x 8 m). Direction of the x and y axes relative to the baseline meter tape (A), extended 5-m search radius (half circle) and example x and y locations of abalone observed (B), and *post hoc* analysis of nearest-neighbor distances using location data (C). Figure not to scale.

Juvenile abalones (< 50 mm) are often highly cryptic, occupying small refuges formed by crevices in the rock, underneath boulders, within urchin spine canopy, and under macroalgae, so divers used lights to look for abalone in crevices, moved aside macroalgae, and also gently lifted larger rocks when feasible to search for juveniles and cryptic adults. Divers collected all empty shells, which can be used to identify missing size cohorts, the absence of which may indicate recruitment failure or differential

survivorship (Micheli et al. 2008). All shells found on sites were collected and brought up to the surface. Shells were identified to species and measured to the nearest millimeter.

I calculated transect densities and variance-to-mean ratios (VMR) of transect counts for each of four depth strata— 13-16 m, 17-20 m, 21-23 m and 24-30 m— within each forest (La Jolla and Point Loma). At sites where additional transects were surveyed, I subsampled the site and used data collected for the transect that I and my dive buddy surveyed to include in within-site density calculations and to standardize effort across all sites. To evaluate pinto abalone demographics within the framework of the ARMP (CDFW 2005), I first compared size distribution data to criterion 1, which requires a broad size distribution of emergent pinto abalone adults within two size categories: 1) intermediate (76-102 mm) and 2) large (102-187 mm) based on the historic minimum legal fishery size for pinto abalone in California (CDFW 2005; Geiger & Owen 2012). I grouped live pinto abalone sizes into 5-mm bins and calculated the percentage of these bins that contained non-zero values. Of the 5-mm bins, adult sizes must occupy at least 90% of the intermediate and 25% of the large size bins (CDFW 2005). I grouped empty shells using the same classification scheme as that of live abalone to evaluate additional or missing size classes in live size frequencies. Second, I compared transect densities to criterion 2, which requires a minimum viable population size, or density, of 0.2 abalone/m². Most importantly, recovery success is dependent upon a final assessment of whether *both* criteria are met at individual *index sites* in *key locations* within larger *recovery areas* throughout the range of each species. Recovery areas were defined using historic commercial landings data and known fishing areas (CDFW 2005). In San Diego, CDFW has identified three key locations to evaluate recovery criteria for pinto abalone:

1) the La Jolla kelp forest from Point La Jolla to Bird Rock; 2) Mission Bay to Ratkay Point in north Point Loma; and 3) Ratkay Point to Ballast Point in south Point Loma; (see Table 6-8 in CDFW 2005). Both criteria must be met at a single index site within each key location, however, the size of index sites in southern California has not been formally established as has been done for red abalone index sites in northern California and thus, my transect areas may not represent an equivalent comparison to a CDFW index site. However, density and size distribution data are still useful in understanding changes in population parameters over time (Taniguchi, personal communication).

I explored nearest-neighbor distance values for individual pinto abalone using two techniques. First, I calculated the proportion of nearest-neighbor distance values in 0.5 m intervals up to 5 m for adult abalone on transects. I compared the proportion of individuals with a nearest-neighbor < 5 m to the proportion with no nearest-neighbor within 5 m (" > 5 m"). Second, I calculated a nearest-neighbor R ratio aggregation index (Clark & Evans 1954) for each transect on which two or more pinto abalone were observed and at least one nearest-neighbor distance < 5 m was calculated to evaluate whether pinto abalone exhibited a random, uniform or aggregated pattern of distribution.

Abalone surveys were conducted over 2.5 pinto abalone spawning seasons (April through July; Campbell et al. 2003) between June 2014 to December 2016. Spawning seasons, spatial distribution patterns, nearest-neighbor distance proportions, and transect counts were all graphed over time and visually inspected to identify potential correlations between measured factors and spawning season. In addition, this study coincided with a recent strong 2014-2016 El Niño event, which began in spring/summer 2014, increased in strength in March 2015, peaked in December 2015, and ended in May/June 2016 (NOAA

Climate Prediction Center). The El Niño was characterized by higher than average sea surface temperatures (SST), reflected in the Oceanic Niño Index (ONI), which gauges changes in SST over three-month periods and provides a relevant measure of the intensity of an El Niño event (NOAA Climate Prediction Center; Figure 3). Given the strength and duration of this event, I compared pinto abalone transect counts and mortalities, as evidenced by the number of shells collected at a site over time, among El Niño periods (pre-, during, and post-El Niño [including La Niña]).

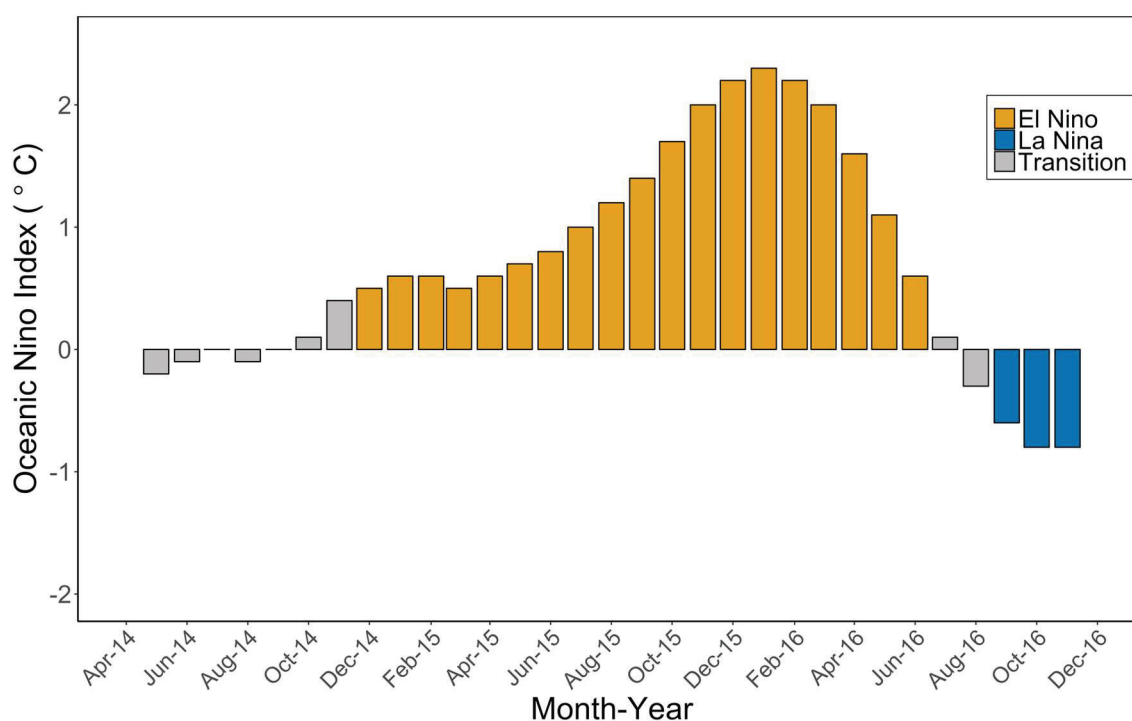


Figure 3. NOAA Oceanic Niño Index (ONI) values for February 2014 to May 2018, which indicate deviations in average sea surface temperatures (°C) over a 3-month period in the east-central tropical Pacific between 120°-170°W over the same months in a 30-year time period. NOAA identifies periods when the ONI is > 0.5 as warmer than average El Niño periods (orange bars) and > -0.5 as lower than average La Niña periods (blue bars). Adapted from: NOAA.gov.

To evaluate water temperatures in San Diego during the study period, I used SST data collected daily from the sea surface at Scripps Institution of Oceanography Pier in La Jolla, CA (available at:

data/data-sio/). I calculated monthly SST averages for June 2014 to December 2016, corresponding to the beginning and ending months of my survey dates. In addition, I averaged minimum bottom temperatures recorded on a Petrel 1 dive computer (Shearwater Research, Richmond, B.C., Canada) during surveys to make comparisons between temperature at survey depth and SST for all survey dates.

Habitat Associations

To obtain information on abalone habitat use, I recorded characteristics within a $\sim 1\text{-m}^2$ area surrounding each abalone, including animals found outside transect areas. Divers recorded abalone exposure (*exposed* on a rock surface or *cryptic* within a deep crevice or underneath a rock), use of each substratum type, abalone positioning on substratum relative to the benthos (“relief”), and the maximum substratum relief within 1m^2 of each abalone observed (Table 2).

Broad habitat characteristics for each site surveyed were quantified using *Species Checklist* methods derived from the National Park Service, Channel Islands National Park Kelp Forest Monitoring Program (Davis 1988) to estimate relative abundances and percent cover of select species and physical features (Table 2). Relative abundances were defined using the following classification scheme (Davis 1988):

- 0 – Absent: an effort was made to look for an organism that was not found
- 1 – Rare: few organisms found
- 2 - Common: organism found in moderate numbers
- 3 - Moderately abundant: organism found over most of the site or in high-density patches
- 4 - Abundant: organism present in higher than normal densities

In addition, at the beginning and end of each survey, one diver team recorded a video of the length of each side of the transect using an underwater video camera, a GoPro Hero (subsequently Hero 4; GoPro, San Mateo, CA), swimming slowly and ~ 1 m above the seafloor, capturing approximately 2 m to either side of the baseline transect. I assigned a subjective habitat score characterizing each site as *Excellent*, *Fair*, or *Poor*. This score was based on the opinion of the dive team of the overall quality of the habitat including physical and biological aspects of the site as well as the potential to support each of four abalone species observed at the depths surveyed (red, pink, pinto and white).

To evaluate preferences for substratum type, I compared counts of pinto abalone use of substrata to the proportion available among all sites using estimates of percent cover (Table 2; Manly et al. 1993). For relief, I made two different comparisons. First, I compared the relief of individual pinto abalone (*observed*) to the highest rock relief within a 1-m² area around each individual (*expected*) to examine whether they positioned themselves at a relief different than the surrounding available substratum relief. Second, I compared the total proportion of available relief for all sites to the proportion of rock relief within a 1-m² area around each individual to evaluate whether pinto abalone might be located adjacent to low-relief habitat disproportionately from what is available over the site. Substratum type and relief were recorded for all 95 pinto abalone found. Relief within a 1-m² area was recorded for 85 individuals.

To test for differences in overall use of available habitats, I used the statistical package *adehabitatHS* (Calenge 2006) in RStudio (version 1.1.383, RStudio Team 2015), which contains a function, *widesI*, for analyzing habitat selection per Manly et al. (1993). The function first performs a log-likelihood chi-squared test on all proportions of used

versus available habitat. Second, it calculates selection ratios (used/available; w_i), standard error (se) for each ratio is approximated, and the differences between selection ratios are tested, producing a set of log-likelihood chi-squared statistics (X_L^2) and p values, one for each habitat category, indicating whether the category is used significantly more than expected from the proportion of available habitat. For each habitat type here, there are four categories and the value of α was set at $0.05/4 = 0.0125$. Similarly, significance levels used for testing $\{(w_i-1)/se(w_i)\}^2$ with critical values from a chi-squared distribution is α/I so there will be a probability of approximately $\alpha = 0.05$ of getting a significant result if there is no selection. To interpret confidence intervals, the selection ratio is significantly different from 1 if the confidence interval for w_i does not contain the value 1; a minimum confidence limit greater than one indicates that selection for that category is greater than expected and an upper confidence limit less than one indicates that selection is less than expected. Of note, the validity of these confidence intervals depends on the selection ratios, and thus the sample used proportions, being normally distributed. For this assumption to hold, the count values of habitat categories used should be five or more for each category. If this condition is not met for certain categories (e.g., sand and cobble substratum types, medium and high relief), the corresponding confidence intervals should be treated with caution.

Table 2. Habitat Variables and Values Used in Pinto Abalone Habitat Association Analyses Adapted from Davis (1988)

Habitat Variable Type	Species / Variable Description	Values / Range of Values
Species' Relative Abundances		
Macroalgae	<i>Macrocystis pyrifera</i>	<i>Desmarestia ligulatum</i>
	<i>Pelagophycus porra</i>	Other brown algae
	<i>Eisenia arborea</i>	<i>Gigartina spp.</i>
	<i>Pterygophora californica</i>	Other red algae
	<i>Laminaria farlowii</i>	Encrusting coralline
	<i>Agarum fimbriatum</i>	Articulated coralline
	<i>Cystoseira osmundacea</i>	
Invertebrates	<i>Strongylocentrotus purpuratus</i>	
	<i>Strongylocentrotus franciscanus</i>	
	All other mobile invertebrates	
Estimated Percent (%) Cover		<u>Estimated % Cover</u>
Substratum type	Bedrock - continuous bedrock, smooth or with crevices/depressions/ridges	0 - 100%
	Boulder - rocks > 30cm in length (cannot move)	
	Cobble - rocks < 30cm and > 7-9cm (can move with one hand)	
	Sand - deep enough to provide little or no attachment/hard substrate	
Substratum roughness	Rough (like volcanic rock; highly porous)	
	Smooth (like sandstone)	
Relief	Flat (0 – 10 cm)	
	Low (10 cm – 1 m)	
	Medium (1 – 2 m)	
	High (> 2 m)	
Invertebrates	All encrusting invertebrates (bryozoans, sponges, tunicates, etc.)	
Macroalgae	Canopy (approx. > 3 m tall to surface), Understory (> 10 cm, < 3 m), Turf (< 10 cm), Encrusting (flat crustose algae), Drift (not attached)	

CHAPTER 3

RESULTS

Pinto Abalone Abundance, Density, and Size Distribution

Between June 2014 and December 2016, 55 sites were surveyed, 19 in La Jolla and 36 in Point Loma (Figure 1). A total of 95 pinto abalone were found among all sites, 66 of which were found on transects (Table 3). The greatest number observed was 15 individuals on a site (both on/off transect) and 10 on a single transect (Figure 4; Table 3). Mean pinto abalone density ($\pm SD$) for all sites (0.003 ± 0.006 abalone/m²; $N = 55$) was far below a critical density threshold of 0.2 abalone/m² identified in the ARMP, a threshold that was not met for any site (Table 3).

The vast majority of pinto abalone were found at sites in Point Loma and predominantly the southern portion of Point Loma; only four individuals were found among three sites in La Jolla (Figure 1; Tables 3 and 4). The mean number of pinto abalone encountered per transect showed a small peak between 17 and 23 m in Point Loma (Table 4). For all depth strata in Point Loma, the VMR was > 1 and increased with increasing depth, indicating a general clumped pattern of spatial dispersion among sites, which became more pronounced with increasing depth (Table 4).

Table 3. Pinto Abalone (*Haliotis kamtschatkana*) Counts on Transects (#/Transect) and on an Entire Site (#/Site), Density (+/-SD), and Mean Live and Empty Shell Numbers, Sizes (mm), and Size Ranges for All Sites in La Jolla (LJ) and Point Loma (PL) Arranged by Forest and Date/El Niño Period Surveyed in San Diego, CA between June 2014 and December 2016

Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/-SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/-SD)
6/10/14	Pre-El Niño	LJ01	17	400	0	0	0	-	-	-	-
7/29/14	Pre-El Niño	LJ03	18	400	0	0	0	-	-	-	-
8/19/14	Pre-El Niño	LJ04	20	400	1	0.0025	1	145	145	-	-
8/19/14	Pre-El Niño	LJ05	19	400	0	0	0	-	-	-	-
3/28/15	El Niño	LJ06	15	400	0	0	0	-	-	-	-
4/12/15	El Niño	LJ07	16	400	0	0	0	-	-	-	-
4/20/15	El Niño	LJ08	16	400	0	0	0	-	-	-	-
4/20/15	El Niño	LJ09	17	400	0	0	0	-	-	-	-
4/21/15	El Niño	LJ10	20	400	0	0	0	-	-	-	-
4/21/15	El Niño	LJ11	20	400	0	0	0	-	-	-	-
11/8/15	El Niño	LJ12	25	400	1	0.0025	2	120-130	125 (7)	1	24
11/8/15	El Niño	LJ13	22	400	0	0	0	-	-	-	-
11/14/15	El Niño	LJ14	21	400	0	0	0	-	-	0	0
11/14/15	El Niño	LJ15	23	400	0	0	0	-	-	0	0
11/20/15	El Niño	LJ16	20	400	0	0	0	-	-	1	134
11/21/15	El Niño	LJ17	26	400	0	0	0	-	-	-	-
11/21/15	El Niño	LJ18	21	400	0	0	0	-	-	1	56

Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
11/23/15	El Niño	LJ19	23	400	1	0.0025	1	131	131	3	85 (42)
5/3/16	El Niño	LJ20	24	400	0	0	0	-	-	3	103 (29)
6/11/14	Pre-El Niño	PL01	15	400	0	0	0	-	-	-	-
6/11/14	Pre-El Niño	PL02	14	400	0	0	3	108-145	121 (21)	-	-
6/13/14	Pre-El Niño	PL03	23	400	6	0.0150	6	60-143	111 (28)	-	-
6/13/14	Pre-El Niño	PL04	16	400	1	0.0025	1	59	59	-	-
6/15/14	Pre-El Niño	PL06	19	400	1	0.0025	1	13	13	-	-
6/15/14	Pre-El Niño	PL07	17	400	2	0.0050	2	56-61	59 (4)	-	-
6/20/14	Pre-El Niño	PL08	16	400	0	0	0	-	-	-	-
6/22/14	Pre-El Niño	PL09	26	400	0	0	3	118-140	131 (12)	-	-
6/23/14	Pre-El Niño	PL10	25	400	2	0.0050	2	101-126	114 (18)	-	-
6/23/14	Pre-El Niño	PL11	14	400	0	0	0	-	-	-	-
6/24/14	Pre-El Niño	PL12	23	400	3	0.0075	3	34-85	53 (28)	1	40
6/25/14	Pre-El Niño	PL13	20	400	0	0	0	-	-	-	-
6/25/14	Pre-El Niño	PL14	25	400	0	0	0	-	-	-	-
7/1/14	Pre-El Niño	PL15	19	400	1	0.0025	1	100	100	-	-
7/8/14	Pre-El Niño	PL16	23	400	3	0.0075	3	128-137	133 (5)	1	81
7/9/14	Pre-El Niño	PL17	23	400	1	0.0025	2	64-75	70 (8)	1	104
7/15/14	Pre-El Niño	PL18	16	400	0	0	0	-	-	-	-

Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
7/16/14	Pre-El Niño	PL19	15	400	0	0	0	-	-	-	-
7/23/14	Pre-El Niño	PL20	18	400	0	0	0	-	-	-	-
8/6/14	Pre-El Niño	PL21	14	400	0	0	0	-	-	-	-
8/12/14	Pre-El Niño	PL22	17	400	0	0	0	-	-	2	74 (0)
8/13/14	Pre-El Niño	PL23	22	400	0	0	0	-	-	-	-
8/18/14	Pre-El Niño	PL24	15	400	0	0	0	-	-	-	-
10/25/14	Pre-El Niño	PL25	17	400	4	0.0100	4	79-103	96 (12)	-	-
10/25/14	Pre-El Niño	PL26	15	400	2	0.0050	7	73-124	93 (21)	-	-
4/23/15	El Niño	PL27	18	400	2	0.0050	6	114-125	122 (4)	1	109
9/26/15	El Niño	PL28	19	300*	9	0.0300	9	87-131	105 (16)	-	-
10/23/15	El Niño	PL29	22	400	1	0.0025	3	105-130	120 (13)	7	59 (24)
10/24/15	El Niño	PL30	29	400	0	0	1	121	121	1	119
10/24/15	El Niño	PL31	20	400	6	0.0150	9	105-142	131 (11)	3	121 (17)
2/9/16	El Niño	PL32	22	400	10	0.0250	10	95-146	126 (14)	2	113 (15)
3/18/16	El Niño	PL33	27	400	9	0.0225	15	93-135	118 (14)	6	114 (35)
3/18/16	El Niño	PL34	25	400	0	0	0	-	-	1	76
4/19/16	El Niño	PL35	23	400	0	0	0	-	-	2	123 (6)
9/20/16	El Niño	PL36	21	400	0	0	0	-	-	2	93 (10)
12/1/16	Post-El Niño	PL38	21	400	0	0	0	-	-	2	91 (40)

*Transect area < 400 m²; extrapolated from density to estimate count/400-m² transect in Table 4; numbers here are exact transect counts

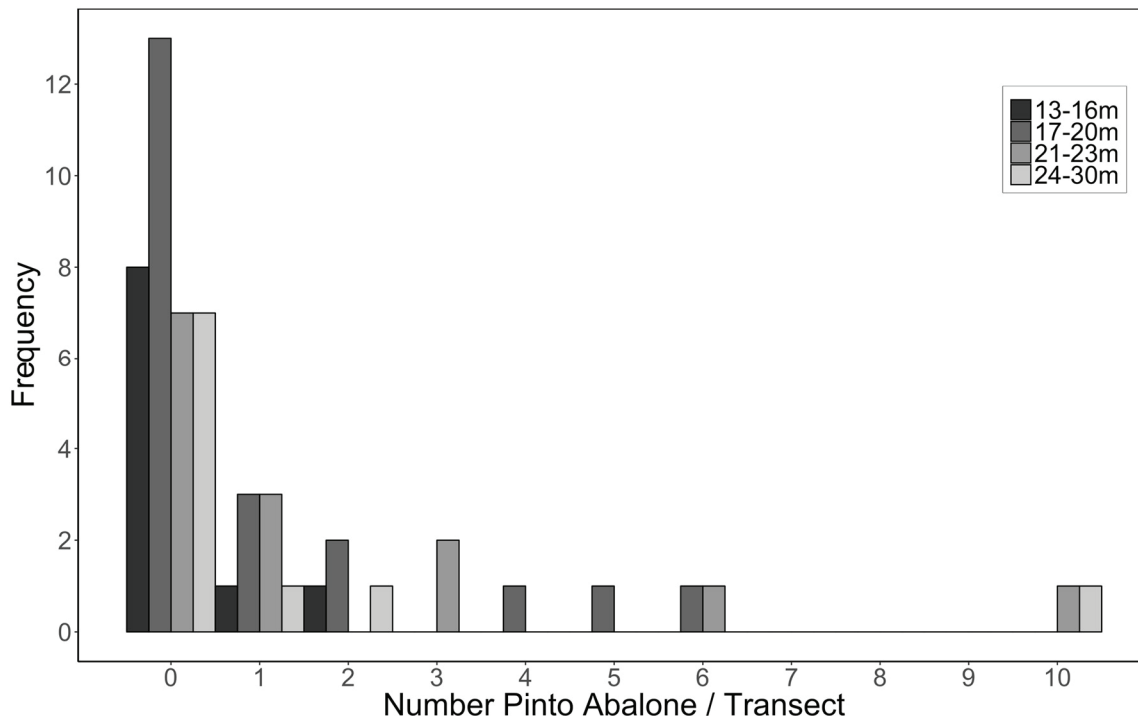


Figure 4. Number of pinto abalone counted for each transect ($N = 55$) and by depth stratum (m) in Point Loma and La Jolla in San Diego, CA between June 2014 and December 2016.

Table 4. Distribution of Pinto Abalone Counted Per 400-m² Transect (#/Transect), Number of Transects Surveyed (N), Mean Transect Densities (#/m²), and Variance-To-Mean Ratios (VMR) Grouped by Forest (La Jolla and Point Loma) and Depth Stratum (m) for Surveys Conducted in San Diego, CA Between June 2014 and December 2016

Forest & Depth Stratum	N	Frequency of Counts												Total # Pintos	#/ Transect	#/m ²	VMR						
		0	1	2	3	4	5	6	7	8	9	10	11					12					
La Jolla																							
13-16 m	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.0000	-		
17-20 m	10	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.10	0.0003	1.00			
21-23 m	5	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20	0.0005	1.00			
24-30 m	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33	0.0008	1.00			
	19																3	0.16	0.0004	1.00			
Point Loma																							
13-16 m	9	7	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.33	0.0008	1.50			
17-20 m	11	4	2	2	0	0	1	1	0	0	0	0	0	1*	0	0	30	2.73	0.0068	2.46			
21-23 m	9	3	2	0	2	0	0	1	0	0	0	1	0	0	0	0	24	2.67	0.0067	4.31			
24-30 m	7	5	0	1	0	0	0	0	0	0	0	0	1	0	0	0	12	1.71	0.0043	8.11			
	36																69	1.92	0.0048	4.10			

*Transect area < 400 m²; extrapolated from density at PL28 to estimate count/400-m² transect

Older, larger individuals represented a majority of the size frequency distribution for all individuals combined from all sites. The mean shell length ($\pm SD$) of all live pinto abalone in San Diego was 110.8 ± 27.2 mm ($N = 86$), ranging from 13 to 146 mm (Figure 5; Table 3). Intermediate (76 -102 mm) and large (102-187 mm) size classes represented 15% and 73% of all sizes, respectively. Though small abalones are typically highly cryptic, 10 individuals < 76 mm were found, three < 50 mm. In terms of the ARMP size distribution criterion, 90% of intermediate and 25% of large size bins (in 5-mm bins) must be occupied (CDFW 2005). This criterion was met for the distribution of sizes for *all* sites combined (Figure 5) and for Point Loma only but not for any individual site.

I collected and measured 41 empty pinto abalone shells ranging from 24 to 167 mm (Table 3; Figure 6). Mean size ($\pm SD$) of all empty and empty/live shells combined was 91.5 ± 33.9 mm and 104.6 ± 30.8 mm, respectively (Figure 6). Site and transect counts, densities, and size ranges for all other abalone species encountered at survey sites are presented in Appendix A.

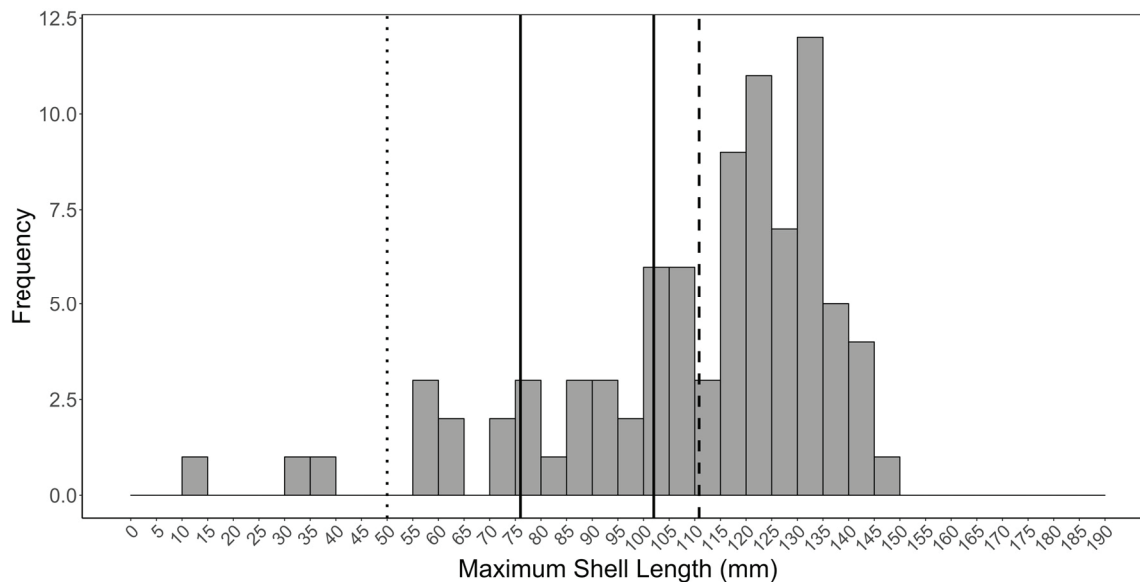


Figure 5. Size distribution of live pinto abalone observed on sites surveyed between June 2014 and December 2016 in San Diego, CA. The dotted line represents approximate size at which pinto abalone reach sexual maturity (50 mm; Campbell et al. 2003). The dashed line represents mean size ($\pm SD$) for all live pinto abalone (110.8 ± 27.2 mm; $N = 86$). The two solid lines represent the minimum size for intermediate (76-102 mm) and large (102-187 mm) size classes as per Criterion 1 in the California Department of Fish and Wildlife Abalone Recovery and Management Plan (CDFW 2005).

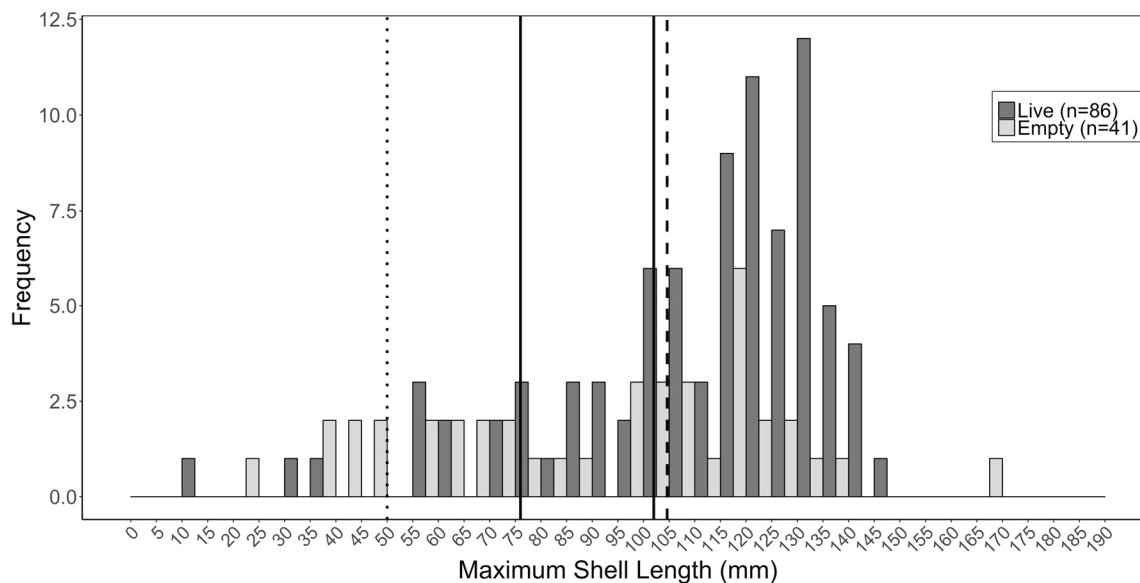


Figure 6. Size distribution of empty pinto abalone shells and live pinto abalone observed on sites surveyed between June 2014 and December 2016 in San Diego, CA. The dotted line represents approximate size at which pinto abalone reach sexual maturity (50 mm; Campbell et al. 2003). The dashed line represents mean size ($\pm SD$) for empty and live pinto shell sizes combined (104.6 ± 30.8 mm). The two solid lines represent the minimum size for intermediate (76-102 mm) and large (102-187 mm) size classes as per Criterion 1 in the California Department of Fish and Wildlife Abalone Recovery and Management Plan (CDFW 2005).

El Niño conditions were first observed in April 2014 and an El Niño event was officially recognized in December 2014 (NOAA Climate Prediction Center). Mean bottom temperature ($\pm SD$) at survey sites in Point Loma and La Jolla ($13.6 \pm 3.7^{\circ}\text{C}$; mean depth = 19.0 ± 3.3 m) was, on average, 6°C cooler than mean SST ($\pm SD$) recorded at the SIO pier in La Jolla ($19.6 \pm 3.7^{\circ}\text{C}$). The highest bottom and sea surface temperatures were observed in September 2015; the maximum bottom temperature recorded was 17.7°C at 19 m depth at one site in Point Loma and mean monthly SST for that month was 24°C . Average monthly SST and bottom temperatures recorded during survey dives are shown in Figures 7 and 8 for Point Loma and La Jolla, respectively.

The majority of surveys ($N = 29$) were conducted in 2014 during the transition period between La Niña and El Niño (pre-El Niño) events when weak El Niño conditions were already present (Table 5). In Point Loma, 25 of these surveys were conducted during the transition period before the El Niño, but the highest counts were observed during the El Niño and mean site depths for these surveys were deeper on average than sites surveyed prior to the El Niño (Figure 7; Table 5). A vast majority of sites in La Jolla were surveyed during the El Niño, which had very low numbers of pinto abalone overall (Figure 8; Table 5). Mean densities ($\pm SD$) were lower during spawning seasons (0.002 ± 0.003 abalone/ m^2 ; $N = 29$ transects) compared to all other months (0.004 ± 0.007 abalone/ m^2 ; $N = 26$ transects). A greater number of empty pinto abalone shells were collected during the El Niño period (Figure 9; Table 3).

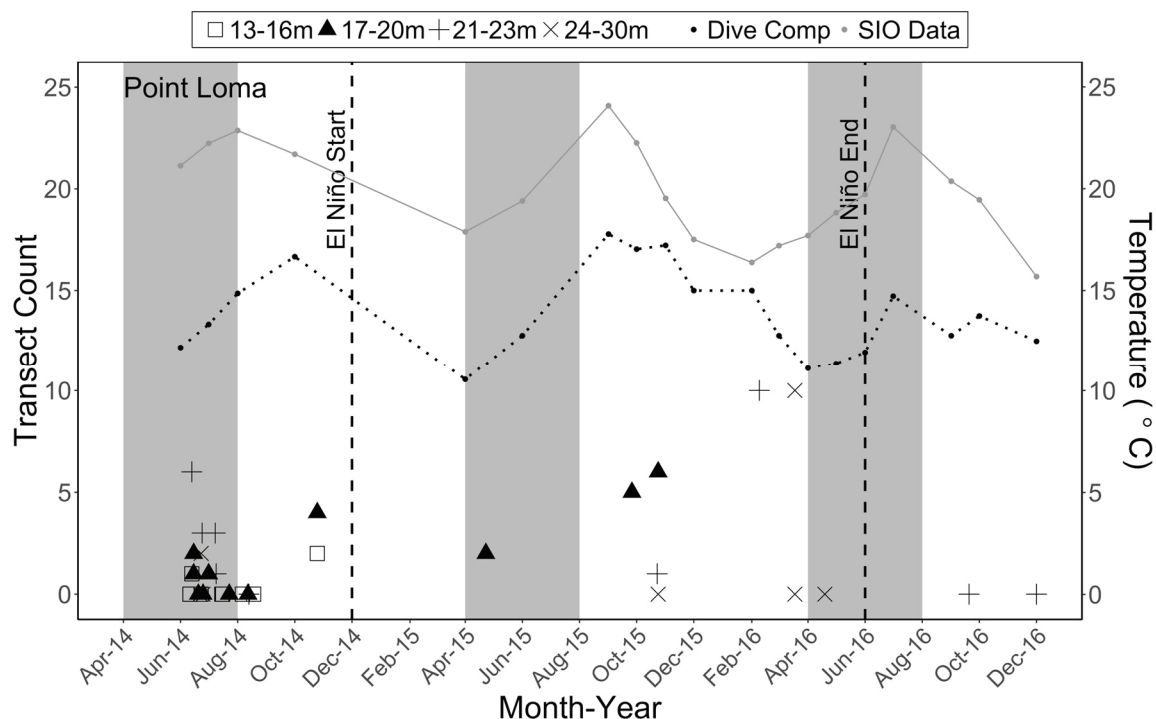


Figure 7. Number of pinto abalone counted for each transect in Point Loma ($N = 36$) by survey date and depth stratum, average monthly water temperature ($^{\circ}\text{C}$) collected at the surface (solid lines and points) at Scripps Institute of Oceanography Pier in La Jolla, and temperature ($^{\circ}\text{C}$) recorded on a Shearwater Petrel 1 dive computer (dotted lines and points) at depth at each pinto abalone survey site by survey date between June 2014 and December 2016 in San Diego, CA. Shaded date ranges indicate pinto abalone spawning seasons (April – July; Campbell et al. 2003). Dashed lines correspond to the beginning (December 2014) and end (June 2016) of an El Niño period based on NOAA's Oceanic Niño Index (NOAA Climate Prediction Center).

Table 5. Total Number of Pinto Abalone Counted Per 400-m² transect (#/Transect), Number of Transects Surveyed (N), Mean Transect Densities (#/m²), and Variance-To-Mean Ratios (VMR) Grouped by Forest (La Jolla and Point Loma) and El Niño Period for Surveys Conducted in San Diego, CA Between June 2014 and December 2016

ENSO Period	N	Total # Pinto Abalone	#/ Transect	Density (#/m ²)	VMR	Mean Depth (m)
La Jolla						
Pre-El Niño (2014)	4	1	0.25	0.0006	1.00	18.5
El Niño (2015/2016)	15	2	0.13	0.0003	0.93	20.6
Post-El Niño (2016)	0	-	-	-	-	-
Point Loma						
Pre-El Niño (2014)	25	26	1.04	0.0026	2.36	18.7
El Niño (2015/2016)	9	34	3.78	0.0094	4.55	22.8
Post-El Niño (2016)	2	0	0.00	0.0000	-	20.7

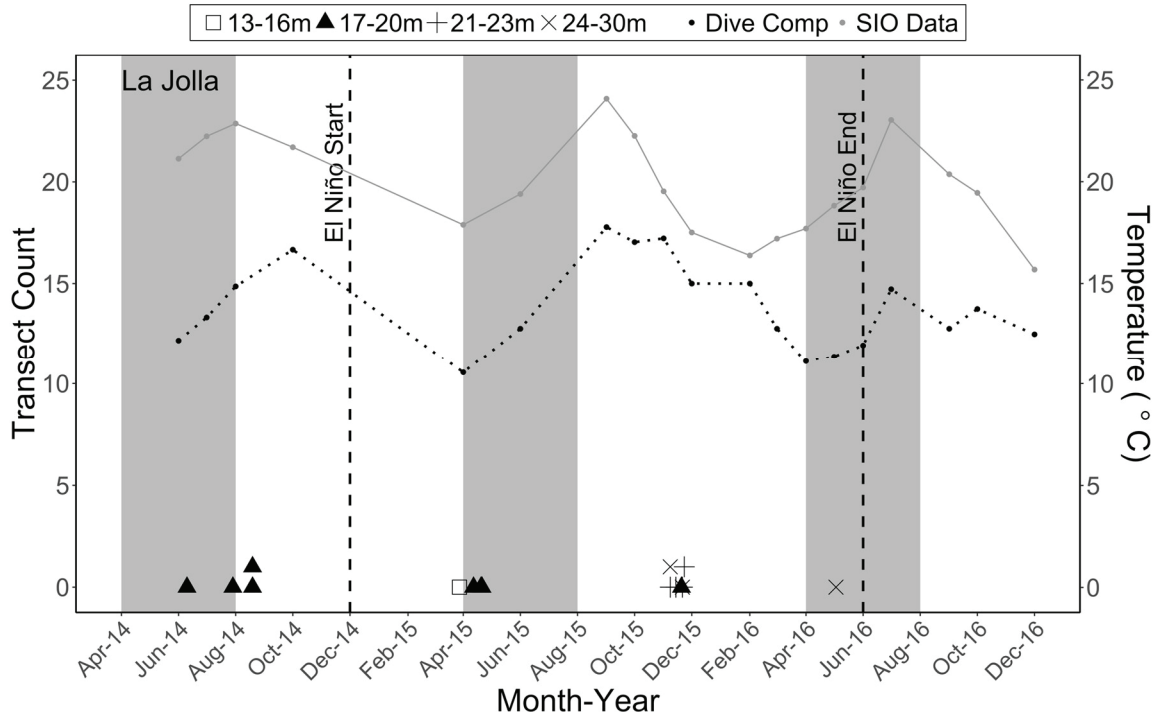


Figure 8. Number of pinto abalone counted for each transect in La Jolla ($N = 19$) by survey date and depth stratum, average monthly water temperature ($^{\circ}\text{C}$) collected at the surface (solid lines and points) at Scripps Institute of Oceanography Pier in La Jolla, and temperature ($^{\circ}\text{C}$) recorded on a Shearwater Petrel 1 dive computer (dotted lines and points) at depth at each pinto abalone survey site by survey date between June 2014 and December 2016 in San Diego, CA. Shaded date ranges indicate pinto abalone spawning seasons (April – July; Campbell et al. 2003). Dashed lines correspond to the beginning (December 2014) and end (June 2016) of an El Niño period based on NOAA’s Oceanic Niño Index (NOAA Climate Prediction Center).

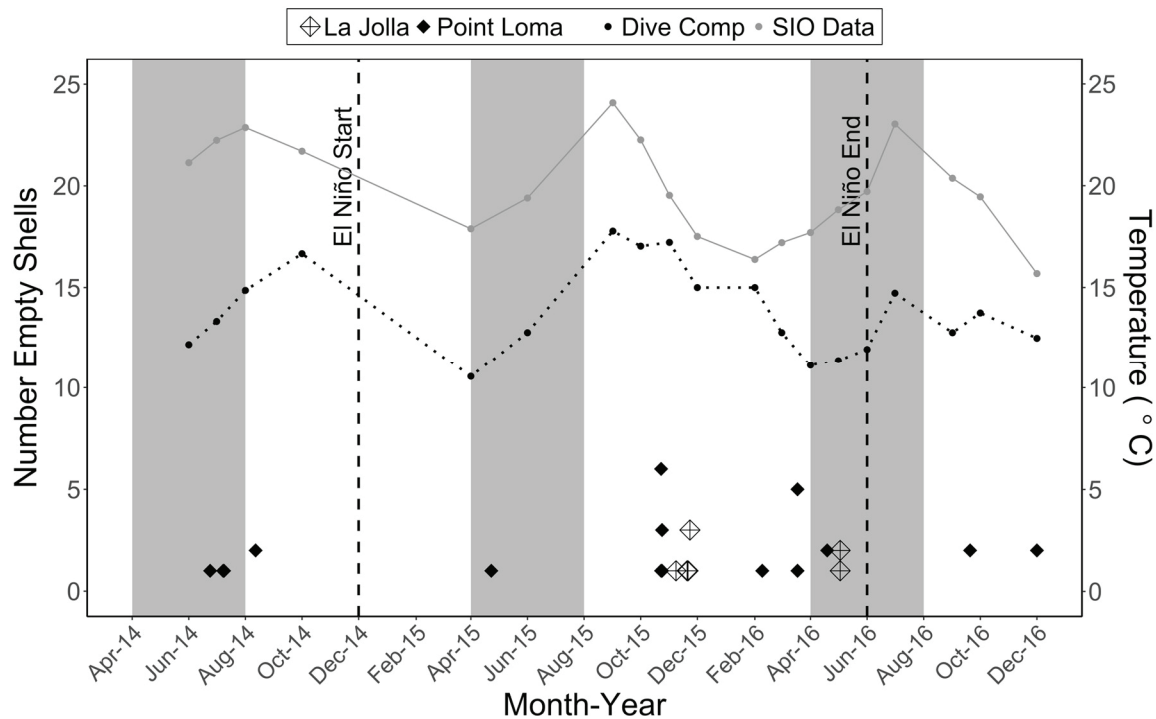


Figure 9. Number of empty pinto abalone shells collected on pinto abalone survey sites in La Jolla ($N = 9$ shells) and Point Loma ($N = 32$ shells), average monthly water temperature ($^{\circ}\text{C}$) collected at the surface (solid lines and points) at Scripps Institute of Oceanography Pier in La Jolla, and temperature ($^{\circ}\text{C}$) recorded on a Shearwater Petrel 1 dive computer (dotted lines and points) at depth at each pinto abalone survey site by survey date between June 2014 and December 2016 in San Diego, CA. Shaded date ranges indicate pinto abalone spawning seasons (April – July; Campbell et al. 2003). Dashed lines correspond to the beginning (December 2014) and end (June 2016) of an El Niño period based on NOAA’s Oceanic Niño Index (NOAA Climate Prediction Center).

Nearest-Neighbor Distances and Spatial Distribution

Nearest-neighbor distances were measured for 63 pinto abalone. A majority (65%) of individuals had a nearest neighbor within 5 m (Figure 10) both in and out of spawning seasons (Table 6). In terms of a critical fertilization radius (Babcock & Keesing 1999), 11% of individuals had a conspecific within 2 m during spawning seasons, compared to 45% at other times of the year (Figure 11).

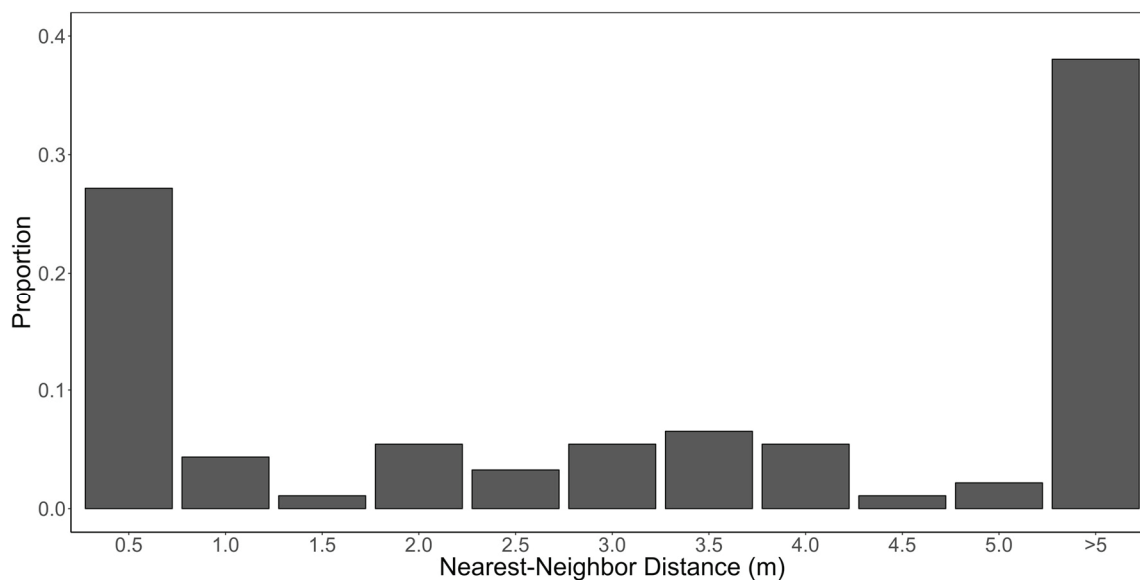


Figure 10. Proportions of nearest-neighbor distances grouped to the nearest 0.5 m for all adult pinto abalone (> 50 mm size; $N = 63$) found in San Diego, CA from June 2014 to December 2016. Individuals with no nearest-neighbor within 5 m are classified as > 5 m.

Table 6. Counts, Proportions, and Cumulative Proportions of Nearest-Neighbor Distances Grouped to the Nearest 1 m and by Spawning Season for All Adult Pinto Abalone (> 50 mm size) Surveyed in San Diego, CA from June 2014 to December 2016. Pinto Abalone Spawning Season Occurs Between April and July (Campbell et al. 2003)

Nearest-Neighbor Distance (m)	In Spawning Season			Out of Spawning Season		
	Count	Proportion	Cumulative Proportion	Count	Proportion	Cumulative Proportion
up to 1 m	2	0.11	0.11	17	0.39	0.39
2 m	0	0.00	0.11	3	0.07	0.45
3 m	5	0.26	0.37	2	0.05	0.50
4 m	4	0.21	0.58	6	0.14	0.64
5 m	0	0.00	0.58	2	0.05	0.68
> 5 m	8	0.42	1.00	14	0.32	1.00
Total	19			44		

Nearest-neighbor R ratios indicated that pinto abalone were significantly aggregated at four of nine sites that had more than two pinto abalone with a nearest-

neighbor on transect (Table 7). Pinto abalone were most often significantly aggregated at sites surveyed outside of spawning seasons and were most often randomly distributed during spawning seasons (Figure 11) though sample sizes of both the number of sites and number of abalone per site were low. Mean R ratios were below 1 for all sites and seasons except one and no sites exhibited a *regular*, or uniform pattern of dispersion.

Table 7. Number of Pinto Abalone with a Nearest-Neighbor Within a 400-m² Transect Area, Transect Density (#/m²), Mean Nearest-Neighbor Distance (m), and Values of the R Statistic (Clark & Evans 1954) for Sites in Point Loma, CA Surveyed Between June 2014 and December 2016 Where Two or More Pinto Abalone Were Observed. The Distribution Pattern (*Aggregated*, *Random*, or *Regular*) is Indicated with Results of Significance Tests (* $p < 0.05$, ** $p < 0.01$) Based on the Z Test Statistic. No Transects Showed a Significant *Regular* Distribution Pattern. Shaded Rows Identify Sites Within the Pinto Abalone Spawning Season (April – July; Campbell et al. 2003)

Date surveyed	Site ID	# Abalone with nearest-neighbor	#/ Transect	Density (#/m ²)	Mean nearest-neighbor distance (m)	R	z Test Statistic	Distribution
6/13/14	PL03	5	6	0.0150	3.68	0.90	-0.43	Random
6/15/14	PL07	2	2	0.0050	3.45	0.49	-1.39	Random
6/23/14	PL10	2	2	0.0050	0.10	0.01	-2.67	Aggregated**
7/8/14	PL16	3	3	0.0075	2.55	0.44	-1.85	Random
10/25/14	PL25	3	4	0.0100	1.99	0.40	-2.00	Aggregated*
9/26/15	PL28	8	9	0.0300	1.21	0.42	-3.14	Aggregated**
10/24/15	PL31	6	6	0.0150	4.54	1.11	0.52	Random
2/9/16	PL32	10	10	0.0250	2.50	0.79	-1.28	Random
3/18/16	PL33	9	9	0.0225	1.80	0.54	-2.64	Aggregated**

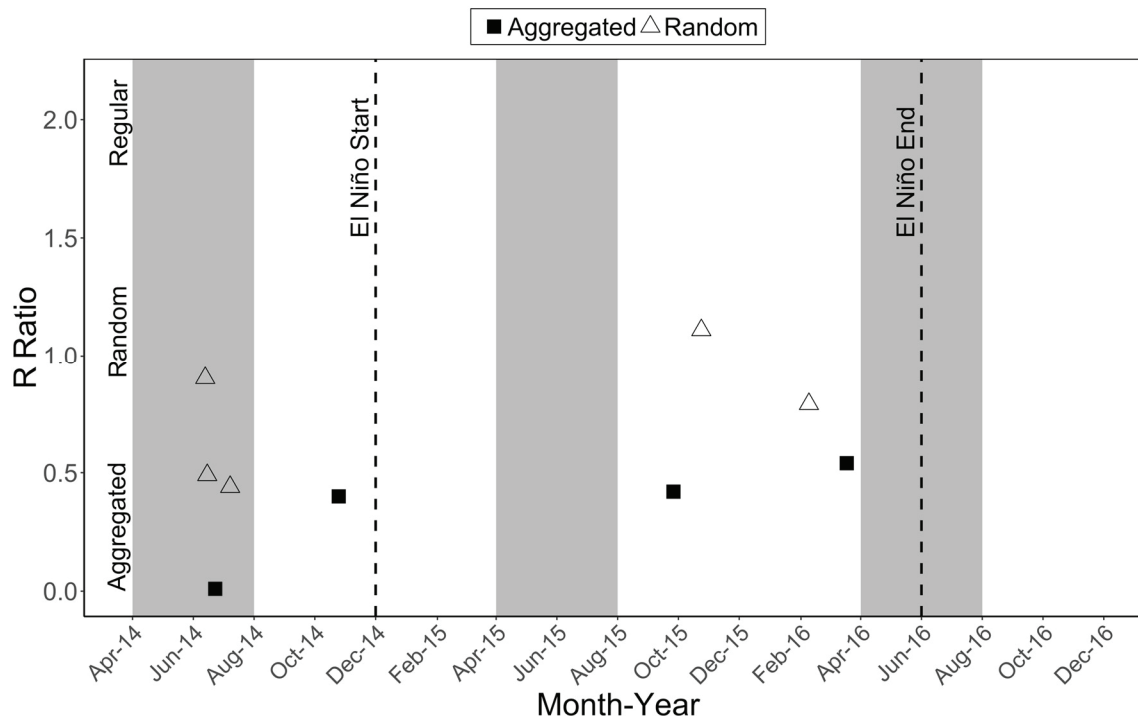


Figure 11. R ratios (Clark & Evans 1954) for each transect in Point Loma, CA where two or more pinto abalone were present and nearest-neighbor distances were measured ($N = 9$) surveyed between June 2014 and December 2016. Filled squares indicate significant ($p < 0.05$) departure from a random distribution (in this case only significantly *Aggregated*) and open triangles a random distribution for each transect. No transects showed a significant *Regular* spatial distribution. Shaded date ranges indicate pinto abalone spawning seasons (April – July; Campbell et al. 2003). Dashed lines correspond to the beginning (December 2014) and end (June 2016) of an El Niño period based on NOAA’s Oceanic Niño Index (NOAA Climate Prediction Center).

Habitat Associations

The greatest proportion (75%) of pinto abalone of all sizes were observed exposed on hard substrate, or easily visible and not tucked in crevices or under rocks (Figure 12A). Seventy-percent (70%; 7 individuals) of animals smaller than 76 mm (juveniles and small adults) were found in crevices, two underneath boulders. Pinto abalone were most often found on boulders (60%; Figure 12B) and located < 10 cm above the benthos at a flat relief (63%; Figure 12C), which includes individuals found a) attached to flat substrate (e.g., bedrock) or 2) attached to the base of boulders at the boulder/sand or boulder/bedrock interface. No individuals were found more than 1 m above the benthos.

Abalone habitat use and available habitat (estimated percent cover for each site) metadata for all species observed are in Appendices B and C, respectively.

Habitat for all sites consisted primarily of bedrock (59%) and flat-relief substratum (64%; Table 8). However, the majority of relief within a 1 m² area around pinto abalone was of low-relief (73%; Figure 12D), which includes both boulders and raised portions of the bedrock (“reefs”). No individuals were found on sand or at medium and high relief positions on substrata. Over all sites, there was very little medium (5%) and high (2%) relief substratum, and cobble and sand represented only 13% and 3% of substratum types available, respectively. Different from pinto abalone, of 90 red and 70 pink abalone observed, 68% and 54% were found in cryptic positions, respectively, either in crevices or under rocks (Appendix D). However, similar to pinto abalone, a majority of both species were found on boulders (red = 75%; pink = 89%), at a position < 10 cm above the benthos (red = 69%; pink = 80%), and most often adjacent to low-relief substratum (red = 88%; pink = 97%; Appendix D).

Pinto abalone use of substratum type ($X_L^2 = 62.27$; $df = 3$; $p = 1.91e-13$), their relief relative to surrounding 1 m² relief ($X_L^2 = 70.67$; $df = 3$; $p = 3.1e-15$), and 1 m² relief used relative to site relief ($X_L^2 = 77.07$; $df = 3$; $p = 1.11e-16$) were all significantly different than expected (Table 8). However, results should be treated with caution as cobble, sand, medium and high relief values were < 5 and thus do not meet conditions required for the chi-squared test, so multiple comparisons were made to evaluate individual categories.

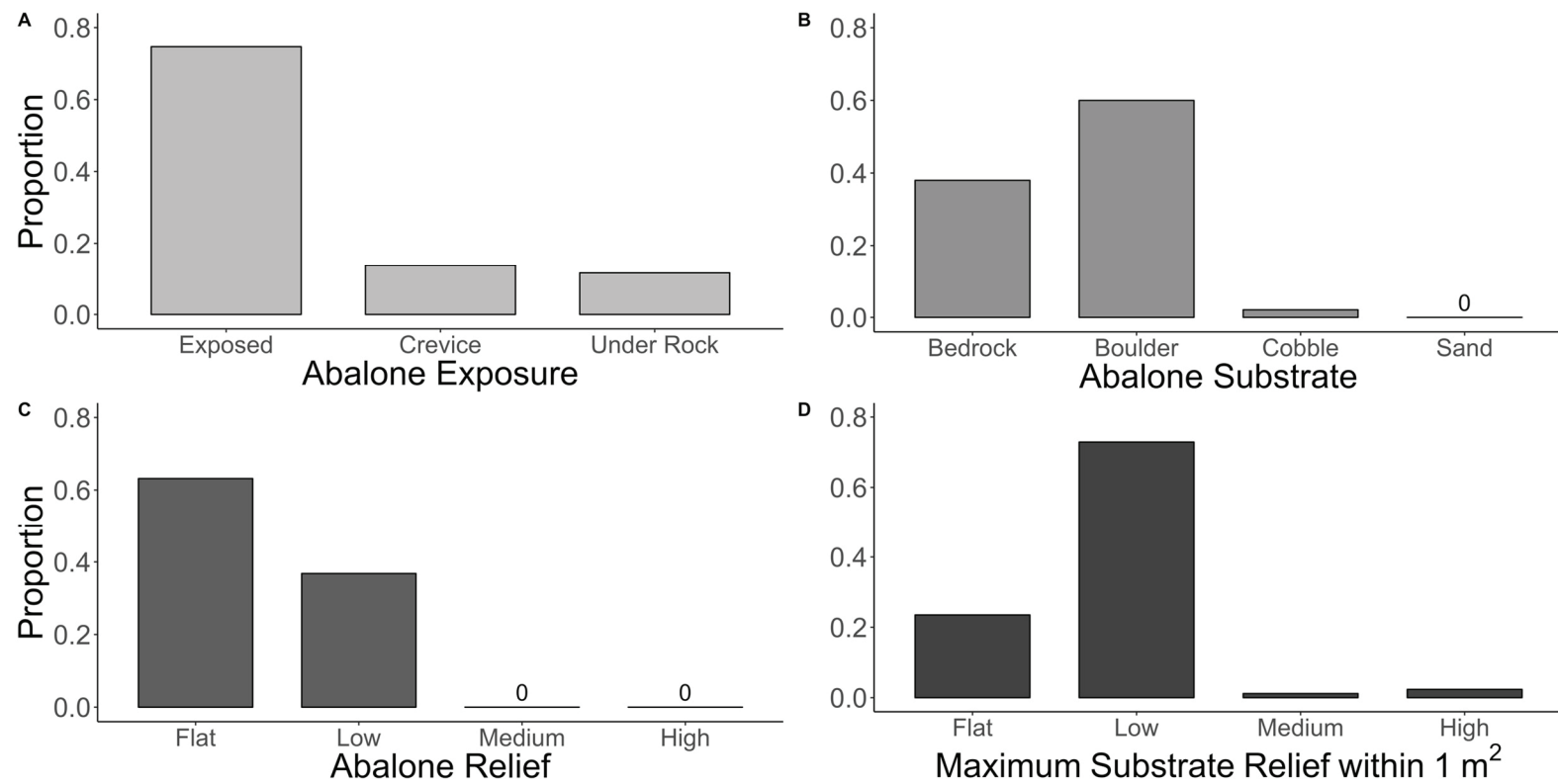


Figure 12. Proportions of pinto abalone associated with specific microhabitat features. (A) abalone exposure, or visibility on the seafloor, (B), substrate type an abalone was attached to, (C), relief of the abalone relative to the seafloor, and (D) highest rock relief within 1m² of an abalone. Substrate relief categories include: 1) flat: 0 – 10 cm; 2) low: 10 cm – 1 m; 3) medium: 1 – 2 m; and 4) high: > 2 m.

Table 8. Estimation of Pinto Abalone Habitat Selection Ratios ($w_i = o_i/\pi_i$) Based on Proportions of Available (π_i) and Used (o_i) Substratum Type and Relief Categories, Standard Errors of the Selection Ratios (se), *P* Values and Confidence Limits for Selection Ratios, and Standardized Ratios (B_i) Per Manly et al. (1993) for All Sites Where Pinto Abalone Were Present ($N = 23$) in San Diego, CA Between June 2014 and December 2016

Substratum category	Population (available) proportion (π_i)	Sample count (u_i)	Sample (used) proportion (o_i)	Selection ratio (w_i)	Standardized ratio (B_i)	se (w_i)	<i>p</i> value	Confidence Limits	
								Lower	Upper
Substratum Type									
Bedrock	0.5929	36	0.3789	0.6392	0.1970	0.0840	0.0000	0.4507	0.8272
Boulder	0.2452	57	0.6000	2.4466	0.7550	0.2050	0.0000	1.9875	2.9064
Cobble	0.1371	2	0.0211	0.1535	0.0470	0.1070	0.0000	0.0000*	0.3938
Sand	0.0248	0	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Relief (1 m ² /site)									
Flat (0 - 10 cm)	0.6405	20	0.2353	0.3670	0.0880	0.0720	0.0000	0.2056	0.5284
Low (10 cm - 1 m)	0.2762	62	0.7294	2.6410	0.6300	0.1740	0.0000	2.2510	3.0310
Medium (1 - 2 m)	0.0595	1	0.0118	0.1980	0.0470	0.1960	0.0000	0.0000	0.6373
High (> 2 m)	0.0238	2	0.0235	0.9880	0.2360	0.6910	0.0000	0.0000	2.5368
Relief (abalone/1 m ²)									
Flat (0 - 10 cm)	0.2353	60	0.6316	2.6842	0.8420	0.2100	0.0000	2.2135	3.1548
Low (10 cm - 1 m)	0.7294	35	0.3684	0.5051	0.1580	0.0680	0.0000	0.3526	0.6575
Medium (1 - 2 m)	0.0118	0	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
High (> 2 m)	0.0235	0	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

*A negative lower limit for the confidence interval for medium and high relief and cobble has been replaced by 0.0000 as negative values for selection indices are impossible (Manly et al. 1993).

While a majority of habitat for sites where pinto abalone were present consisted of bedrock, pinto abalone used bedrock habitat significantly less ($p < 0.0001$) and boulder significantly more ($p < 0.0001$) than was available (Table 8). Pinto abalone were most often located < 10 cm above the bottom (“flat relief”), and this was the most abundant substratum relief for all sites where pinto abalone were present. However, the majority of relief within a 1 m^2 area around pinto abalone was of low-relief and pinto abalone were located < 10 cm (flat relief) above the benthos significantly more than expected from this surrounding relief ($p < 0.0001$; Table 8). Further, pinto abalone were located on or within 1 m^2 of low-relief substratum significantly more often than it was available at sites ($p < 0.0001$; Table 8). Cobble and sand substratum types and medium and high relief categories were selected less than expected, but results should also be interpreted with caution given use counts less than 5. Confidence intervals for the other categories with counts > 5 are considered reliable (Manly et al. 1993).

Using the selection and standardized ratios, which allow for direct comparisons between values for each habitat category, pinto abalone are predicted to select boulder habitat 75% of the time ($B_{10} = 0.755$), or at about 3.8 times more than bedrock habitat ($B_9 = 0.197, B_{10} = 0.755$, and $w_9 = 0.6392, w_{10} = 2.4466$; Table 8) and pinto abalone should be located < 10 cm above the benthos 84% of the time, or 5.3 times more than at low relief ($B_1 = 0.8420, B_2 = 0.1580$, and $w_1 = 2.6842, w_2 = 0.5051$; Table 8) if all categories are available in the same proportions as the original population. Similarly, pinto abalone may be located within 1 m^2 of low-relief substratum 63% of the time, and are 7 times more likely to be next to low- than flat-relief substratum ($w_5 = 0.367, w_6 = 2.641$).

Both pink and red abalone observed in this study showed similar and slightly stronger preferences for substratum type and relief than pinto abalone (Appendix D); they occupied boulders and were < 10 cm above the seafloor significantly more often than expected ($p < 0.0001$ for all categories; Appendix E). Based on selection and standardized ratios, red and pink abalone are expected to be found on boulders 84% and 94% of the time and at < 10 cm relief 96% and 99% of the time, respectively. At sites where pink and red abalone were present, the majority of habitat available over the site was bedrock (55-57%) and flat relief (62-68%), respectively. Conversely, 86-97% of available habitat within a 1 m² area around pink and red abalone was of low-relief, respectively. Manly selection ratios, standardized ratios and proportions of used versus available habitat types are presented in Appendix E for all abalone species observed.

CHAPTER 4

DISCUSSION

This study provides the first assessment of demographic and habitat information for pinto abalone in San Diego, California two decades after the closure of all abalone fisheries in southern California. Current low densities are far below critical thresholds for successful spawning and recruitment identified for other abalone species (0.15-0.30 abalone/m²; Babcock & Keesing 1999). Within the framework of the CDFW ARMP, the guiding document for recovery of depleted abalone populations in California, very low local densities, and thus the absence of a broad size distribution at single sites, suggest that populations in San Diego are not self-sustaining. However, the ARMP recognizes a need to refine target densities based on new data that may differ among species as well as among locations throughout the range of a species (CDFW 2005). Here, the distribution of pinto abalone was found to be very patchy throughout San Diego. Some, albeit extremely limited, evidence that recruitment appears to have occurred over the past two decades was observed, with multiple size classes being filled when using *both* live and empty shell size data, and evidence of recent (2013/2014) recruitment with the presence of individuals < 50 mm in size. Recruitment was much too limited and possibly episodic to allow an estimation of magnitude and frequency of such events. Some sites showed significant aggregation of adult pinto abalone, though the mechanism behind this, whether as mate-seeking behavior, by chance, or as a function of habitat preference, is

unknown. Studies of aggregation related to reproduction are likewise mostly lacking (see below), even in better studied and cultivated abalone species. It is likely that the frequency, timing, and broad spatial distribution of these surveys, as well as observed low densities, was not sufficient to measure meaningful patterns in recruitment or spatial distribution among spawning seasons and sites. Further, these surveys were conducted over a strong El Niño event, which certainly had observed negative impacts on kelp forest habitat, the primary food source of abalone. Interestingly, I observed some of the highest counts of abalone during the El Niño event, but with limited surveys, it is difficult to correlate these counts specifically with the El Niño event, as counts could have also been elevated randomly, due to depth, or due to other factors. In general, survey duration was not adequate to measure potential effects of El Niño on pinto abalone populations or habitat. While this study provides baseline demographic information, regular monitoring surveys are needed to assess long-term changes in population structure and habitat.

Pinto Abalone Population Structure and Distribution in San Diego, CA

Pinto abalone densities in San Diego are far below critical density thresholds (0.15-0.30 abalone/m²) identified for other abalone species (Babcock & Keesing 1999), below which successful fertilization may be compromised and abalone populations have been observed to experience recruitment failure (Shepherd & Brown 1993; Shepherd & Partington 1995). The highest density observed at a single site in this study (0.03/m²) was nearly an order of magnitude below the minimum viable population size of 0.2 abalone/m² as defined in the ARMP for a self-sustaining population (CDFW 2005), a criterion that equates to 80 animals per 400-m² transect, the standard area surveyed in this study. Further, the ARMP size distribution criterion was not met for any site in San

Diego; this was only met for all sites combined in San Diego, or all sites in Point Loma only (approximately 14,000 m² area surveyed). However, the size of an ARMP index site has not been defined for southern California; index sites (~ 2,160 m² total survey area) have only been defined for the recreational red abalone fishery in northern California and are not comparable to areas surveyed in this study. However, densities measured here provide useful baseline information for future recovery assessments (Taniguchi, personal communication).

Pinto abalone were patchily distributed throughout San Diego based on the variance-to-mean ratios of transect counts; there were many sites where neither live pinto abalone nor empty shells were found. Pinto abalone were more abundant in Point Loma, particularly at the southern extent of Point Loma, than in La Jolla. However, exploratory surveys among approximately 20 sites conducted prior to this study (April 2010 to September 2014) in La Jolla indicate that higher-density areas exist, with counts at sites ranging from one to just under a dozen individuals, including several juveniles, on SCUBA dive surveys ranging from 40-60 minutes in duration (Hagey et al. unpublished data). Potential explanations for observed differences in abundances among forests include (but are not limited to), differences in the spatial extent of survey effort, depth, habitat composition, and environmental conditions, as well as through random selection of sites. I surveyed 19 sites in La Jolla (compared to 36 in Point Loma); survey effort was distributed among the two forests based on the presence and proportion of *Macrocystis pyrifera* canopy cover using available aerial canopy survey data (CDFW 2014; Figure 1). These data are visual aerial observations of surface canopy cover. Ocean conditions, including strong currents and tidal height, as well as declines in canopy cover in warmer

years, may, either in combination or independently, lead to underestimates of canopy cover (Stekoll et al. 2007; Parnell 2015). Parnell (2015) used an acoustic method to estimate kelp canopy cover that indicated much higher spatial kelp coverage compared to aerial survey estimates (and more equal coverage among the two forests). He suggested using this method during times of highest kelp abundance in combination with seasonal aerial surveys to offset underestimation. Thus, survey effort should have been distributed more equally among the forests.

In addition, Parnell (2015) identified another important deeper macroalgal community present in San Diego structured by *Pelagophycus porra* that was likely not represented in *Macrocystis* canopy calculations. He found that *Macrocystis* decreases around 22 m in depth and is largely absent at depths greater than 25 m in both La Jolla and Point Loma whereas *Pelagophycus*, which is also canopy-forming but more often grows to just beneath the surface of the water, is dominant beyond 23 m in depth. Based on geology of the seafloor, La Jolla in particular has more hard substrata at depths ideal for *Pelagophycus* compared to Point Loma (Parnell 2015). I surveyed six sites in Point Loma and nine in La Jolla in deeper (21-30m) habitat characterized by relatively abundant *Pelagophycus porra* and understory brown algae including *Laminaria farlowii*, *Pterygophora californica*, and *Agarum fimbriatum* (Appendix C) as described by Parnell (2015). The fewest number of surveys among all survey dates were conducted in the shallowest (13-16 m) and deepest (24-30 m) strata but there was equal effort among these two strata and far more pinto abalone were observed in the deepest strata compared to the shallowest, particularly in Point Loma. The three sites with the highest counts of pinto abalone in Point Loma were found in deeper habitat (19-27m). All pinto abalone

observed in La Jolla were found at sites between 20 and 25 m maximum depth. The depth distribution of transect counts in Point Loma suggest that there may be a greater number of areas deeper than 17 m that support higher numbers of pinto abalone, which is maintained in qualitative descriptions by Geiger and Owen (2012) that pinto abalone in the southern portion of their range are most common between 20 and 30 m.

It is possible that improved diver experience in identifying and locating pinto abalone may have contributed to an increase in the frequency of higher pinto abalone counts over time. In addition, abalone movement and degree of aggregation may have influenced counts. While adult pinto abalone are generally sedentary, especially when food is abundant, they may move several meters each day (Sloan & Breen 1988). Further, if abalone are more dispersed over space at certain times, small survey areas may not effectively capture local abundance, particularly at a single point in time. The distribution of these surveys over large spatial areas and conducted irregularly over a two-year period, provide limited information on population trends. Future survey efforts should focus on: 1) comparing pinto abalone population parameters among depths and within distinct macroalgal communities as described by Parnell (2015) to explore depth and habitat relationships, and 2) carefully evaluating long-term fluctuations in abalone abundance through regular index site surveys to assess natural demographic and habitat changes and those associated with climate-related events, such as El Niño periods.

Reproductive Potential

While very few juvenile abalone (< 50 mm in size) were observed in this study, they are often very difficult to find as they are tucked in deep crevices, underneath boulders and urchin spine canopy, or within *Macrocystis* holdfasts (Tegner & Dayton

1977; Rogers-Bennett & Pearse 1998). The cryptic nature of small abalones makes measuring recruitment, particularly over short periods of time, difficult. Stevick (2010) calculated a “show factor” for outplanted juvenile pinto abalone in Washington to determine the proportion of animals observed during *noninvasive* surveys in which emergent abalone are searched for without destructively sampling habitat to find all abalone. She conducted an outplant experiment at three sites in Washington using pinto abalone ~ 25 mm in size and determined the number of individuals at the end of one year (post-outplanting) observed using both noninvasive and invasive (she overturned rocks and cobble to find all abalone) survey techniques. She found that only 31% of outplanted juvenile pinto, which had grown 21 mm in length on average over one year, were observed during noninvasive surveys compared to invasive surveys. Similarly, Hines and Pearse (1982) found that invasive sampling for small red abalone in central California increased density estimates from 1.8 to 2.8 abalone/10m². In this study, I found 10 animals smaller than 76 mm (the minimum size within the intermediate size class per the ARMP) and three < 50 mm, one of which was 13 mm and likely produced within the past 1-2 years (2013-2014; Quayle 1971). Fresh empty shell sizes filled in several pinto abalone size classes and, when combined with live pinto abalone sizes, brought the mean size down from 111 to 105 mm. In addition, 12 shells collected were less than 76 mm, six of which were less than 50 mm, which is about the age at pinto abalone sexual maturity (Quayle 1971). While we turned rocks and cobble to look for juveniles in this study, we did not do so to the extent required to find all cryptic animals (Stevick 2010) and much habitat was inaccessible but capable of supporting small abalone (e.g., deep bedrock reef ledges, large boulders, multiple layers of boulders, urchin spine canopy, and kelp

holdfasts). The presence of live juvenile pinto abalone and shells indicates that limited recruitment has been occurring in San Diego, and the frequency of counts of smaller individuals may be higher than observed based on a relatively low “show factor” for noninvasive survey methods (Stevick 2010).

One explanation for the observation of recruitment events despite low adult densities is the potential for reproductive adults to aggregate during spawning events (Breen & Adkins 1980). Seamone and Boulding (2011) calculated R ratio aggregation indices (Clark & Evans 1954) to analyze spatial distributions of pinto abalone in British Columbia, Canada and found that adults were significantly aggregated during a spawning season (July) in all three low-density populations they surveyed (R ratios = 0.389-0.761). However, the lowest site density, each site being only 50m², was 0.12/m², nearly an order of magnitude greater than the highest within-site density in this study and no surveys were conducted outside of spawning season. Studies of pink abalone conducted from 2006 to 2007 in Point Loma used location data from transect mapping methods (similar to this study) during the peak spawning season for pink abalone and found that, at densities ranging from 0.023-0.007 abalone/m², which are perhaps most comparable to pinto abalone in Point Loma, adult pink abalone maintained a relatively high degree of aggregation (Catton & Rogers-Bennett 2013).

This study was the first to examine nearest-neighbor distances and spatial distribution for pinto abalone in southern California. In this study, only 30% of individuals had a neighbor within a critical distance of 2 m identified for successful fertilization of gametes for other abalone species (Babcock & Keesing 1999). However, a majority (65%) had a neighbor within 5 m. Interestingly, nearly half of individuals had

nearest-neighbor distances less than 2 m outside of the spawning season (April – July) identified for pinto abalone in the northern portion of their range (Campbell et al. 2003). While some sites exhibited patterns of significant aggregation, there was no distinguishable pattern over time in and out of spawning seasons. Though these surveys were conducted over multiple spawning seasons, they were not done at regular intervals over the study period and both the frequency and duration of surveys was likely not enough to adequately capture potential aggregative behaviors and make meaningful comparisons over time and space. However, the observation of a majority of individuals within 5 m of an adult conspecific and evidence of significant aggregation at some sites, may suggest that pinto abalone can aggregate in San Diego or are at least close enough to move towards a conspecific if they exhibit active aggregation to spawn. Future work should focus on this aspect of reproduction at low densities and use these metrics alongside densities as an additional indication of reproductive potential and long-term population viability (Button 2008; Catton & Rogers-Bennett 2008; Stierhoff et al. 2012).

Beyond whether pinto abalone may overcome the physical limitations of reproducing at low densities, reproduction and recruitment may not be successful each year due to several other factors. Successful reproduction may vary considerably with abalone gonad maturity and health (fecundity), timing and duration of single spawning events, and fluctuations in environmental conditions that may impact both. Northern pinto abalone reach sexual maturity at a size of ~ 50-70 mm shell length (~ 2-5 years of age; Campbell et al. 1992) and are thought to have a spawning season between April and July with ripe gonads year-round (Campbell et al. 2003; Sloan & Breen 1988). CDFW (2005) has identified a season of April to June for pinto abalone in California, however,

there have been no observations of spawning for pinto abalone in southern California. Female pinto abalone may carry several millions of eggs, however, fewer have been released during spawning events, which suggests they have the potential to spawn several times per spawning season (Campbell et al. 2003) but this has not been observed (NMFS 2014). Fecundity generally increases with size/age in abalones (Tutschulte 1976) and varies with water temperature and the quality and abundance of food (Leighton 2000; CDFW 2005). Very little is known about spawning duration and frequency in pinto abalone (NMFS 2014). A spawning event was observed in pinto abalone in British Columbia, Canada in July 1979 by Breen and Adkins (1980), though a small number of animals had been collected and tagged during the event, which may or may not have influenced spawning. Spawning lasted for at least 3.5 hours and was characterized by animals climbing to the highest points on the substratum and nearest to one another, producing small aggregations and releasing gametes. The frequency of such spawning events, though, may be sporadic or may only occur once each year as in white abalone (Leighton 2000) if at all. If the act of spawning cues aggregative behavior, successful reproduction still requires synchronicity in timing, close proximity, and the presence of adults capable of spawning quality gametes (especially if densities are low) as well as ideal environmental conditions.

In terms of larval survival and recruitment, higher water temperatures may negatively affect larval survival (Leighton 1974; Bouma 2007). However, warm-water events have also been suggested as potential drivers of settlement success in pink abalone in California (Tegner & Dayton 1987). Temperature is an important cue for spawning in adult abalone (Young & DeMartini 1970; Uki & Kikuchi 1984; Leighton 2000) and may

influence the variable annual spawning periods observed among haliotids (Shepherd & Laws 1974; Mottet 1978). Shifts in oceanographic current regimes, particularly among El Niño periods, have been suggested to impact patterns of larval dispersal (Tegner et al. 2001). Most studies to date suggest that abalone larvae are dispersed in the water column over relatively short distances (Prince et al. 1987; McShane et al. 1988; Gruenthal 2007; Gruenthal et al. 2007) but the potential for transport ranges from short- to long-distances (Miyake et al. 2017). The genetic structure of pinto abalone suggest it could be on the order of 1,000 km (Withler et al. 2001; NMFS 2014). Recruitment was observed for red, pink, and pinto abalone in this study though juvenile abalone (< 50 mm) were observed at sites both with and without adults within the areas searched (which were fairly limited in size) and over all three years of the study period. The number of juveniles was too small to assess variation among years or sites. Variation in spawning success, larval dispersal patterns, and recruitment introduce uncertainty in assessing long-term reproductive potential regardless of the ability of animals to aggregate to spawn. Environmental changes, such as El Niño events, combined with variable reproductive strategies, may contribute to the observed sporadic nature of recruitment seen in pinto abalone over the past two decades (NMFS 2014). Again, the timing and duration of these surveys did not allow for an assessment of changes in pinto abalone abundance and recruitment, particularly associated with the El Niño and among a diversity of habitats.

Habitat Preferences and Relationship to Spatial Distribution

Local distribution of pinto abalone may fluctuate over time depending on reproductive strategies and environmental conditions as well as the presence of suitable habitat. Further, the distribution of individuals on a small scale (tens of meters) within a

habitat, may vary based on habitat features, which could also indirectly influence aggregation. Pinto abalone observed in this study show a strong preference for boulder habitat though bedrock was the most available substratum type at all sites where they were present. They positioned themselves at a lower relief (closer to the benthos) than was available in the surrounding rock relief, particularly < 10 cm above the benthos, attached to the sides of boulders at the boulder/bedrock or boulder/sand interface or on the bedrock next to a higher-relief boulder. While they were most frequently found on the most available substratum relief (flat), they were also most often on or adjacent to substratum of a higher relief. Several of these findings are in line with prior qualitative observations of pinto abalone adults being more exposed on substratum throughout their range (Cox 1972; Hines & Pearse 1982; Sloan & Breen 1988; Rogers-Bennett et al. 2011; Geiger & Owen 2012).

Abalone habitat preferences may vary among species, but some preferences may overlap. In this study, both pink and red abalone almost exclusively preferred boulder substrata and were < 10 cm above the seafloor. These preferences were somewhat stronger than pinto abalone. Conversely, 70% of red abalone in this study were found in crevices or underneath reef ledges or boulders compared to 25% of pinto abalone (Figure 12; Appendix D). Pink abalone were intermediate, exposed 54% of the time. In another study where red and pinto abalone were both observed, the authors qualitatively noted that nearly all pinto abalone observed on sites, though very rare, were exposed on rocks though a majority of red abalone (whose exposure was quantified) were almost exclusively in crevices in an area where sea otters had been present for nearly two

decades (Hines & Pearse 1982). Hines and Pearse (1982) also found that red abalone were more exposed in similar habitat without sea otters.

At several locations in southern California, Lafferty et al. (2004) observed a pattern of positioning in endangered white abalone similar to that of pinto abalone in this study; white abalone adults were disproportionately located at positions low to the seafloor on the vertical face of large rocks (at the rock/sand interface). White abalone overlap in habitat with pinto abalone in southern California– at one site I observed individuals of both species next to one another on the same boulder – and white abalone adults, like pinto abalone, have been widely observed to occupy exposed positions on the substratum (Lafferty et al. 2004; NMFS 2008; A. Bird, personal observation; and this study). White abalone are considered a deep abalone species, found commonly between 25 and 30 m but > 40 m in some areas (Tutschulte 1976). It has been qualitatively observed that while they could survive at shallower depths, their emergent (exposed) nature and thin shell may have limited them to deeper habitats due to competition with other abalone species and potentially predation (octopus and, formerly sea otters; Tutschulte 1976; USFWS 2015). However, fishermen reported white abalone as shallow as 10-20 m deep (Lafferty et al. 2004) and this study has observed them as shallow as 15 m. Five adult white abalone ranging in size from 151 to 191 mm were found in San Diego and all were exposed on the substratum, three on boulders and two on bedrock, and all but one were within 1 m² of low-relief substratum the other being near flat relief.

Abalone preferences for specific substratum types and positions on the substratum may be directly related to these habitat features but may also be the result of a combination of factors. For example, in the study by Hines and Pearse (1982) and in a

similar more recent study by Micheli et al. (2008) for both red and black abalone in the same areas of central California, red abalone occupied crevice habitat almost exclusively. It was indicated in both studies that food availability in such positions was likely not limiting and recruitment was occurring despite predation by sea otters. Micheli et al. (2008) suggested that populations may have remained relatively stable for the past 30 years due to a combination of abundant algae, predator avoidance, and increased fertilization success due to high-density occupation of crevice habitat. Shepherd (1986b) reported that *H. laevigata* movement varied with the amount of crevice habitat, which may indicate preference; animals were more mobile when less crevice habitat was available and vice versa. Lafferty et al. (2004) hypothesized that white abalone positioning at the boulder/sand interface may increase access to negatively buoyant drift algae, which may be “captured” in crevices formed between boulders, for example, or by urchins that occupy similar positions relative to the substratum, but individuals were much deeper (> 40 m) and sea otters were not present. Water movement may also contribute to abalone habitat occupation. Several studies that have quantified broad habitat associations for pinto abalone in British Columbia, Canada indicated that moderate wave exposure was ideal and few or no animals were observed in high-velocity environments (Sloan & Breen 1988; Tomascik & Holmes 2003; Lessard & Campbell 2007). In shallower habitats, such as those where pinto abalone are most common in the northern part of their range, wave exposure and algal abundance may interact to provide sufficient food. In deeper habitats, such as the extensive marginal shelves along coastal areas of southern California (Parnell 2015), abalone may prefer more exposed positions in order to capture drift algae more effectively as has been suggested by Lafferty et al.

(2004) for white abalone. However, red and pinto abalone found co-occurring in San Diego show different preferences for exposed and cryptic positions but both appear capable of acquiring food in such positions (many individuals were observed feeding on drift algae) and explanations for these behaviors deserve further study.

At nearly all sites, sand represented very little of overall habitat, thus hard substrate in general was likely not limiting. Boulder and low-relief substrata represented only ~ 25% of what was available though, pinto abalone showed preference for this combination of habitat types. Such habitat is not uniform over space and thus could contribute to aggregation of abalone unrelated to proximity to a potential mate. Seamone and Boulding (2011) found that pinto abalone abundance increased with the abundance of boulder and bedrock containing crevices and the unequal distribution of this habitat within and outside their study sites (it was more abundant outside survey sites) may have underestimated observed densities. They reported that at one site, abalone appeared to be concentrated on a raised portion of flat bedrock. In addition, male abalone at one site were significantly aggregated around a single female but this may have also been attributed to individuals aggregating in suitable habitat (Seamone & Boulding 2011). At higher densities, if such a preference exists and is related to growth and survival, habitat in these areas could be limiting (Shepherd 1986b), particularly for juvenile abalone who rely on crevice habitat for protection from predators. Northern pinto abalone have been observed to aggregate during spawning events and, interestingly, they were reported to climb to the highest relief within the area including on top of one another and up kelp stipes, to spawn (Breen & Adkins 1980; Stekoll & Shirley 1993). So while they have the

ability to aggregate to reproduce, thus increasing potential for successful fertilization, habitat structure may also indirectly facilitate this during spawning events.

When a portion of habitat is used disproportionately to its availability, this may indicate some level of preference, particularly if a resource is selected when offered on an equal basis with others (Manly et al. 1993). There is some criticism regarding the validity of analyses of whether animals are using habitats in proportion to their availability, particularly when measured at only one point in time (Cherry 1998). Use of habitat is subject to change given changes in an organism's habitat needs over spatial and temporal scales. Habitat may also change irrespective of an organism's needs. Further, at low densities, such as for pinto abalone in this study, it could be argued that habitats are "undersaturated" and though selection may appear to be significant, it may truly be random. Alternatively, it could also be argued that at low densities, abalone are incredibly selective, choosing only the preferred habitat. Observations of habitat use were made only once for each animal in this study in a small portion of the range of pinto abalone in San Diego, CA and provide limited information on how habitat preferences may change over time and over the range of pinto abalone. To address these issues, methods developed here could be expanded to new areas and measured at multiple points in time for individual abalone. Continued research to evaluate habitat preferences, particularly for substratum type and relief, depth (and temperature at depth), and macroalgal abundance could be used to inform habitat models to identify areas with ideal habitat for pinto abalone. Habitat model creation has been done for white abalone in southern California (Okano 2009) and more recently for pinto abalone in San Diego using preliminary habitat information from this study (Ostrowski 2016). If naturally-occurring

patterns in substratum type and relief contribute to aggregation of reproductive individuals and growth and survival of abalone at multiple life stages, a better understanding of these patterns, among other habitat characteristics, could inform several aspects of abalone recovery. Combined with species-specific habitat models, habitat preferences could be used to identify ideal habitat for outplanting juvenile abalone to enhance wild populations and critical habitat that should be protected as well as unexplored areas where abalone may be present.

Current Status and Potential Threats to Pinto Abalone in Southern California

Much of the uncertainty regarding the current status of pinto abalone populations in southern California is related to the highly variable nature of observed recruitment events and patchy distribution of adults, which makes long-term recovery assessment in already low-density populations very difficult. Prior to this study, reports of pinto abalone in southern California were rare during the 1980s and 1990s (NMFS 2014). However, beginning around 1997 and continuing up until the present, pinto abalone adults and young recruits have been observed more frequently throughout the Southern California Bight with sizes ranging from 11-135 mm on Santa Cruz Island and 40-150 mm in Point Loma in San Diego, for example (NMFS 2014). Between 2008 and 2012, densities observed among non-targeted surveys ranged from 0.0002/m² at San Miguel Island to 0.0286/m² in Point Loma (CDFW, unpublished data, cited in Neuman et al. in prep). This study, conducted between June 2014 and December 2016 in San Diego and targeting pinto abalone, documented densities ranging from 0.0025 to 0.0300 abalone/m² for sites where pinto abalone were present, and do not appear to be vastly different from those reported since 2008. Further, despite low densities, multiple size classes ranging from 13

to 167 mm are represented in both live and empty shell size distributions, suggesting recruitment, though very limited, has occurred in San Diego over the past two decades and there is evidence of recent recruitment.

Throughout the range of pinto abalone, populations appear to be slowly recovering at some long-term monitoring sites (NMFS 2014). Index sites in British Columbia, Canada have been surveyed regularly since 1978 and experienced 75-80% declines in abundance from the 1970s to the mid-2000s. Densities for large and mature abalone ($0.03\text{-}0.29/\text{m}^2$) were very low in 2007, but have since shown slow increases in areas where sea otters are not present where predation pressure may hinder recovery (Hankewich et al. 2008; Chadés et al. 2012; Chandler et al. 2017; Neuman et al. in prep). Near Sitka, Alaska, at the northernmost range of pinto abalone, regular monitoring surveys at sites targeting pinto abalone aggregations have recorded absolute adult densities above $0.2/\text{m}^2$ as well as new recruits (< 20 mm) at nearly all sites (Bell et al. in prep). Conversely, in Washington, specifically in the San Juan Islands, there have been steady declines of adult densities from 1992 ($0.18/\text{m}^2$) to 2017 ($0.005/\text{m}^2$; Rothaus et al. 2008; NMFS 2014) and recruitment failure appears to be occurring (Bouma et al. 2012).

There have been instances in which abalone populations below critical density thresholds in California have recovered to densities at or above these thresholds; populations of endangered black abalone along mainland California show signs of recruitment despite very low densities (Eckdahl 2015). Depleted abalone populations may be capable of successful reproduction even at densities below critical thresholds but our understanding of thresholds, particularly on a species-specific level, is still limited (Neuman et al. in prep). Potential aggregative behaviors— whether in seeking potential

mates or whether preferences for habitat features indirectly promote naturally-aggregated patterns of spatial dispersion— may be facilitating recruitment despite very low densities.

For a diversity of taxa (but not without exceptions), species are often more abundant near the center of their range, gradually declining in abundance towards the edges of the range depending on a suite of environmental conditions (Brown 1984; Brown et al. 1996). It has been suggested that pinto abalone in southern California may have been less abundant than their northern counterparts even prior to being exploited in modern fisheries (Rogers-Bennett et al. 2002; NMFS 2014). It could be that pinto abalone in southern California exhibit characteristics of a species at the edge of its range; they exhibit lower abundances and are found in deeper habitat compared to those in more central areas of the range, similar to red and flat abalone (Cox 1962). At local scales, recruitment is clearly an important mechanism to sustain local populations (Prince et al. 1987, 1988; McShane et al. 1988) but the potential to disperse widely exists, depending on timing of spawning and larval duration and behavior (Miyake et al. 2017). A combination of ideal oceanographic conditions such as temperature and shifting current patterns may produce ideal conditions for transport beyond historic dispersal boundaries (Zacherl et al. 2003) and may play a role in maintaining pinto abalone populations in areas approaching the southern edge of their range such as southern California. However, local larval production in low-density areas may be too limited at range edges (Bahn et al. 2006) despite input from distant sources to maintain populations long-term. Mortality of pinto abalone and widespread and negative impacts on macroalgal communities may be exacerbated with predicted effects of climate-change, particularly warm water events and shifts in oceanographic currents associated with El Niño events (Tegner et al. 2001;

Edwards & Estes 2006). This raises concerns regarding the persistence of populations in the face of climate change and other environmental stressors (e.g., disease) particularly those that may be at the edge their range and at already low abundances. There is extensive evidence of climate-related shifts in both terrestrial and aquatic species' composition, abundance, and vertical and latitudinal distributions (Barry et al. 1995; Parmesan 1996; Sagarin et al. 1999). Species' abundance and distribution in the ocean are likely related to changes in recruitment and survival of offspring, not movement of adults (Shepherd et al. 1982), which is affected by oceanographic regimes, as well as adult densities. However, the dynamics of abalone larval dispersal among a suite of environmental conditions and adult densities remains to be understood and whether or not populations in San Diego at current levels are capable of the degree of recruitment necessary for long-term recovery is questionable. The persistence of pinto abalone in the southern edge of their range can only be measured using long-term studies.

The purpose of this study was to provide a baseline characterization of pinto abalone demographics and habitat associations in San Diego. There continue to be limitations in our understanding of critical density thresholds, local and regional fluctuations in abundance and recruitment, and long-term reproductive potential. There is a critical need for consistent long-term studies of pinto abalone in southern California to capture trends over time and among differing environmental regimes and to assess changes in population structure near the edge of the range for this rather interesting species with a broad geographic distribution. The conservation of this and other abalone species depends on our continued and combined efforts to understand demographic and environmental processes affecting recovery of abalone populations.

APPENDIX A

DEMOGRAPHIC INFORMATION FOR OTHER ABALONE SPECIES

Table A1. White Abalone (*Haliotis sorenseni*) Counts on Transects (#/Transect) and on an Entire Site (#/Site), Density (+/- SD), and Mean Live and Empty Shell Numbers, Sizes (mm), and Size Ranges for All Sites in La Jolla (LJ) and Point Loma (PL) Arranged by Forest and Date/El Niño Period Surveyed in San Diego, CA between June 2014 and December 2016

White abalone (<i>Haliotis sorenseni</i>)											
Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
6/10/14	Pre-El Niño	LJ01	17	400	0	0	0	-	-	-	-
7/29/14	Pre-El Niño	LJ03	18	400	0	0	0	-	-	-	-
8/19/14	Pre-El Niño	LJ04	20	400	0	0	0	-	-	-	-
8/19/14	Pre-El Niño	LJ05	19	400	0	0	0	-	-	-	-
3/28/15	El Niño	LJ06	15	400	0	0	0	-	-	-	-
4/12/15	El Niño	LJ07	16	400	0	0	0	-	-	-	-
4/20/15	El Niño	LJ08	16	400	0	0	0	-	-	-	-
4/20/15	El Niño	LJ09	17	400	0	0	0	-	-	-	-
4/21/15	El Niño	LJ10	20	400	0	0	0	-	-	-	-
4/21/15	El Niño	LJ11	20	400	0	0	0	-	-	-	-
11/8/15	El Niño	LJ12	25	400	0	0	0	-	-	-	-
11/8/15	El Niño	LJ13	22	400	0	0	0	-	-	-	-
11/14/15	El Niño	LJ14	21	400	0	0	0	-	-	-	-
11/14/15	El Niño	LJ15	23	400	0	0	0	-	-	-	-
11/20/15	El Niño	LJ16	20	400	1	0.0025	2	190-191	190.5 (0.7)	-	-
11/21/15	El Niño	LJ17	26	400	0	0	0	-	-	-	-
11/21/15	El Niño	LJ18	21	400	0	0	0	-	-	-	-
11/23/15	El Niño	LJ19	23	400	0	0	0	-	-	-	-
5/3/16	El Niño	LJ20	24	400	0	0	0	-	-	-	-
6/11/14	Pre-El Niño	PL01	15	400	0	0	0	-	-	-	-
6/11/14	Pre-El Niño	PL02	14	400	0	0	1	151	151	-	-
6/13/14	Pre-El Niño	PL03	23	400	0	0	0	-	-	-	-
6/13/14	Pre-El Niño	PL04	16	400	1	0.0025	1	165	165	-	-
6/15/14	Pre-El Niño	PL06	19	400	0	0	0	-	-	-	-

White abalone (<i>Haliotis sorenseni</i>)											
Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
6/15/14	Pre-El Niño	PL07	17	400	0	0	0	-	-	-	-
6/20/14	Pre-El Niño	PL08	16	400	0	0	0	-	-	-	-
6/22/14	Pre-El Niño	PL09	26	400	0	0	0	-	-	-	-
6/23/14	Pre-El Niño	PL10	25	400	0	0	0	-	-	-	-
6/23/14	Pre-El Niño	PL11	14	400	0	0	0	-	-	-	-
6/24/14	Pre-El Niño	PL12	23	400	0	0	0	-	-	-	-
6/25/14	Pre-El Niño	PL13	20	400	0	0	0	-	-	-	-
6/25/14	Pre-El Niño	PL14	25	400	0	0	0	-	-	-	-
7/1/14	Pre-El Niño	PL15	19	400	0	0	0	-	-	-	-
7/8/14	Pre-El Niño	PL16	23	400	0	0	0	-	-	-	-
7/9/14	Pre-El Niño	PL17	23	400	0	0	0	-	-	-	-
7/15/14	Pre-El Niño	PL18	16	400	0	0	0	-	-	-	-
7/16/14	Pre-El Niño	PL19	15	400	0	0	0	-	-	-	-
7/23/14	Pre-El Niño	PL20	18	400	0	0	0	-	-	-	-
8/6/14	Pre-El Niño	PL21	14	400	0	0	0	-	-	-	-
8/12/14	Pre-El Niño	PL22	17	400	0	0	0	-	-	-	-
8/13/14	Pre-El Niño	PL23	22	400	0	0	0	-	-	-	-
8/18/14	Pre-El Niño	PL24	15	400	0	0	0	-	-	-	-
10/25/14	Pre-El Niño	PL25	17	400	0	0	0	-	-	-	-
10/25/14	Pre-El Niño	PL26	15	400	0	0	0	-	-	-	-
4/23/15	El Niño	PL27	18	400	1	0.0025	1	173	173	-	-
9/26/15	El Niño	PL28	19	300	0	0	0	-	-	-	-
10/23/15	El Niño	PL29	22	400	0	0	0	-	-	-	-
10/24/15	El Niño	PL30	29	400	0	0	0	-	-	-	-
10/24/15	El Niño	PL31	20	400	0	0	0	-	-	-	-
2/9/16	El Niño	PL32	22	400	0	0	0	-	-	-	-
3/18/16	El Niño	PL33	27	400	0	0	0	-	-	-	-
3/18/16	El Niño	PL34	25	400	0	0	0	-	-	-	-
4/19/16	El Niño	PL35	23	400	0	0	0	-	-	-	-
9/20/16	Post-El Niño	PL36	21	400	0	0	0	-	-	-	-
12/1/16	Post-El Niño	PL38	21	400	0	0	0	-	-	-	-

Table A2. Red Abalone (*Haliotis rufescens*) Counts on Transects (#/Transect) and on an Entire Site (#/Site), Density (+/-SD), and Mean Live and Empty Shell Numbers, Sizes (mm), and Size Ranges for All Sites in La Jolla (LJ) and Point Loma (PL) Arranged by Forest and Date/El Niño Period Surveyed in San Diego, CA between June 2014 and December 2016

Red abalone (<i>Haliotis rufescens</i>)											
Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
6/10/14	Pre-El Niño	LJ01	17	400	0	0	0	0	0	-	-
7/29/14	Pre-El Niño	LJ03	18	400	1	0.0025	1	203	203	-	-
8/19/14	Pre-El Niño	LJ04	20	400	8	0.02	10	54-205	152 (46)	-	-
8/19/14	Pre-El Niño	LJ05	19	400	7	0.0175	7	127-181	159 (17)	1	162
3/28/15	El Niño	LJ06	15	400	0	0	0	0	0	-	-
4/12/15	El Niño	LJ07	16	400	0	0	0	0	0	-	-
4/20/15	El Niño	LJ08	16	400	0	0	0	0	0	-	-
4/20/15	El Niño	LJ09	17	400	0	0	0	0	0	-	-
4/21/15	El Niño	LJ10	20	400	0	0	0	0	0	-	-
4/21/15	El Niño	LJ11	20	400	0	0	0	0	0	-	-
11/8/15	El Niño	LJ12	25	400	0	0	0	0	0	-	-
11/8/15	El Niño	LJ13	22	400	1	0.0025	2	105-143	124 (27)	9	89 (51)
11/14/15	El Niño	LJ14	21	400	1	0.0025	6	164-213	198 (18)	-	-
11/14/15	El Niño	LJ15	23	400	2	0.005	2	183-200	192 (12)	-	-
11/20/15	El Niño	LJ16	20	400	0	0	0	0	0	1	140
11/21/15	El Niño	LJ17	26	400	0	0	0	0	0	2	104 (45)
11/21/15	El Niño	LJ18	21	400	0	0	0	0	0	1	99
11/23/15	El Niño	LJ19	23	400	3	0.0075	7	39-200	138 (49)	1	190
5/3/16	El Niño	LJ20	24	400	3	0.0075	10	120-220	181 (31)	1	118
6/11/14	Pre-El Niño	PL01	15	400	0	0	0	0	0	-	-
6/11/14	Pre-El Niño	PL02	14	400	0	0	2	196-206	201 (7)	-	-
6/13/14	Pre-El Niño	PL03	23	400	0	0	0	0	0	-	-
6/13/14	Pre-El Niño	PL04	16	400	0	0	0	0	0	-	-
6/15/14	Pre-El Niño	PL06	19	400	0	0	0	0	0	-	-
6/15/14	Pre-El Niño	PL07	17	400	0	0	0	0	0	-	-
6/20/14	Pre-El Niño	PL08	16	400	0	0	1	134	134	-	-
6/22/14	Pre-El Niño	PL09	26	400	0	0	0	0	0	-	-
6/23/14	Pre-El Niño	PL10	25	400	1	0.0025	1	175	175	1	150
6/23/14	Pre-El Niño	PL11	14	400	0	0	0	0	0	-	-

Red abalone (<i>Haliotis rufescens</i>)											
Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
6/24/14	Pre-El Niño	PL12	23	400	3	0.0075	3	131-162	149 (16)	-	-
6/25/14	Pre-El Niño	PL13	20	400	0	0	0	0	0	-	-
6/25/14	Pre-El Niño	PL14	25	400	0	0	0	0	0	-	-
7/1/14	Pre-El Niño	PL15	19	400	9	0.0225	9	40-200	138 (45)	3	169 (19)
7/8/14	Pre-El Niño	PL16	23	400	4	0.01	4	163-242	198 (39)	2	160 (0)
7/9/14	Pre-El Niño	PL17	23	400	3	0.0075	3	135-255	203 (61)	-	-
7/15/14	Pre-El Niño	PL18	16	400	2	0.005	3	149-191	163 (24)	1	153
7/16/14	Pre-El Niño	PL19	15	400	3	0.0075	3	160-250	207 (45)	-	-
7/23/14	Pre-El Niño	PL20	18	400	0	0	0	0	0	-	-
8/6/14	Pre-El Niño	PL21	14	400	0	0	0	0	0	1	35
8/12/14	Pre-El Niño	PL22	17	400	2	0.005	2	160-177	169 (12)	1	60
8/13/14	Pre-El Niño	PL23	22	400	0	0	0	0	0	-	-
8/18/14	Pre-El Niño	PL24	15	400	0	0	0	0	0	-	-
10/25/14	Pre-El Niño	PL25	17	400	0	0	0	0	0	-	-
10/25/14	Pre-El Niño	PL26	15	400	0	0	0	0	0	-	-
4/23/15	El Niño	PL27	18	400	6	0.015	16	94-215	162 (43)	-	-
9/26/15	El Niño	PL28	19	300	0	0	0	0	0	-	-
10/23/15	El Niño	PL29	22	400	0	0	0	0	0	-	-
10/24/15	El Niño	PL30	29	400	0	0	0	0	0	-	-
10/24/15	El Niño	PL31	20	400	6	0.015	6	135-220	172 (37)	-	-
2/9/16	El Niño	PL32	22	400	0	0	0	0	0	-	-
3/18/16	El Niño	PL33	27	400	0	0	0	0	0	-	-
3/18/16	El Niño	PL34	25	400	0	0	0	0	0	-	-
4/19/16	El Niño	PL35	23	400	0	0	0	0	0	-	-
9/20/16	Post-El Niño	PL36	21	400	0	0	0	0	0	-	-
12/1/16	Post-El Niño	PL38	21	400	0	0	0	0	0	1	77

Table A3. Pink Abalone (*Haliotis corrugata*) Counts on Transects (#/Transect) and on an Entire Site (#/Site), Density (+/-SD), and Mean Live and Empty Shell Numbers, Sizes (mm), and Size Ranges for All Sites in La Jolla (LJ) and Point Loma (PL) Arranged by Forest and Date/El Niño Period Surveyed in San Diego, CA between June 2014 and December 2016

Pink abalone (<i>Haliotis corrugata</i>)											
Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
6/10/14	Pre-El Niño	LJ01	17	400	1	0.0025	0	0	0	-	-
7/29/14	Pre-El Niño	LJ03	18	400	2	0.005	4	155-160	157 (3)	-	-
8/19/14	Pre-El Niño	LJ04	20	400	3	0.0075	3	119-130	125 (6)	-	-
8/19/14	Pre-El Niño	LJ05	19	400	1	0.0025	1	86	86	-	-
3/28/15	El Niño	LJ06	15	400	2	0.005	2	143-183	163 (28)	-	-
4/12/15	El Niño	LJ07	16	400	2	0.005	3	188-205	194 (9)	-	-
4/20/15	El Niño	LJ08	16	400	1	0.0025	7	96-218	166 (41)	-	-
4/20/15	El Niño	LJ09	17	400	1	0.0025	2	159-165	162 (4)	-	-
4/21/15	El Niño	LJ10	20	400	1	0.0025	1	180	180	-	-
4/21/15	El Niño	LJ11	20	400	1	0.0025	4	120-178	150 (25)	-	-
11/8/15	El Niño	LJ12	25	400	0	0	0	0	0	-	-
11/8/15	El Niño	LJ13	22	400	0	0	1	141	141	-	-
11/14/15	El Niño	LJ14	21	400	0	0	0	0	0	-	-
11/14/15	El Niño	LJ15	23	400	0	0	0	0	0	-	-
11/20/15	El Niño	LJ16	20	400	3	0.0075	5	151-172	163 (10)	-	-
11/21/15	El Niño	LJ17	26	400	0	0	0	0	0	-	-
11/21/15	El Niño	LJ18	21	400	1	0.0025	1	187	187	-	-
11/23/15	El Niño	LJ19	23	400	9	0.0225	9	115-180	155 (21)	2	158 (1.4)
5/3/16	El Niño	LJ20	24	400	0	0	0	0	0	-	-
6/11/14	Pre-El Niño	PL01	15	400	0	0	0	0	0	-	-
6/11/14	Pre-El Niño	PL02	14	400	2	0.005	2	120-136	128 (11)	-	-
6/13/14	Pre-El Niño	PL03	23	400	0	0	0	0	0	-	-
6/13/14	Pre-El Niño	PL04	16	400	0	0	0	0	0	-	-
6/15/14	Pre-El Niño	PL06	19	400	0	0	0	0	0	1	98
6/15/14	Pre-El Niño	PL07	17	400	0	0	0	0	0	-	-
6/20/14	Pre-El Niño	PL08	16	400	0	0	1	150	150	-	-
6/22/14	Pre-El Niño	PL09	26	400	0	0	0	0	0	-	-
6/23/14	Pre-El Niño	PL10	25	400	0	0	0	0	0	-	-
6/23/14	Pre-El Niño	PL11	14	400	0	0	0	0	0	-	-

Pink abalone (<i>Haliotis corrugata</i>)											
Date surveyed	El Niño Period	Site ID	Max Site Depth (m)	Total Area (m ²)	#/Transect	Density (#/m ²)	#/Site	Size Range (mm)	Mean Size (mm) (+/- SD)	# Empty Shells	Mean Empty Shell Size (mm) (+/- SD)
6/24/14	Pre-El Niño	PL12	23	400	1	0.0025	1	113	113	-	-
6/25/14	Pre-El Niño	PL13	20	400	0	0	0	0	0	-	-
6/25/14	Pre-El Niño	PL14	25	400	0	0	0	0	0	-	-
7/1/14	Pre-El Niño	PL15	19	400	1	0.0025	1	141	141	-	-
7/8/14	Pre-El Niño	PL16	23	400	0	0	0	0	0	-	-
7/9/14	Pre-El Niño	PL17	23	400	0	0	0	0	0	-	-
7/15/14	Pre-El Niño	PL18	16	400	4	0.01	6	140-162	148 (8)	-	-
7/16/14	Pre-El Niño	PL19	15	400	3	0.0075	3	149-174	158 (14)	-	-
7/23/14	Pre-El Niño	PL20	18	400	5	0.0125	5	79-156	119 (33)	-	-
8/6/14	Pre-El Niño	PL21	14	400	3	0.0075	5	127-165	146 (17)	-	-
8/12/14	Pre-El Niño	PL22	17	400	1	0.0025	1	112	112	-	-
8/13/14	Pre-El Niño	PL23	22	400	0	0	0	0	0	-	-
8/18/14	Pre-El Niño	PL24	15	400	4	0.01	4	119-174	158 (26)	-	-
10/25/14	Pre-El Niño	PL25	17	400	0	0	0	0	0	-	-
10/25/14	Pre-El Niño	PL26	15	400	0	0	1	58	58	-	-
4/23/15	El Niño	PL27	18	400	0	0	0	0	0	-	-
9/26/15	El Niño	PL28	19	300	0	0	0	0	0	-	-
10/23/15	El Niño	PL29	22	400	0	0	0	0	0	-	-
10/24/15	El Niño	PL30	29	400	0	0	0	0	0	-	-
10/24/15	El Niño	PL31	20	400	0	0	0	0	0	-	-
2/9/16	El Niño	PL32	22	400	0	0	0	0	0	-	-
3/18/16	El Niño	PL33	27	400	0	0	0	0	0	-	-
3/18/16	El Niño	PL34	25	400	0	0	0	0	0	-	-
4/19/16	El Niño	PL35	23	400	0	0	0	0	0	-	-
9/20/16	Post-El Niño	PL36	21	400	0	0	0	0	0	-	-
12/1/16	Post-El Niño	PL38	21	400	1	0.0025	1	46	46	1	46

APPENDIX B

ABALONE HABITAT USE METADATA

Table B. Number and Size (Maximum Shell Length) of All Species Observed, Depth, Exposure, Type of Substratum and Relief for Individual Abalone, and Surrounding Relief Within 1m² of Each Live Abalone Observed for All Sites in La Jolla (LJ) and Point Loma (PL) in San Diego, CA Surveyed Between June 2014 and December 2016

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
6/10/14	LJ01	NA	0	NA	NA	NA	NA	NA	NA
6/11/14	PL01	NA	0	NA	NA	NA	NA	NA	NA
6/11/14	PL02	Pink	1	120	42	exposed	bedrock	flat	flat
6/11/14	PL02	Pink	1	136	43	exposed	bedrock	low	low
6/11/14	PL02	Red	1	196	41	exposed	bedrock	low	low
6/11/14	PL02	Red	1	206	44	exposed	bedrock	low	low
6/11/14	PL02	Pinto	1	108	42	exposed	bedrock	flat	flat
6/11/14	PL02	Pinto	1	110	42	exposed	bedrock	flat	flat
6/11/14	PL02	Pinto	1	145	43	exposed	bedrock	flat	low
6/11/14	PL02	White	1	151	43	exposed	bedrock	low	low
6/13/14	PL03	Pinto	1	108	67	exposed	boulder	low	low
6/13/14	PL03	Pinto	1	60	70	crevice	bedrock	flat	low
6/13/14	PL03	Pinto	1	114	70	exposed	boulder	low	low
6/13/14	PL03	Pinto	1	115	72	crevice	boulder	low	low
6/13/14	PL03	Pinto	1	143	72	exposed	boulder	low	low
6/13/14	PL03	Pinto	1	125	75	exposed	boulder	low	low
6/13/14	PL04	Pinto	1	59	50	exposed	boulder	flat	low
6/13/14	PL04	White	1	165	61	exposed	boulder	flat	low
6/15/14	PL06	Pinto	1	13	61	underrock	boulder	flat	low
6/15/14	PL07	Pinto	1	56	56	underrock	boulder	flat	NA
6/15/14	PL07	Pinto	1	61	57	underrock	boulder	flat	NA

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
6/20/14	PL08	Pink	1	150	53	underrock	boulder	flat	low
6/20/14	PL08	Red	1	134	56	underrock	boulder	flat	low
6/22/14	PL09	Pinto	1	136	80	crevice	boulder	low	high
6/22/14	PL09	Pinto	1	140	80	crevice	boulder	low	high
6/22/14	PL09	Pinto	1	118	86	crevice	boulder	low	medium
6/23/14	PL10	Red	1	175	81	crevice	bedrock	low	high
6/23/14	PL10	Pinto	1	101	82	underrock	boulder	flat	low
6/23/14	PL10	Pinto	1	126	82	underrock	boulder	flat	low
6/23/14	PL11	NA	0	NA	NA	NA	NA	NA	NA
6/24/14	PL12	Pink	1	113	65	exposed	boulder	NA	flat
6/24/14	PL12	Red	1	131	66	crevice	bedrock	flat	low
6/24/14	PL12	Red	1	162	65	crevice	boulder	flat	low
6/24/14	PL12	Red	1	154	65	exposed	bedrock	flat	low
6/24/14	PL12	Pinto	1	40	50	exposed	boulder	flat	low
6/24/14	PL12	Pinto	1	34	70	crevice	bedrock	flat	low
6/24/14	PL12	Pinto	1	85	74	crevice	boulder	flat	low
6/25/14	PL13	NA	0	NA	NA	NA	NA	NA	NA
6/25/14	PL14	NA	0	NA	NA	NA	NA	NA	NA
7/1/14	PL15	Pink	1	141	62	crevice	boulder	low	low
7/1/14	PL15	Red	1	NA	60	crevice	boulder	low	low
7/1/14	PL15	Red	1	148	60	underrock	boulder	flat	low
7/1/14	PL15	Red	1	148	60	underrock	boulder	flat	low
7/1/14	PL15	Red	1	148	60	underrock	boulder	flat	low
7/1/14	PL15	Red	1	148	60	underrock	boulder	flat	low
7/1/14	PL15	Red	1	148	60	underrock	boulder	flat	low
7/1/14	PL15	Red	1	40	61	crevice	bedrock	flat	medium
7/1/14	PL15	Red	1	120	60	underrock	boulder	flat	low
7/1/14	PL15	Red	1	200	63	underrock	boulder	flat	low
7/1/14	PL15	Pinto	1	100	60	underrock	boulder	flat	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
7/8/14	PL16	Red	1	168	71	crevice	boulder	flat	flat
7/8/14	PL16	Red	1	242	71	crevice	bedrock	flat	flat
7/8/14	PL16	Red	1	218	71	exposed	bedrock	flat	flat
7/8/14	PL16	Red	1	163	71	exposed	boulder	low	low
7/8/14	PL16	Pinto	1	128	71	exposed	boulder	low	low
7/8/14	PL16	Pinto	1	135	71	exposed	boulder	low	low
7/8/14	PL16	Pinto	1	137	71	exposed	boulder	low	low
7/9/14	PL17	Red	1	135	75	underrock	boulder	flat	low
7/9/14	PL17	Red	1	255	75	underrock	boulder	flat	low
7/9/14	PL17	Red	1	218	75	underrock	boulder	flat	low
7/9/14	PL17	Pinto	1	64	74	crevice	boulder	flat	low
7/9/14	PL17	Pinto	1	75	74	crevice	boulder	flat	low
7/15/14	PL18	Pink	1	144	50	exposed	bedrock	flat	low
7/15/14	PL18	Pink	1	152	50	exposed	bedrock	flat	low
7/15/14	PL18	Pink	1	140	50	crevice	bedrock	flat	low
7/15/14	PL18	Pink	1	149	54	exposed	boulder	flat	low
7/15/14	PL18	Pink	1	140	54	exposed	bedrock	flat	low
7/15/14	PL18	Pink	1	162	56	exposed	bedrock	flat	medium
7/15/14	PL18	Red	1	150	53	crevice	bedrock	low	low
7/15/14	PL18	Red	1	149	50	crevice	bedrock	flat	low
7/15/14	PL18	Red	1	191	56	crevice	bedrock	flat	medium
7/16/14	PL19	Pink	1	149	50	underrock	boulder	flat	low
7/16/14	PL19	Pink	1	174	47	crevice	boulder	flat	low
7/16/14	PL19	Pink	1	152	50	crevice	boulder	low	low
7/16/14	PL19	Red	1	160	50	underrock	bedrock	flat	low
7/16/14	PL19	Red	1	210	50	underrock	boulder	flat	low
7/16/14	PL19	Red	1	250	50	underrock	boulder	flat	low
7/23/14	PL20	Pink	1	156	60	exposed	boulder	flat	low
7/23/14	PL20	Pink	1	79	58	exposed	boulder	flat	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
7/23/14	PL20	Pink	1	90	59	crevice	boulder	flat	low
7/23/14	PL20	Pink	1	142	57	underrock	boulder	flat	low
7/23/14	PL20	Pink	1	127	57	crevice	boulder	flat	low
7/29/14	LJ03	Pink	1	155	57	exposed	boulder	flat	low
7/29/14	LJ03	Pink	1	160	57	crevice	boulder	low	low
7/29/14	LJ03	Pink	1	159	58	crevice	boulder	flat	low
7/29/14	LJ03	Pink	1	155	58	crevice	boulder	flat	low
7/29/14	LJ03	Red	1	203	59	crevice	boulder	low	low
8/6/14	PL21	Pink	1	147	45	crevice	boulder	flat	low
8/6/14	PL21	Pink	1	130	49	underrock	boulder	flat	low
8/6/14	PL21	Pink	1	160	49	exposed	boulder	flat	low
8/6/14	PL21	Pink	1	165	49	exposed	boulder	flat	low
8/6/14	PL21	Pink	1	127	49	exposed	boulder	flat	low
8/12/14	PL22	Pink	1	112	58	exposed	boulder	flat	low
8/12/14	PL22	Red	1	160	58	exposed	boulder	low	low
8/12/14	PL22	Red	1	177	58	exposed	boulder	low	low
8/13/14	PL23	NA	0	NA	NA	NA	NA	NA	NA
8/18/14	PL24	Pink	1	170	48	underrock	boulder	flat	low
8/18/14	PL24	Pink	1	170	48	underrock	boulder	flat	low
8/18/14	PL24	Pink	1	174	48	underrock	boulder	flat	low
8/18/14	PL24	Pink	1	119	46	underrock	boulder	flat	low
8/19/14	LJ04	Pink	1	130	64	crevice	boulder	flat	low
8/19/14	LJ04	Pink	1	119	62	crevice	boulder	NA	low
8/19/14	LJ04	Pink	1	125	62	crevice	boulder	NA	low
8/19/14	LJ04	Red	1	97	65	crevice	boulder	NA	low
8/19/14	LJ04	Red	1	139	65	crevice	boulder	NA	low
8/19/14	LJ04	Red	1	157	65	crevice	boulder	NA	low
8/19/14	LJ04	Red	1	154	65	exposed	boulder	NA	low
8/19/14	LJ04	Red	1	187	63	crevice	boulder	NA	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
8/19/14	LJ04	Red	1	54	63	crevice	boulder	NA	low
8/19/14	LJ04	Red	1	205	65	crevice	boulder	NA	low
8/19/14	LJ04	Red	1	165	63	crevice	boulder	NA	low
8/19/14	LJ04	Red	1	175	64	exposed	boulder	flat	low
8/19/14	LJ04	Red	1	185	62	crevice	boulder	NA	low
8/19/14	LJ04	Pinto	1	145	64	exposed	boulder	low	low
8/19/14	LJ05	Pink	1	86	62	exposed	boulder	low	low
8/19/14	LJ05	Red	1	165	62	underrock	boulder	flat	low
8/19/14	LJ05	Red	1	160	62	underrock	boulder	flat	low
8/19/14	LJ05	Red	1	127	62	crevice	bedrock	flat	low
8/19/14	LJ05	Red	1	151	62	underrock	boulder	flat	low
8/19/14	LJ05	Red	1	161	62	underrock	boulder	flat	low
8/19/14	LJ05	Red	1	171	62	underrock	boulder	flat	low
8/19/14	LJ05	Red	1	181	62	underrock	boulder	flat	low
10/25/14	PL25	Pinto	1	79	57	exposed	boulder	low	low
10/25/14	PL25	Pinto	1	99	57	exposed	boulder	low	low
10/25/14	PL25	Pinto	1	103	57	exposed	boulder	low	low
10/25/14	PL25	Pinto	1	103	57	exposed	boulder	low	low
10/25/14	PL26	Pink	1	58	51	underrock	boulder	flat	low
10/25/14	PL26	Pinto	1	106	49	exposed	boulder	low	low
10/25/14	PL26	Pinto	1	NA	49	exposed	boulder	low	low
10/25/14	PL26	Pinto	1	73	51	exposed	boulder	low	low
10/25/14	PL26	Pinto	1	76	51	exposed	boulder	low	low
10/25/14	PL26	Pinto	1	76	51	exposed	boulder	flat	low
10/25/14	PL26	Pinto	1	103	51	exposed	boulder	low	low
10/25/14	PL26	Pinto	1	124	51	exposed	boulder	flat	low
3/28/15	LJ06	Pink	1	143	51	exposed	boulder	flat	low
3/28/15	LJ06	Pink	1	183	49	crevice	boulder	flat	low
4/12/15	LJ07	Pink	1	188	49	crevice	boulder	low	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
4/12/15	LJ07	Pink	1	190	49	crevice	boulder	flat	low
4/12/15	LJ07	Pink	1	205	54	NA	NA	NA	NA
4/20/15	LJ08	Green	1	206	54	exposed	boulder	flat	low
4/20/15	LJ08	Pink	1	159	51	crevice	boulder	flat	low
4/20/15	LJ08	Pink	1	96	55	exposed	boulder	low	low
4/20/15	LJ08	Pink	1	147	55	underrock	boulder	low	low
4/20/15	LJ08	Pink	1	151	55	exposed	boulder	low	low
4/20/15	LJ08	Pink	1	191	53	crevice	boulder	low	low
4/20/15	LJ08	Pink	1	200	51	crevice	boulder	flat	low
4/20/15	LJ08	Pink	1	218	51	crevice	boulder	flat	low
4/20/15	LJ09	Pink	1	165	53	exposed	boulder	low	low
4/20/15	LJ09	Pink	1	159	53	exposed	boulder	flat	low
4/21/15	LJ10	Pink	1	180	61	crevice	boulder	flat	low
4/21/15	LJ11	Pink	1	178	64	exposed	boulder	flat	low
4/21/15	LJ11	Pink	1	120	67	underrock	boulder	flat	low
4/21/15	LJ11	Pink	1	140	65	underrock	boulder	flat	low
4/21/15	LJ11	Pink	1	160	64	underrock	boulder	flat	low
4/23/15	PL27	Red	1	94	57	underrock	boulder	flat	low
4/23/15	PL27	Red	1	145	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	140	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	215	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	150	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	186	57	exposed	bedrock	flat	flat
4/23/15	PL27	Red	1	207	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	boulder	flat	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
4/23/15	PL27	Red	1	NA	57	exposed	boulder	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	boulder	low	low
4/23/15	PL27	Red	1	NA	57	exposed	boulder	low	low
4/23/15	PL27	Red	1	NA	57	exposed	bedrock	flat	low
4/23/15	PL27	Red	1	NA	57	exposed	bedrock	flat	flat
4/23/15	PL27	Pinto	1	123	57	exposed	boulder	low	low
4/23/15	PL27	Pinto	1	125	57	exposed	boulder	low	low
4/23/15	PL27	Pinto	1	114	58	exposed	boulder	low	low
4/23/15	PL27	Pinto	1	125	58	exposed	bedrock	flat	flat
4/23/15	PL27	Pinto	1	125	58	exposed	bedrock	flat	flat
4/23/15	PL27	Pinto	1	122	60	exposed	boulder	low	low
4/23/15	PL27	White	1	173	59	exposed	bedrock	flat	flat
9/26/15	PL28	Pinto	1	106	60	exposed	bedrock	flat	flat
9/26/15	PL28	Pinto	1	116	60	exposed	bedrock	flat	flat
9/26/15	PL28	Pinto	1	119	60	exposed	cobble	flat	low
9/26/15	PL28	Pinto	1	131	60	exposed	boulder	low	low
9/26/15	PL28	Pinto	1	87	62	underrock	boulder	flat	flat
9/26/15	PL28	Pinto	1	89	62	underrock	boulder	flat	flat
9/26/15	PL28	Pinto	1	90	62	underrock	boulder	flat	flat
9/26/15	PL28	Pinto	1	92	62	underrock	boulder	flat	flat
9/26/15	PL28	Pinto	1	119	62	underrock	boulder	flat	flat
10/23/15	PL29	Pinto	1	130	66	exposed	bedrock	flat	flat
10/23/15	PL29	Pinto	1	126	69	exposed	bedrock	flat	flat
10/23/15	PL29	Pinto	1	105	70	exposed	bedrock	flat	flat
10/24/15	PL30	Pinto	1	121	79	exposed	boulder	low	low
10/24/15	PL31	Red	1	204	61	crevice	boulder	flat	low
10/24/15	PL31	Red	1	139	61	crevice	boulder	flat	low
10/24/15	PL31	Red	1	145	61	underrock	boulder	low	low
10/24/15	PL31	Red	1	135	61	underrock	boulder	low	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
10/24/15	PL31	Red	1	220	62	crevice	boulder	low	medium
10/24/15	PL31	Red	1	190	62	crevice	boulder	flat	low
10/24/15	PL31	Pinto	1	133	60	exposed	boulder	low	low
10/24/15	PL31	Pinto	1	133	61	exposed	boulder	low	low
10/24/15	PL31	Pinto	1	138	61	exposed	boulder	low	low
10/24/15	PL31	Pinto	1	140	61	exposed	cobble	flat	low
10/24/15	PL31	Pinto	1	105	63	crevice	bedrock	flat	low
10/24/15	PL31	Pinto	1	121	63	exposed	bedrock	flat	low
10/24/15	PL31	Pinto	1	133	63	exposed	bedrock	flat	low
10/24/15	PL31	Pinto	1	133	63	exposed	boulder	low	low
10/24/15	PL31	Pinto	1	142	63	exposed	boulder	low	low
11/8/15	LJ12	Pinto	1	130	75	exposed	bedrock	low	low
11/8/15	LJ12	Pinto	1	120	81	exposed	boulder	flat	flat
11/8/15	LJ13	Pink	1	141	70	underrock	boulder	flat	low
11/8/15	LJ13	Red	1	105	70	underrock	boulder	flat	low
11/8/15	LJ13	Red	1	143	69	underrock	boulder	flat	low
11/14/15	LJ14	Red	1	213	64	underrock	boulder	low	low
11/14/15	LJ14	Red	1	198	65	underrock	boulder	low	low
11/14/15	LJ14	Red	1	164	65	underrock	boulder	low	low
11/14/15	LJ14	Red	1	195	65	underrock	boulder	low	low
11/14/15	LJ14	Red	1	205	65	underrock	boulder	low	low
11/14/15	LJ14	Red	1	213	65	underrock	boulder	low	low
11/14/15	LJ15	Red	1	183	75	underrock	boulder	flat	low
11/14/15	LJ15	Red	1	200	75	underrock	boulder	flat	low
11/20/15	LJ16	Pink	1	151	61	underrock	bedrock	flat	low
11/20/15	LJ16	Pink	1	156	61	exposed	boulder	flat	low
11/20/15	LJ16	Pink	1	172	61	underrock	boulder	flat	low
11/20/15	LJ16	Pink	1	166	61	exposed	boulder	low	low
11/20/15	LJ16	Pink	1	172	64	underrock	boulder	flat	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
11/20/15	LJ16	White	1	191	63	exposed	boulder	low	low
11/20/15	LJ16	White	1	190	65	exposed	boulder	flat	low
11/21/15	LJ17	NA	0	NA	NA	NA	NA	NA	NA
11/21/15	LJ18	Pink	1	187	66	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	159	72	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	115	71	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	165	71	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	180	71	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	179	71	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	143	73	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	157	73	exposed	boulder	flat	low
11/23/15	LJ19	Pink	1	162	73	exposed	boulder	low	low
11/23/15	LJ19	Pink	1	134	70	underrock	boulder	flat	low
11/23/15	LJ19	Red	1	135	73	underrock	boulder	flat	low
11/23/15	LJ19	Red	1	140	73	underrock	boulder	flat	low
11/23/15	LJ19	Red	1	160	73	exposed	boulder	flat	low
11/23/15	LJ19	Red	1	146	71	underrock	boulder	flat	low
11/23/15	LJ19	Red	1	146	71	underrock	boulder	flat	low
11/23/15	LJ19	Red	1	200	71	exposed	boulder	flat	low
11/23/15	LJ19	Red	1	39	70	underrock	boulder	flat	low
11/23/15	LJ19	Pinto	1	131	71	exposed	boulder	flat	low
2/9/16	PL32	Pinto	1	95	70	crevice	boulder	low	low
2/9/16	PL32	Pinto	1	118	70	exposed	bedrock	flat	low
2/9/16	PL32	Pinto	1	118	70	exposed	bedrock	flat	low
2/9/16	PL32	Pinto	1	124	70	exposed	bedrock	flat	low
2/9/16	PL32	Pinto	1	128	70	exposed	bedrock	flat	low
2/9/16	PL32	Pinto	1	131	70	exposed	bedrock	flat	flat
2/9/16	PL32	Pinto	1	132	70	exposed	boulder	low	low
2/9/16	PL32	Pinto	1	134	70	exposed	bedrock	flat	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
2/9/16	PL32	Pinto	1	134	70	exposed	bedrock	flat	low
2/9/16	PL32	Pinto	1	146	70	exposed	bedrock	flat	low
3/18/16	PL33	Pinto	1	93	86	exposed	bedrock	flat	flat
3/18/16	PL33	Pinto	1	117	86	exposed	bedrock	flat	flat
3/18/16	PL33	Pinto	1	118	86	crevice	boulder	flat	low
3/18/16	PL33	Pinto	1	123	86	crevice	boulder	flat	low
3/18/16	PL33	Pinto	1	130	86	exposed	bedrock	flat	flat
3/18/16	PL33	Pinto	1	135	86	exposed	boulder	flat	low
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	NA	86	exposed	bedrock	flat	NA
3/18/16	PL33	Pinto	1	110	88	exposed	bedrock	flat	flat
3/18/16	PL34	NA	0	NA	NA	NA	NA	NA	NA
4/19/16	PL35	NA	0	NA	NA	NA	NA	NA	NA
5/3/16	LJ20	Red	1	182	76	crevice	boulder	flat	low
5/3/16	LJ20	Red	1	158	75	crevice	boulder	flat	low
5/3/16	LJ20	Red	1	167	75	crevice	boulder	flat	low
5/3/16	LJ20	Red	1	220	75	crevice	boulder	flat	medium
5/3/16	LJ20	Red	1	220	75	crevice	boulder	flat	medium
5/3/16	LJ20	Red	1	206	74	crevice	boulder	low	low
5/3/16	LJ20	Red	1	186	73	underrock	boulder	flat	low
5/3/16	LJ20	Red	1	165	73	crevice	boulder	flat	low
5/3/16	LJ20	Red	1	120	70	exposed	boulder	medium	medium
5/3/16	LJ20	Red	1	185	71	crevice	boulder	flat	low

Survey Date	Site ID	Species	Count	Shell Length (mm)	Abalone Depth	Abalone Exposure	Abalone Substrate	Abalone Relief	Relief 1m ²
9/20/16	PL36	NA	0	NA	NA	NA	NA	NA	NA
12/1/16	PL38	Pink	1	46	59	underrock	boulder	low	low

APPENDIX C

SITE (AVAILABLE) HABITAT METADATA

Table C. Species' Relative Abundances and Estimated Percent Cover for Macroalgae, Invertebrates, and Substratum Type and Relief and Subjective Habitat Scores for Each Site Surveyed in La Jolla (LJ) and Point Loma (PL) in San Diego, California from June 2014 to December 2016.

Species / Variable Description	Site ID										
	LJ01	LJ03	LJ04	LJ05	LJ06	LJ07	LJ08	LJ09	LJ10	LJ11	LJ12
Relative Abundance											
<i>Macrocystis pyrifera</i>	2	3	3	3	3	NA	NA	NA	NA	NA	3
<i>Pelagophycus porra</i>	0	0	0	2	0	NA	NA	NA	NA	NA	3
<i>Eisenia arborea</i>	0	0	2	1	NA	NA	NA	NA	NA	NA	2
<i>Pterygophora californica</i>	4	2	2	2	NA	NA	NA	NA	NA	NA	2
<i>Laminaria farlowii</i>	3	2	3	3	NA	NA	NA	NA	NA	NA	2
<i>Agarum fimbriatum</i>	0	1	1	2	NA	NA	NA	NA	NA	NA	2
<i>Cystoseira osmundacea</i>	1	0	3	3	NA	NA	NA	NA	NA	NA	2
<i>Desmarestia ligulatum</i>	0	0	1	2	NA	NA	NA	NA	NA	NA	1
Other brown algae	2	2	2	3	NA	NA	NA	NA	NA	NA	1
<i>Gigartina spp.</i>	0	1	2	3	NA	NA	NA	NA	NA	NA	3
Other red algae	3	2	3	3	2	NA	NA	NA	NA	NA	2
Encrusting coralline	3	3	3	3	NA	NA	NA	NA	NA	NA	3
Articulated coralline	3	3	3	3	NA	NA	NA	NA	NA	NA	2
All mobile invertebrates	1	1	1	1	NA	NA	NA	NA	NA	NA	1
Percent (%) Cover											
All encrusting invertebrates	20	10	20	20	NA	NA	NA	NA	NA	NA	15
Flat (0 - 10cm)	60	60	60	80	90	NA	NA	NA	NA	NA	60
Low (10cm - 1m)	38	40	40	20	10	NA	NA	NA	NA	NA	40

Species / Variable Description	Site ID										
	LJ01	LJ03	LJ04	LJ05	LJ06	LJ07	LJ08	LJ09	LJ10	LJ11	LJ12
Medium (1 - 2m)	1	0	0	0	0	NA	NA	NA	NA	NA	0
High (> 2 m)	1	0	0	0	0	NA	NA	NA	NA	NA	0
Bedrock	75	10	40	50	65	NA	NA	NA	NA	NA	45
Boulder	25	30	30	20	25	NA	NA	NA	NA	NA	30
Cobble	0	10	20	5	10	NA	NA	NA	NA	NA	5
Mix soft/hard	0	50	10	25	0	NA	NA	NA	NA	NA	10
Sand	0	0	0	0	0	NA	NA	NA	NA	NA	10
Rough	90	20	0	10	60	NA	NA	NA	NA	NA	0
Smooth	10	80	100	90	40	NA	NA	NA	NA	NA	100
Canopy	25	40	25	30	NA	NA	NA	NA	NA	NA	50
Understory algae	75	10	50	70	NA	NA	NA	NA	NA	NA	20
Turf algae	50	20	50	75	NA	NA	NA	NA	NA	NA	20
Encrusting algae	50	50	75	75	NA	NA	NA	NA	NA	NA	50
Drift algae	10	5	20	20	NA	NA	NA	NA	NA	NA	5
White abalone SHC	Poor	Fair	Excellent	Excellent	NA	NA	NA	NA	NA	NA	Fair
Pinto abalone SHC	Poor	Fair	Excellent	Excellent	NA	NA	NA	NA	NA	NA	Fair
Red abalone SHC	Fair	Fair	Excellent	Excellent	NA	NA	NA	NA	NA	NA	Fair
Pink abalone SHC	Fair	Fair	Excellent	Excellent	NA	NA	NA	NA	NA	NA	Fair

Species / Variable Description	Site ID										
	LJ13	LJ14	LJ15	LJ16	LJ17	LJ18	LJ19	LJ20	PL01	PL02	PL03
Relative Abundance											
<i>Macrocystis pyrifera</i>	3	3	2	4	2	4	2	3	4	3	2
<i>Pelagophycus porra</i>	1	0	1	0	2	0	1	1	1	1	4
<i>Eisenia arborea</i>	0	2	0	0	0	0	0	0	0	0	0
<i>Pterygophora californica</i>	2	4	3	0	3	1	4	1	0	2	1
<i>Laminaria farlowii</i>	1	3	3	1	3	1	3	1	1	1	2
<i>Agarum fimbriatum</i>	2	3	2	1	3	1	3	1	0	0	2
<i>Cystoseira osmundacea</i>	1	3	1	0	2	1	2	1	0	0	1
<i>Desmarestia ligulatum</i>	1	1	1	0	1	1	1	1	1	3	NA
Other brown algae	1	2	2	1	2	1	2	1	2	2	1
<i>Gigartina spp.</i>	2	1	2	0	3	2	3	1	2	1	1
Other red algae	2	3	3	1	3	2	3	1	1	2	1
Encrusting coralline	2	2	3	4	2	4	3	3	3	2	2
Articulated coralline	2	4	3	2	3	3	3	1	1	1	1
All mobile invertebrates	1	2	1	1	1	2	2	2	2	2	2
Percent (%) Cover											
All encrusting invertebrates	15	30	10	10	10	20	20	25	20	25	30
Flat (0 - 10cm)	80	55	90	60	80	80	90	60	90	80	40
Low (10cm - 1m)	20	40	10	40	20	20	10	20	10	20	50
Medium (1 - 2m)	0	5	0	0	0	0	0	20	0	0	10
High (> 2 m)	0	0	0	0	0	0	0	0	0	0	0
Bedrock	40	50	40	40	20	65	50	50	90	75	25
Boulder	20	30	10	40	5	20	10	20	10	20	50
Cobble	5	5	40	10	5	10	40	20	0	5	25
Mix soft/hard	10	10	10	10	10	5	0	5	0	0	0
Sand	25	5	0	0	60	0	0	5	0	0	0
Rough	20	30	10	0	70	60	0	30	90	90	80
Smooth	80	70	90	100	30	40	100	70	10	10	20

Species / Variable Description	Site ID										
	LJ13	LJ14	LJ15	LJ16	LJ17	LJ18	LJ19	LJ20	PL01	PL02	PL03
Canopy	60	50	20	70	10	75	20	50	90	75	60
Understory algae	10	75	50	0	40	0	80	0	10	1	20
Turf algae	25	60	50	10	40	25	60	20	10	5	5
Encrusting algae	50	50	75	75	30	75	75	60	60	40	60
Drift algae	5	5	5	5	10	0	5	5	25	10	10
White abalone SHC	Fair	Excellent	Fair	Fair	Poor	Fair	Fair	Fair	Poor	Poor	Fair
Pinto abalone SHC	Fair	Excellent	Fair	Fair	Poor	Fair	Fair	Fair	Poor	Poor	Fair
Red abalone SHC	Fair	Excellent	Fair	Fair	Poor	Fair	Fair	Fair	Poor	Poor	Fair
Pink abalone SHC	Fair	Excellent	Fair	Fair	Poor	Fair	Fair	Fair	Poor	Poor	Fair

Species / Variable Description	Site ID										
	PL04	PL06	PL07	PL08	PL09	PL10	PL11	PL12	PL13	PL14	PL15
Relative Abundance											
<i>Macrocystis pyrifera</i>	3	2	NA	4	3	1	2	3	3	2	3
<i>Pelagophycus porra</i>	1	0	NA	0	3	3	0	3	1	2	0
<i>Eisenia arborea</i>	0	0	NA	0	0	0	4	0	0	0	0
<i>Pterygophora californica</i>	0	3	NA	1	2	1	2	2	1	1	1
<i>Laminaria farlowii</i>	1	3	NA	3	4	2	3	3	2	3	2
<i>Agarum fimbriatum</i>	1	2	NA	1	4	1	0	3	0	3	1
<i>Cystoseira osmundacea</i>	1	3	NA	0	2	4	0	1	0	2	2
<i>Desmarestia ligulatum</i>	3	0	NA	0	NA	0	0	0	1	0	0
Other brown algae	1	2	NA	1	3	1	3	2	2	2	2
<i>Gigartina spp.</i>	3	0	NA	2	NA	0	2	2	2	1	2
Other red algae	2	3	NA	2	4	2	3	3	2	2	2
Encrusting coralline	3	3	NA	4	4	2	3	3	3	3	3
Articulated coralline	1	3	NA	3	4	2	4	3	1	2	2
All mobile invertebrates	3	1	NA	3	3	2	2	2	1	2	1
Percent (%) Cover											
All encrusting invertebrates	25	20	NA	40	75	30	30	75	40	60	50
Flat (0 - 10cm)	90	100	NA	80	5	60	95	70	95	45	60
Low (10cm - 1m)	10	0	NA	20	20	20	1	25	5	20	40
Medium (1 - 2m)	0	0	NA	0	50	15	0	5	0	10	0
High (> 2 m)	0	0	NA	0	25	5	4	0	0	25	0
Bedrock	65	85	NA	70	50	50	99	60	80	60	40
Boulder	25	0	NA	20	40	10	1	30	5	10	30
Cobble	10	10	NA	5	10	10	0	10	10	10	10
Mix soft/hard	0	0	NA	0	0	30	0	0	0	20	20
Sand	0	0	NA	10	5	0	0	0	5	0	0
Rough	60	50	NA	80	90	80	100	60	90	80	10
Smooth	40	50	NA	20	10	20	0	40	10	20	90

Species / Variable Description	Site ID										
	PL04	PL06	PL07	PL08	PL09	PL10	PL11	PL12	PL13	PL14	PL15
Canopy	75	50	NA	50	50	50	10	60	90	40	75
Understory algae	5	50	NA	25	90	50	75	40	10	60	10
Turf algae	25	60	NA	10	75	20	75	30	25	50	20
Encrusting algae	75	80	NA	75	75	50	60	60	50	60	75
Drift algae	25	30	NA	10	NA	25	0	20	10	20	10
White abalone SHC	Fair	Fair	NA	Fair	Fair	Fair	Poor	Fair	Poor	Fair	Fair
Pinto abalone SHC	Fair	Fair	NA	Fair	Fair	Fair	Poor	Fair	Poor	Fair	Fair
Red abalone SHC	Fair	Fair	NA	Fair	Fair	Fair	Poor	Fair	Poor	Fair	Fair
Pink abalone SHC	Fair	Fair	NA	Fair	Fair	Poor	Poor	Fair	Poor	Poor	Fair

Species / Variable Description	Site ID										
	PL16	PL17	PL18	PL19	PL20	PL21	PL22	PL23	PL24	PL25	PL26
Relative Abundance											
<i>Macrocystis pyrifera</i>	NA	3	3	4	3	3	3	4	3	3	3
<i>Pelagophycus porra</i>	NA	3	0	1	2	1	0	3	0	2	1
<i>Eisenia arborea</i>	NA	0	0	0	0	0	0	0	0	0	0
<i>Pterygophora californica</i>	NA	3	3	3	4	3	1	2	1	0	1
<i>Laminaria farlowii</i>	NA	4	3	3	4	3	1	3	1	2	1
<i>Agarum fimbriatum</i>	NA	3	2	2	1	1	0	1	1	2	1
<i>Cystoseira osmundacea</i>	NA	4	3	3	1	2	1	2	1	0	0
<i>Desmarestia ligulatum</i>	NA	0	0	0	0	0	0	2	0	2	1
	NA	3	2	2	2	2	1	2	1	1	1
Other brown algae											
<i>Gigartina spp.</i>	NA	2	1	3	1	1	1	1	1	2	1
	NA	3	1	3	2	3	2	2	1	2	1
Other red algae											
Encrusting coralline	NA	3	3	4	4	3	3	3	3	3	4
Articulated coralline	NA	2	3	4	3	3	1	1	1	1	1
All mobile invertebrates	NA	2	2	2	1	1	1	1	1	1	1
Percent (%) Cover											
All encrusting invertebrates	NA	60	70	25	10	10	10	25	25	20	20
Flat (0 - 10cm)	NA	40	10	40	90	80	60	100	60	75	75
Low (10cm - 1m)	NA	50	85	60	10	20	30	0	40	25	25
Medium (1 - 2m)	NA	10	5	0	0	0	10	0	0	0	0
High (> 2 m)	NA	0	0	0	0	0	0	0	0	0	0
Bedrock	NA	40	20	50	60	70	50	90	50	60	75
Boulder	NA	30	70	20	10	20	30	0	40	30	20
Cobble	NA	0	5	10	20	10	10	0	10	10	5
Mix soft/hard	NA	30	5	20	10	0	10	10	0	0	0
Sand	NA	0	0	0	0	0	0	0	0	0	0
Rough	NA	50	75	0	0	60	50	80	60	75	75
Smooth	NA	50	25	100	100	40	50	20	40	25	25

Species / Variable Description	Site ID										
	PL16	PL17	PL18	PL19	PL20	PL21	PL22	PL23	PL24	PL25	PL26
Canopy	NA	50	75	90	10	60	60	100	75	100	100
Understory algae	NA	80	25	50	90	50	0	50	0	20	25
Turf algae	NA	75	10	30	50	40	10	20	10	20	25
Encrusting algae	NA	70	70	80	80	60	50	50	50	75	75
Drift algae	NA	25	20	20	20	20	15	25	50	50	40
White abalone SHC	NA	Excellent	Excellent	Excellent	Fair	Fair	Fair	Poor	Fair	Fair	Fair
Pinto abalone SHC	NA	Excellent	Excellent	Excellent	Fair	Fair	Fair	Poor	Fair	Fair	Fair
Red abalone SHC	NA	Excellent	Excellent	Excellent	Fair	Fair	Fair	Poor	Fair	Fair	Fair
Pink abalone SHC	NA	Excellent	Excellent	Excellent	Fair	Fair	Fair	Poor	Fair	Fair	Fair

Species / Variable Description	Site ID										
	PL27	PL28	PL29	PL30	PL31	PL32	PL33	PL34	PL35	PL36	PL38
Relative Abundance											
<i>Macrocystis pyrifera</i>	4	3	1	2	3	1	1	1	1	0	3
<i>Pelagophycus porra</i>	2	3	4	3	1	3	2	4	3	3	0
<i>Eisenia arborea</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Pterygophora californica</i>	3	4	2	1	2	3	1	1	4	4	1
<i>Laminaria farlowii</i>	3	4	3	2	2	3	2	2	3	3	1
<i>Agarum fimbriatum</i>	3	3	3	3	2	3	2	2	3	3	1
<i>Cystoseira osmundacea</i>	2	3	2	1	1	3	2	1	3	2	0
<i>Desmarestia ligulatum</i>	2	1	1	1	1	1	1	1	1	1	1
Other brown algae	2	2	2	2	1	1	1	1	2	1	1
<i>Gigartina spp.</i>	3	3	2	1	1	3	2	2	3	2	1
Other red algae	3	4	3	2	2	3	2	2	4	3	1
Encrusting coralline	4	4	4	3	2	4	3	3	4	3	4
Articulated coralline	3	2	3	2	3	3	2	2	4	3	1
All mobile invertebrates	2	1	1	1	1	3	2	1	3	3	2
Percent (%) Cover											
All encrusting invertebrates	30	30	20	60	30	50	40	25	50	50	20
Flat (0 - 10cm)	60	60	90	30	60	60	80	85	60	50	70
Low (10cm - 1m)	40	40	10	20	35	40	20	10	40	50	30
Medium (1 - 2m)	0	0	0	30	5	0	0	5	0	0	0
High (> 2 m)	0	0	0	20	0	0	0	0	0	0	0
Bedrock	55	40	40	70	60	60	60	60	40	40	40
Boulder	40	20	10	20	30	20	20	10	20	20	30
Cobble	5	20	5	10	10	10	10	20	20	10	20
Mix soft/hard	0	20	30	0	0	10	10	10	10	30	10
Sand	0	0	15	0	0	0	0	0	0	0	0
Rough	10	50	10	70	60	40	40	80	60	40	50

Species / Variable Description	Site ID										
	PL27	PL28	PL29	PL30	PL31	PL32	PL33	PL34	PL35	PL36	PL38
Smooth	90	50	90	30	40	60	60	20	40	60	50
Canopy	100	40	50	30	50	10	10	20	25	40	25
Understory algae	50	90	30	50	25	60	10	10	60	75	0
Turf algae	50	60	30	25	25	80	50	10	80	75	10
Encrusting algae	80	85	75	50	50	80	75	60	80	75	80
Drift algae	20	10	5	10	5	5	5	0	5	5	5
White abalone SHC	Excellent	Excellent	Fair	Fair	Fair	Excellent	Fair	Poor	Excellent	Excellent	Fair
Pinto abalone SHC	Excellent	Excellent	Fair	Fair	Fair	Excellent	Fair	Poor	Excellent	Excellent	Fair
Red abalone SHC	Excellent	Excellent	Fair	Fair	Fair	Excellent	Fair	Poor	Excellent	Excellent	Fair
Pink abalone SHC	Excellent	Excellent	Fair	Fair	Fair	Excellent	Fair	Poor	Excellent	Excellent	Fair

APPENDIX D

RED AND PINK ABALONE HABITAT ASSOCIATIONS

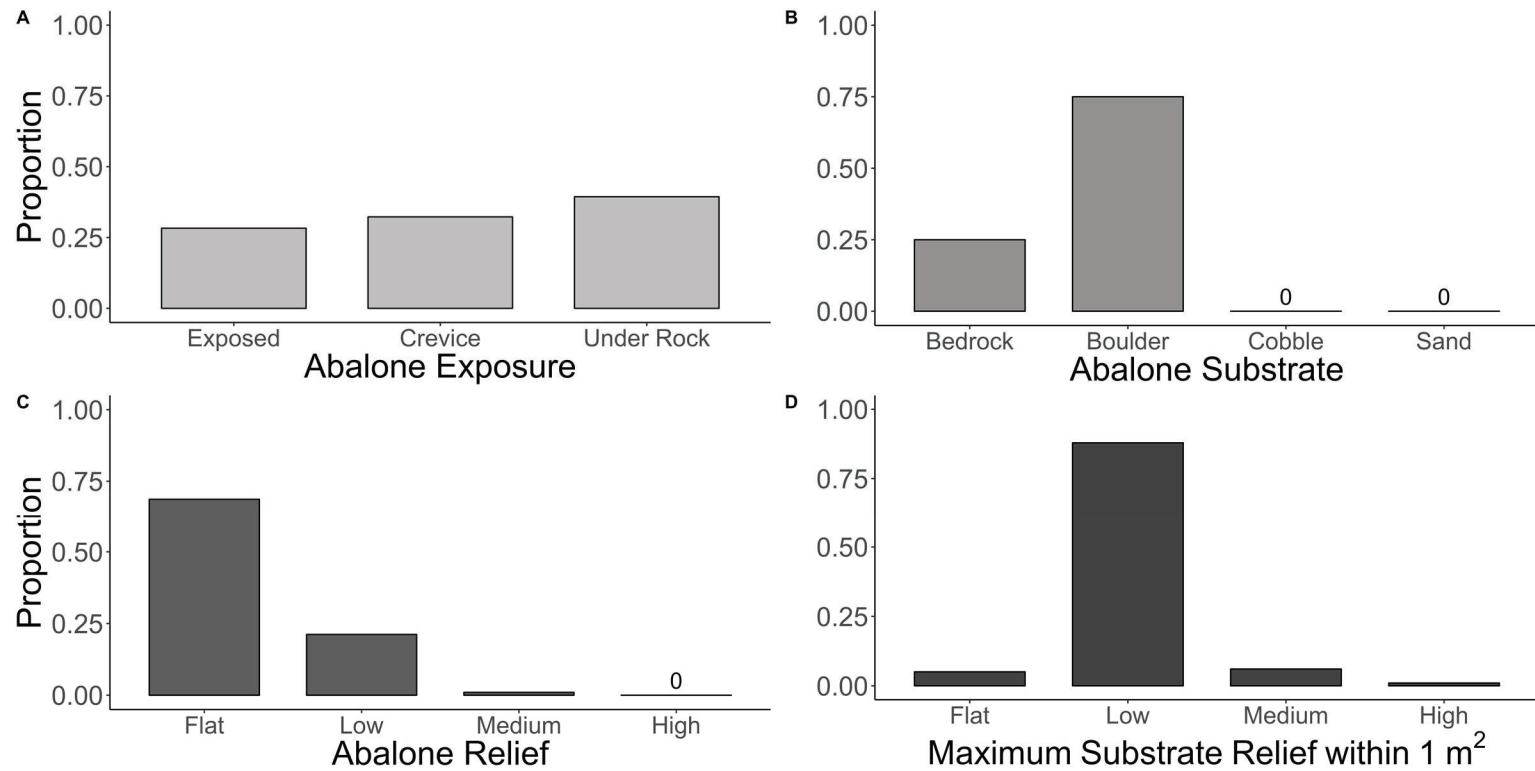


Figure D1. Proportions of red abalone (*Haliotis rufescens*) associated with specific microhabitat features. (A) abalone exposure, or visibility on the seafloor, (B), substrate type an abalone was attached to, (C), relief of the abalone relative to the seafloor, and (D) highest rock relief within 1m² of an abalone. Substrate relief categories include: 1) flat: 0 – 10 cm; 2) low: 10 cm – 1 m; 3) medium: 1 – 2 m; and 4) high: > 2 m.

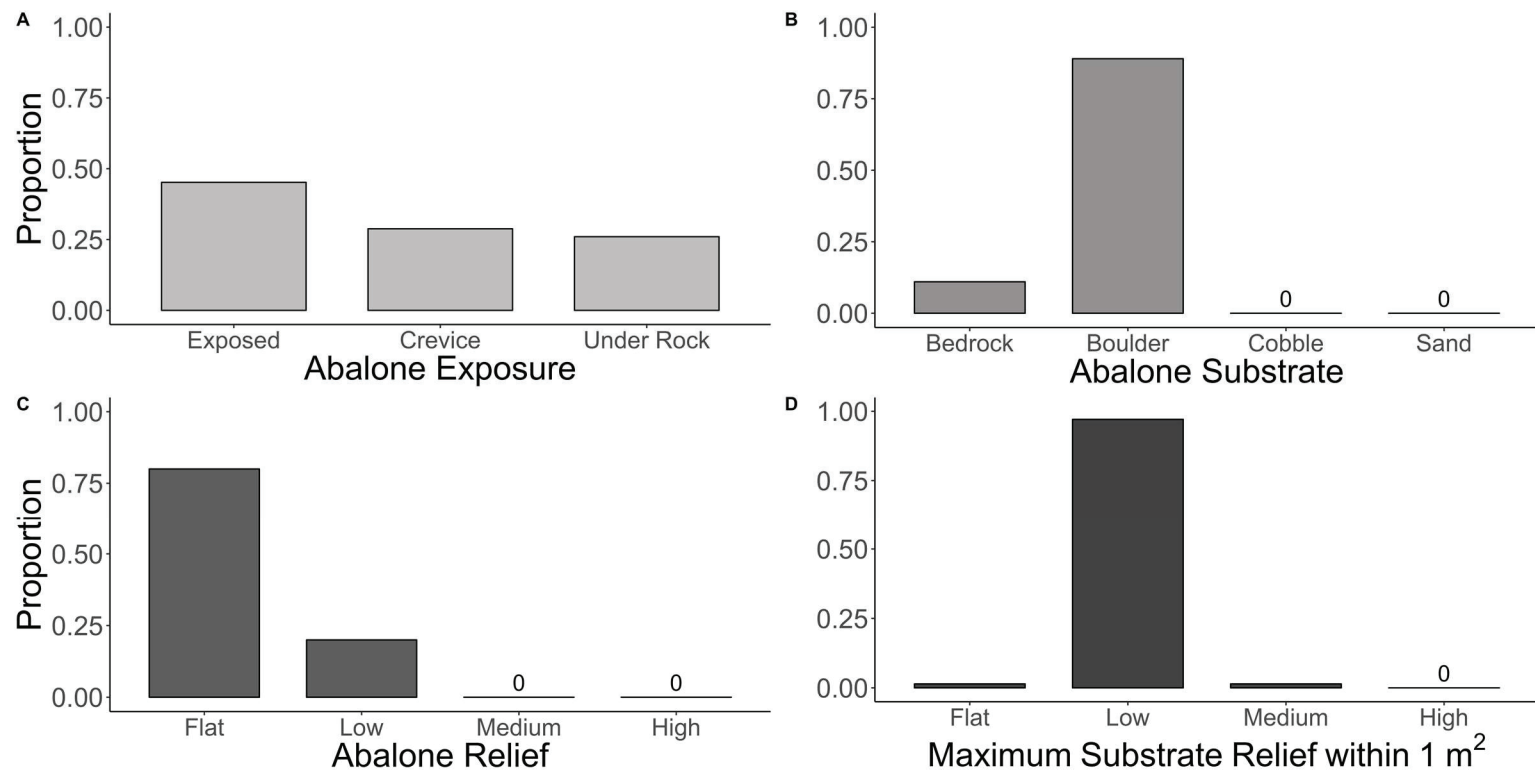


Figure D2. Proportions of pink abalone (*Haliotis corrugata*) associated with specific microhabitat features. (A) abalone exposure, or visibility on the seafloor, (B), substrate type an abalone was attached to, (C), relief of the abalone relative to the seafloor, and (D) highest rock relief within 1m² of an abalone. Substrate relief categories include: 1) flat: 0 – 10 cm; 2) low: 10 cm – 1 m; 3) medium: 1 – 2 m; and 4) high: > 2 m.

APPENDIX E

MANLY HABITAT RESOURCE USE SELECTION RATIOS

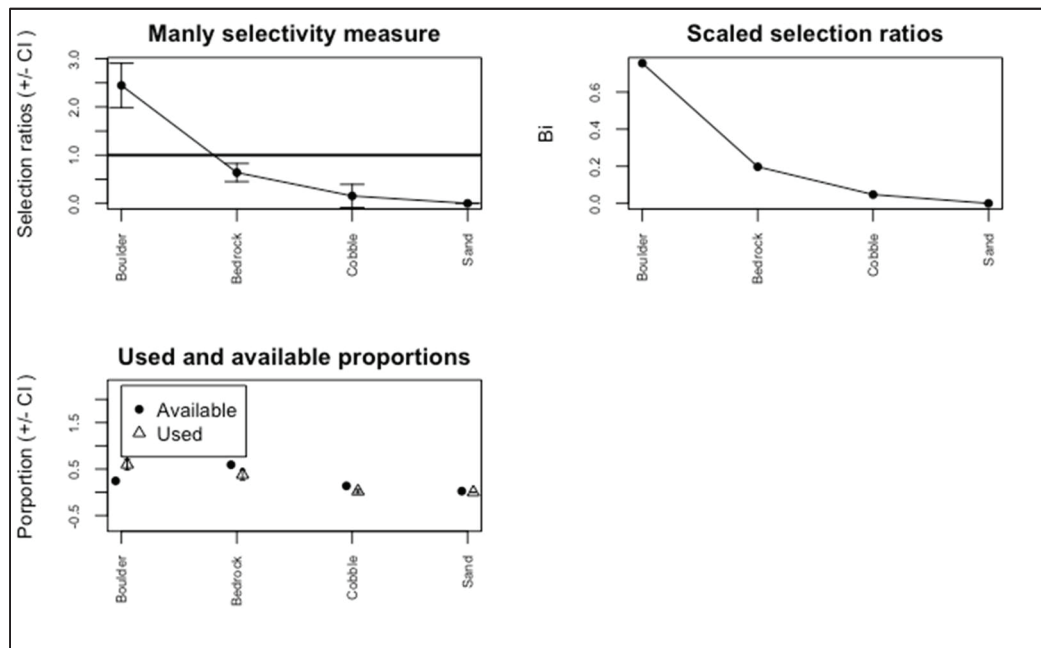


Figure E1. Pinto abalone habitat selection ratios and confidence intervals (top left), standardized selection ratios (top right) and proportions of used and available habitat categories (bottom left) for substratum type categories (boulder, bedrock, cobble and sand) for all pinto abalone observed ($N = 95$) at sites where present ($N = 23$) in San Diego, CA between June 2014 and December 2016. Significant selection for a habitat category is indicated by a confidence interval that is greater than 1 and against if less than 1 (top left).

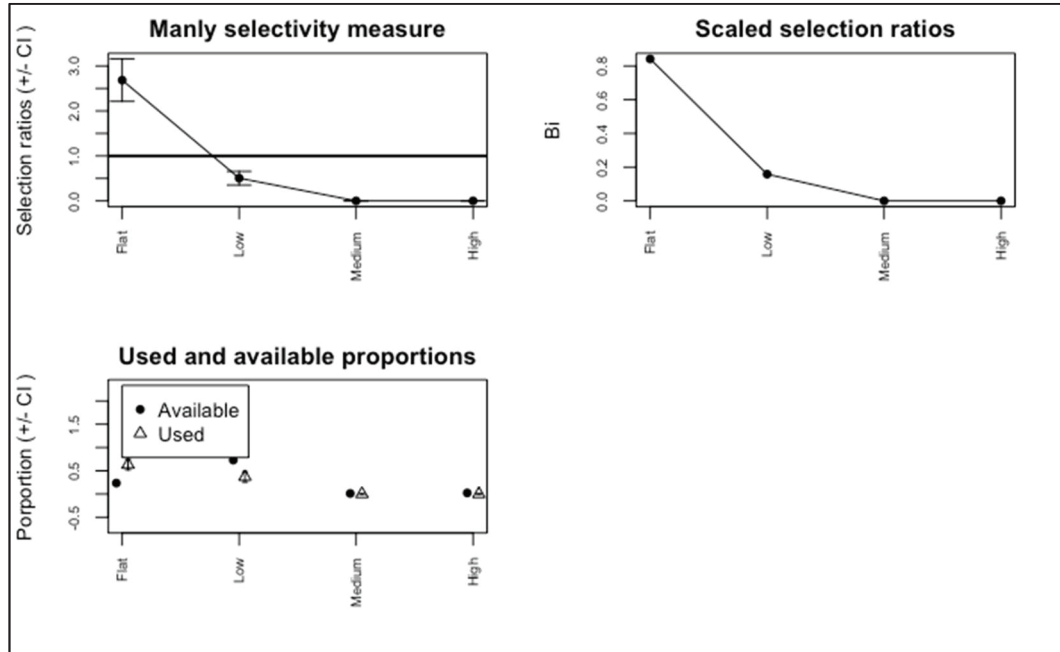


Figure E2. Pinto abalone (*Haliotis kamtschatkana*) habitat selection ratios and confidence intervals (top left), standardized selection ratios (top right) and proportions of used and available habitat categories (bottom left) for substratum relief categories (flat, low, medium, and high) for all pinto abalone observed ($N = 95$) compared to relief available within a 1m^2 area around individuals and at sites where present ($N = 23$) in San Diego, CA between June 2014 and December 2016. Significant selection for a habitat category is indicated by a confidence interval that is greater than 1 and against if less than 1 (top left).

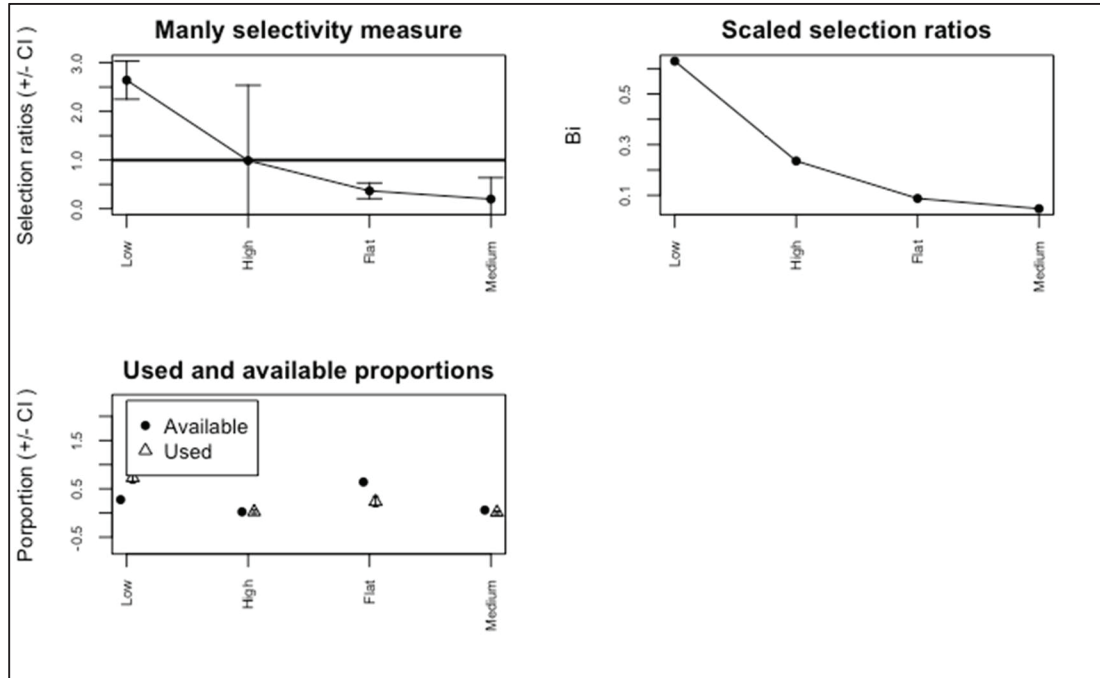


Figure E3. Pinto abalone (*Haliotis kamtschatkana*) habitat selection ratios and confidence intervals (top left), standardized selection ratios (top right) and proportions of used and available habitat categories (bottom left) for substratum relief categories (flat, low, medium, and high) for all pinto abalone observed ($N = 85$) at sites where present ($N = 23$) in San Diego, CA between June 2014 and December 2016. Comparisons made here are relief within a 1m^2 area around individuals to available site relief. Significant selection for a habitat category is indicated by a confidence interval that is greater than 1 and against if less than 1 (top left).

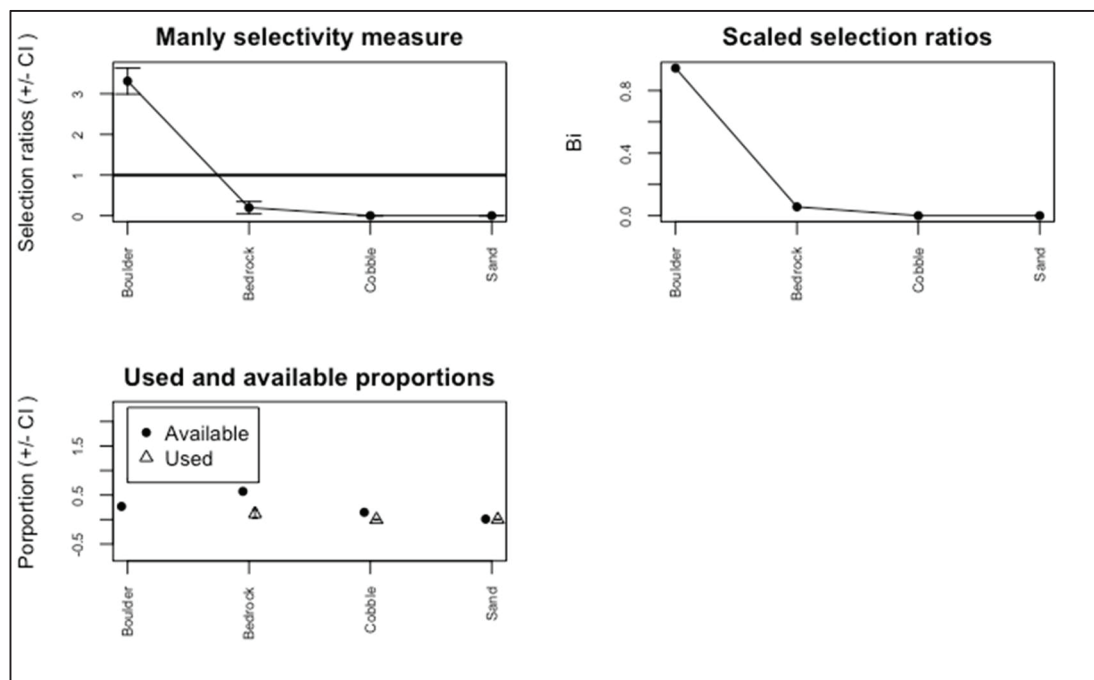


Figure E4. Pink abalone (*Haliotis corrugata*) habitat selection ratios and confidence intervals (top left), standardized selection ratios (top right) and proportions of used and available habitat categories (bottom left) for substratum type categories (boulder, bedrock, cobble and sand) for all pink abalone habitat observations ($N = 70$) and sites where present ($N = 25$). Significant selection for a habitat category is indicated by a confidence interval that is greater than 1 and against if less than 1 (top left). Pink abalone occupied boulder habitat significantly more than expected ($p < 0.0001$) and selected boulders 16.5 times more than bedrock. None were found on cobble or sand.

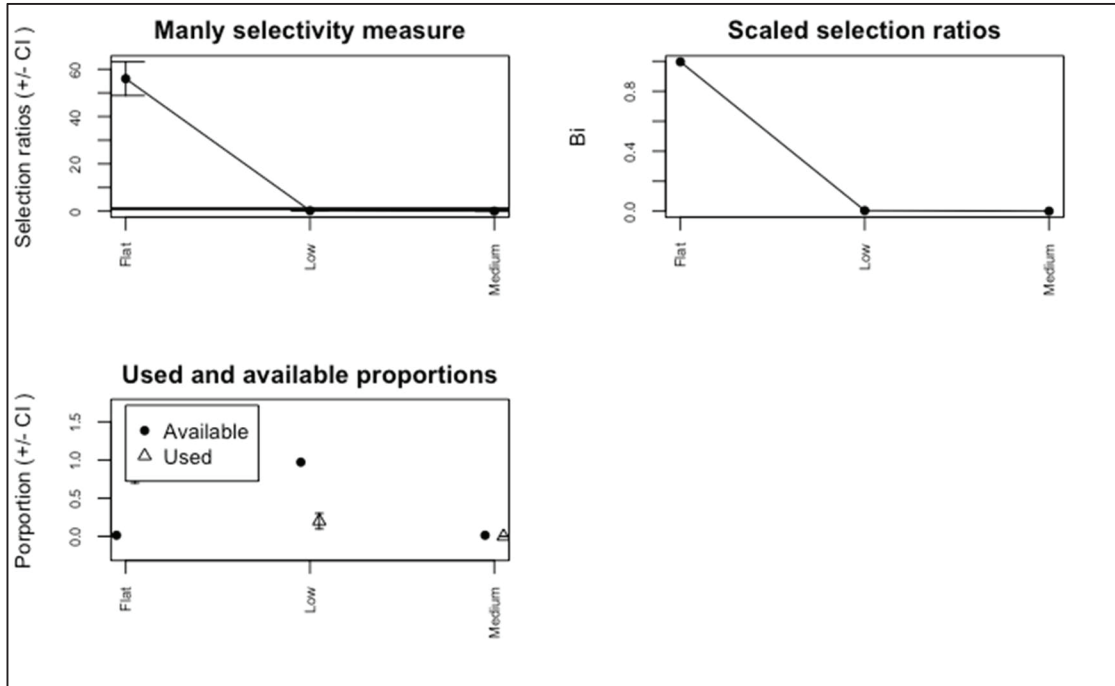


Figure E5. Pink abalone (*Haliotis corrugata*) habitat selection ratios and confidence intervals (top left), standardized selection ratios (top right) and proportions of used and available habitat categories (bottom left) for substratum relief categories (flat, low and medium) for all pink abalone habitat observations ($N = 70$) and sites where present ($N = 25$). Significant selection for a habitat category is indicated by a confidence interval that is greater than 1 and against if less than 1 (top left). Note that the “high” relief category was excluded as no high relief was observed within a 1m^2 area around any pink abalone. Pink abalone were $<10\text{cm}$ above the benthos significantly more than expected ($p < 0.0001$) and may be selected to select a flat position 99.6% of the time. None were found in medium or high relief positions.

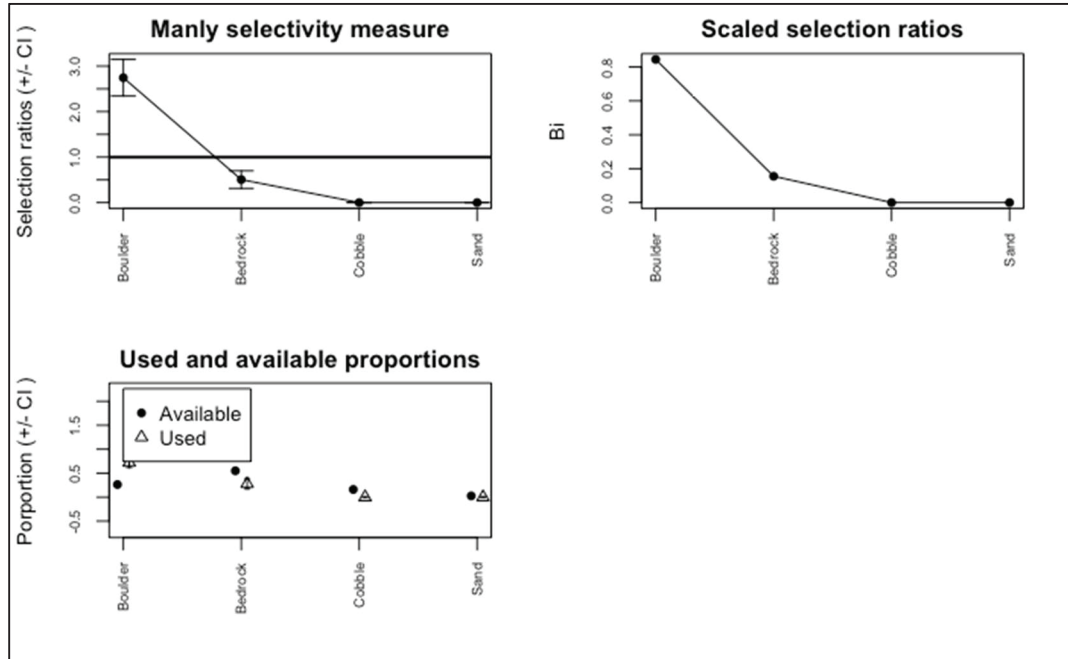


Figure E6. Red abalone (*Haliotis rufescens*) habitat selection ratios and confidence intervals (top left), standardized selection ratios (top right) and proportions of used and available habitat categories (bottom left) for substratum type categories (boulder, bedrock, cobble and sand) for all red abalone habitat observations ($N = 90$) and sites where present ($N = 20$). Significant selection for a habitat category is indicated by a confidence interval that is greater than 1 and against if less than 1 (top left).

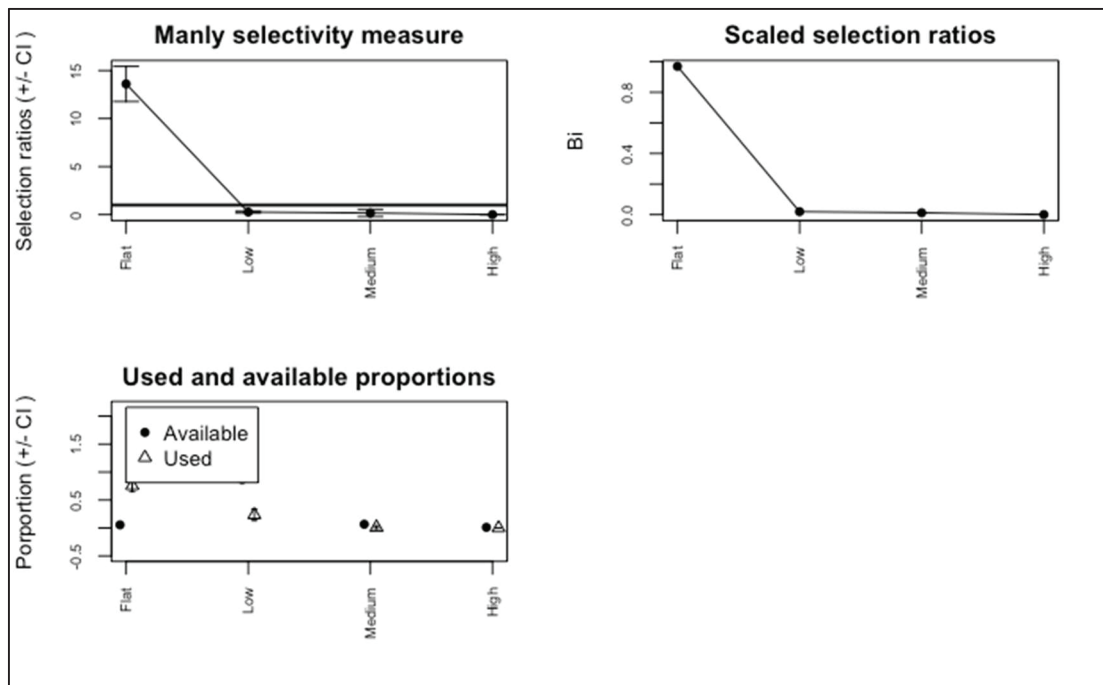


Figure E7. Red abalone (*Haliotis rufescens*) habitat selection ratios and confidence intervals (top left), standardized selection ratios (top right) and proportions of used and available habitat categories (bottom left) for substratum relief categories (flat, low, medium, and high) for all red abalone habitat observations ($N = 90$) and sites where present ($N = 20$). Significant selection for a habitat category is indicated by a confidence interval that is greater than 1 and against if less than 1 (top left).

FEDERAL REGISTER NOTICES

U.S. Federal Register. Volume 66 No. 103. 66 FR 29046, May 29, 2001. Endangered and threatened species; endangered status for white abalone.

U.S. Federal Register. Volume 69 No. 73. 69 FR 19975, April 15, 2004. Endangered and threatened species; establishment of Species of Concern list, addition of species to Species of Concern list.

U.S. Federal Register. Volume 74 No. 9. 74 FR 1937, January 14, 2009. Endangered and Threatened Wildlife and Plants; Endangered Status for Black Abalone

U.S. Federal Register. Volume 70 No. 248. 70 FR 11998, December 29, 2014. Endangered and threatened wildlife and plants; notice of 12-month finding on petitions to list the pinto abalone as threatened or endangered under the Endangered Species Act.

PERSONAL COMMUNICATIONS AND UNPUBLISHED DATA

Hagey, W. Pisces Design. July 2013. Personal communication with Amanda Bird (CSUF) regarding current locations, size distributions, and relative abundance of pinto abalone in San Diego, California from 2010 to 2013.

Hagey, W, Witting, D, and Bird, A, Pisces Design, NOAA Restoration Center, California State University, Fullerton. September 2014. Unpublished data, via personal communication and personal observations of live pinto abalone in San Diego, California from April 2010 to July 2014.

Taniguchi, I. California Department of Fish and Wildlife (CDFW). July 2018. Personal communication with Amanda Bird (CSUF) regarding density and size criteria in the CDFW Abalone Recovery and Management Plan and their applications to pinto abalone demographic assessments in southern California.

Witting, D. NOAA Restoration Center. July 2013. Personal communication with Amanda Bird (CSUF) regarding methods used and results of exploratory surveys of white and pinto abalone in La Jolla and Point Loma in San Diego, California from 2010 to 2013.

LITERATURE CITED

- Allee, W. C. 1931. *Animal Aggregations: A Study in General Sociology*. Chicago, IL: University of Chicago Press. 431 pp.
- Altstatt, J. M., R. F. Ambrose, J. M. Engle, P. L. Haaker, K. D. Lafferty, & P. T. Raimondi. 1996. Recent declines of black abalone *Haliotis cracherodii* on the mainland coast of central California. *Mar. Ecol. Prog. Ser.* 142:185-192.
- Babcock, R. & J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. *Can. J. Fish. Aquat. Sci.* 56:1668-1678.
- Bahn, V., R. J. O'Connor & W. B. Krohn. 2006. Effect of dispersal at range edges on the structure of species ranges. *OIKOS*. 115:89-96.
- Bell, L., T. White, M. Donnellan, K. Hebert & P. Raimondi. 2018. Monitoring pinto abalone populations and recruitment in Sitka Sound, Alaska. In: F.J. Mueter, F. J. M. R. Baker, S. C. Dressel & A. B. Hollowed (eds.), *Impacts of a changing environment on the dynamics of high-latitude fish and fisheries*. Alaska Sea Grant, University of Alaska Fairbanks. Available from: <https://doi.org/10.4027/icedhlff.2018.04>
- Ben-Horin, T., H. S. Lenihan & K. D. Lafferty. 2013. Variable intertidal temperature explains why disease endangers black abalone. *Ecology* 94:161-168.
- Bouma, J. V. 2007. Early life history dynamics of pinto abalone (*Haliotis kamtschatkana*) and implications for recovery. MS Thesis, School of Aquatic and Fisheries Science, University of Washington, Seattle, WA.
- Bouma, J. V., D. P. Rothaus, K. M. Straus, B. Vadopalas & C. S. Friedman. 2012. Low juvenile pinto abalone *Haliotis kamtschatkana kamtschatkana* abundance in the San Juan Archipelago, Washington State. *Trans. Am. Fish. Soc.* 141:76-83.
- Breen, P. A. 1980. Muscled mollusc: the northern abalone. *Diver* 6: 26-28.
- Breen, P. A. & B. E. Adkins. 1980. Spawning in a British Columbia population of northern abalone, *Haliotis kamtschatkana*. *Veliger* 23: 177-179.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *Amer. Nat.* 124: 255-279.

- Brown, J. H., G. C. Stevens & D. W. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.* 27:597-623.
- Button, C. A. 2008. The influence of density-dependent aggregation characteristics on the population biology of benthic broadcast-spawning gastropods: pink abalone (*Haliotis corrugata*), red abalone (*Haliotis rufescens*), and wavy turban snails (*Megastraea undosa*). PhD Dissertation. University of California, San Diego, La Jolla, CA.
- Burge, C. A., C. M. Eakin, C. S. Friedman, B. Froelich, P. K. Hershberger, E. E. Hofmann, L. E. Petes, K. C. Prager, E. Weil, B. L. Willis, S. E. Ford & C. D. Harvell. 2014. Climate change influences on marine infectious diseases: implications for management and society. *Annu. Rev. Mar. Sci.* 6:1.1–1.29.
- Campbell, A., J. Lessard & G. S. Jamieson. 2003. Fecundity and seasonal reproduction of northern abalone, *Haliotis kamtschatkana*, in Barkley Sound, Canada. *J. Shellfish Res.* 22:811-818.
- Campbell, A., I. Manley & W. Carolsfeld. 1992. Size at maturity and fecundity of the abalone, *Haliotis kamtschatkana* in northern British Columbia. *Can. Man. Rep. Fish. Aquat. Sci.* 2169: 47-65.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.* 197:516-519.
- California Department of Fish and Wildlife [Formerly California Department of Fish and Game (CDFW)] Marine Region GIS Unit. 2009. 10 meter bathymetric contour lines to 600 meters depth on the California coast. Available at: <https://www.wildlife.ca.gov/Conservation/Marine/GIS/Downloads>.
- California Department of Fish and Wildlife [Formerly California Department of Fish and Game (CDFW)] Marine Region GIS Unit. 2014. BIO_SCSR_Kelp2011. Available at: <https://www.wildlife.ca.gov/Conservation/Marine/GIS/Downloads>.
- California Department of Fish and Wildlife [Formerly California Department of Fish and Game (CDFW)]. 2005. Abalone Recovery and Management Plan. Prepared by the Marine Region. Adopted by the California Fish and Game Commission. December 9, 2005. 363pp. Available from <http://www.dfg.ca.gov/marine/armp>
- California Department of Fish and Wildlife (CDFW). 2018. North coast red abalone fishery closed for 2018. California Department of Fish and Wildlife News, April 2, 2018. Available from: <https://cdfgnews.wordpress.com/2018/04/02/north-coast-red-abalone-fishery-closed-for-2018/>.
- Catton, C. A & L. Rogers-Bennett. 2013. Assessing the recovery of pink abalone (*Haliotis corrugata*) by incorporating aggregation into a matrix model. *J. Shellfish Res.* 32: 181-187.

- Chadés, I., J. M. R. Curtis & T. G. Martin. 2012. Setting realistic recovery targets for two interacting endangered species, sea otter and northern abalone. *Conserv. Biol.* 26:1016-1025.
- Chandler, P. C., S. A. King & J. Boldt. 2017. State of the physical, biological and selected fishery resources of Pacific Canadian marine ecosystems in 2016. Canadian Technical Report of Fisheries and Aquatic Sciences 3225. Vi + 243pp.
- Cherry, S. 1998. Statistical tests in publications of the Wildlife Society. *Wildl. Soc. Bull.* 26: 947-953.
- Clark, P. J. & F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.
- Coates, J. H., K. A. Hovel, J. L. Butler, A. P. Klimley & S. G. Morgan. 2013. Movement and home range of pink abalone *Haliotis corrugata*: implications for restoration and population recovery. *Mar. Ecol. Prog. Ser.* 486:189-201.
- Cox, K. W. 1962. California abalones, family Haliotidae. California Department of Fish and Game Fish Bulletin 118:1–132.
- Davis, G. E. 1988. Kelp forest monitoring handbook: Channel Islands National Park. U.S. Department of the Interior, National Park Service, Channel Islands National Park, Ventura, CA. Available at:
<https://science.nature.nps.gov/im/units/medn/monitor/kelpforest.cfm>.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, P.B. & K. L. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol. Mon.* 69: 219-250.
- Donnellan, M. & K. Hebert. 2017. Pinto abalone (*Haliotis kamtschatkana* Jonas 1845) surveys in southern Southeast Alaska, 2016. Anchorage, Alaska: Alaska Department of Fish and Game. Fishery Data Series No. 17-40.
- Dowling, N. A., S. J. Hall & R. McGarvey. 2004. Assessing population sustainability and response to fishing in terms of aggregation structure for greenlip abalone (*Haliotis laevigata*) fishery management. *Can. J. Fish. Aquat. Sci.* 61:247–259.
- Eckdahl, K. A. 2015. Endangered black abalone (*Haliotis cracherodii*) abundance and habitat availability in southern California. MS Thesis. Department of Biological Science, California State University, Fullerton, Fullerton, CA. 52 pp.
- Edwards, M. S & J. S. Estes. 2006. Catastrophe, recovery and range limitation in NE Pacific kelp forests: a large-scale perspective. *Mar. Ecol. Prog. Ser.* 320:79-87.

- Fanshawe, S., G. R. VanBlaricom & A. A. Shelly. 2003. Restored top carnivores as detriments to the performance of marine protected areas intended for fishery sustainability: A case study with red abalones and sea otters. *Conserv. Biol.* 17: 273-283.
- Friedman, C. S., K. B. Andree, K. A. Beauchamp, J. D. Moore, T. T. Robbins, J. D. Shields & R. P. Hedrick. 2000. 'Candidatus *Xenohaliotis californiensis*', a newly described pathogen of abalone, *Haliotis* spp., along the west coast of North America. *Int. J. Syst. Evol. Microbiol.* 50:847-855.
- Geiger D. L. 1999. A total evidence cladistic analysis of the Haliotidae (Gastropoda: Vetigastropoda). PhD Dissertation. University of Southern California, Los Angeles, Los Angeles, CA.
- Geiger D. L. 2000. Distribution of and biogeography the recent Haliotidae (Gastropoda: Vetigastropoda) world-wide. *Boll. Malacol.* 35:57-120.
- Geiger, D. & B. Owen. 2012. Abalone: World-wide Haliotidae. ConchBooks, Hackenheim. Viii + 361 pp.
- Gruenthal, K. M. 2007. Conservation genetics of California abalone species. PhD Dissertation. University of California, San Diego. La Jolla, CA.
- Gruenthal, K. M., L. K. Acheson & R. S. Burton. 2007. Genetic structure of natural populations of California red abalone (*Haliotis rufescens*) using multiple genetic markers. *Mar. Biol.* 152: 1237-1248.
- Gruenthal, K. M. & R. S. Burton. 2005. Genetic diversity and species identification in the endangered white abalone (*Haliotis sorenseni*). *Conserv. Genet.* 6: 929-939.
- Hankewich, S., J. Lessard & E. Gebeldinger. 2008. Resurvey of northern abalone, *Haliotis kamtschatkana*, populations in southeast Queen Charlotte Islands, British Columbia, May 2007. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2839. Vii + 39pp.
- Harrison, A. J. 1986. Gastropod fisheries of the Pacific with particular reference to Australian abalone. P. 14-22. In: Jamieson, GS, Bourne, N [ed.]. North Pacific workshop on stock assessment and management of invertebrates. Canadian Special Publications of Fishery and Aquatic Sciences. 92 pp.
- Hines, A. H. & J. S. Pearse. 1982. Abalones, shells, and sea otters: Dynamics of prey populations in central California. *Ecology* 63: 1547-1560.
- Hobday, A. J., M. J. Tegner & P. L. Haaker. 2001. Over-exploitation of a broadcast spawning marine invertebrate: Decline of the white abalone. *Rev. Fish. Biol. Fisher.* 10:493-514.

- Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner & R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-638.
- Lafferty, K. D., M. D. Behrens, G. E. Davis, P. L. Haaker, D. J. Kushner, D. V. Richards, I. K. Taniguchi & M. J. Tegner. 2004. Habitat of endangered white abalone, *Haliotis sorenseni*. *Biol. Conserv.* 116:191-194.
- Leighton, D. L. 1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. *Fish. Bull.* 72:1137-1145.
- Leighton, D. L. 2000. The biology and culture of the California abalones. Pittsburgh, PA: Dorrance Publishing. 216 pp.
- Lessard, J. & A. Campbell. 2007. Describing northern abalone, *Haliotis kamtschatkana*, habitat: Focusing on rebuilding efforts in British Columbia, Canada. *J. Shellfish Res.* 26: 677–686.
- Levitan, D. R., M. A. Sewell & F. Chia. 1992. How distribution and abundance influence fertilization success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73:248-254.
- Levitan, D. R. & C. M. Young. 1995. Reproductive success in large populations: empirical measures and theoretical predictions of fertilization in the sea biscuit *Clypeaster rosaceus*. *J. Exp. Mar. Biol. Ecol.* 190:221-241.
- Manly, B., L. McDonald & D. Thomas. 1993. Resource selection by animals. London, U.K., Chapman and Hall. Vii + 177 pp.
- McLean, J. 1966. West American prosobranch gastropoda: superfamilies Patellaceae, Pleurotomariacea, and Fissurellacea. PhD Dissertation. Stanford University, Stanford, CA. 255 pp.
- McShane, P. E. 1992. Early life history of abalone: a review. In: Abalone of the world: biology, fisheries, culture. Proceedings of the 1st International Symposium on Abalone. Oxford, U.K.: Blackwell Scientific Publications Ltd. Pp. 120-138.
- McShane, P. E., K. P. Black & M. G. Smith. 1988; Recruitment processes in *Haliotis rubra* (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localized dispersal of larvae. *J. Exp. Mar. Biol. Ecol.* 124:175-203.
- Micheli, F., A. O. Shelton, S. M. Bushinsky, A. L. Chiu, A. J. Haupt, K. W. Heiman, C. Kappel, M. C. Lynch, R. G. Martone, R. B. Dunbar & J. Watanabe. 2008. Persistence of depleted abalones in marine reserves of central California. *Biol. Conserv.* 141:1078-1090.

- Miyake, Y., S. Kimura, T. Horii & T. Kawamura. 2017. Larval dispersal of abalone and its three modes: a review. *J. Shellfish Res.* 36:157-167.
- MolluscaBase. 2018. *Haliotis kamtschatkana* Jonas, 1845. Accessed through: World Register of Marine Species at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=405014> on 2018-07-11.
- Mottet, M. 1978. A review of the fishery biology of abalones. Technical report Washington Department of Fisheries. Olympia, WA, Department of Fisheries.
- National Marine Fisheries Service. 2008. White Abalone Recovery Plan (*Haliotis sorenseni*). National Marine Fisheries Service, Southwest Regional Office, Long Beach, CA. October, 2008. 133 p.
- National Marine Fisheries Service. 1 September 2009. 2009 NMFS west coast workshop on abalone species of concern.
- National Marine Fisheries Service. 2014. Status review report for pinto abalone (*Haliotis kamtschatkana*). Long Beach, CA: Report to the National Marine Fisheries Service, West Coast Regional Office. 135 pp.
- Neuman, M. J., B. Tissot & G. R. VanBlaricom. 2010. Overall status and threats assessment of black abalone (*Haliotis cracherodii* Leach, 1814) populations in California, USA. *J. Shellfish Res.* 29:577-586.
- Neuman, M. J., S. Wang, S. Busch, C. Friedman, K. Gruenthal, R. Gustafson, D. Kushner, K. Stierhoff, G. VanBlaricom & S. Wright. 2018. A status review of pinto abalone (*Haliotis kamtschatkana*) along the west coast of North America: Interpreting trends, addressing uncertainty, and assessing risk for a wide-ranging marine invertebrate. *J. Shellfish Res.* 17: 1-42.
- O'Leary, J. K., F. Micheli, L. Airoidi, C. Boch, G. De Leo, R. Elahi, F. Ferretti, N. A. J. Graham, S. Y. Litvin, N. H. Low, S. Lummis, K. J. Nickols & J. Wong. 2017. The resilience of marine ecosystems to climatic disturbances. *BioScience* 67:208-220.
- Ostrowski, E. 2016. Multivariate suitability model for pinto abalone (*Haliotis kamtschatkana*) in San Diego County, California. MS Thesis. Department of Biological Science, California State University, Fullerton, Fullerton, CA. 71 pp.
- Parmesan, C. 1996. Climate and species' range. *Nature* 382:765-766.
- Parnell, P. E. 2015. The effects of seascape pattern on algal patch structure, sea urchin barrens, and ecological processes. *J. Exp. Mar. Biol. Ecol.* 465:64-76.
- Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1987. Experimental evidence for limited dispersal of haliotid larvae (genus: *Haliotis*: Gastropoda: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 106:243-263.

- Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1988. Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 122:91-104.
- Quayle, D. B. 1971. Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamtschatkana* Jonas). Fisheries Research Board of Canada Technical Report. 279: 84p.
- Rogers-Bennett, L. 2007. Is climate change contributing to range reductions and localized extinctions in northern (*Haliotis kamtschatkana*) and flat (*Haliotis walallensis*) abalones? *Bull. Mar. Sci.* 81:283-296.
- Rogers-Bennett L., B. L. Allen & D. P. Rothaus. 2011. Status and habitat associations of the threatened northern abalone: importance of kelp and coralline algae. *Aquat. Conserv. Mar. Fresh. Ecosyst.* 21:573–581.
- Rogers-Bennett L., P. L. Haaker, T. O. Huff & P. K. Dayton. 2002. Estimating baseline abundances of abalone in California for restoration. CalCOFI Report, 43:97-111.
- Rogers-Bennett, L., Pearse, JS. 2001. Indirect benefits of marine protected areas for juvenile abalone. *Conservation Biology*, 15(3):642-647.
- Rothaus, D. P., B. Vadopalas & C. S. Friedman. 2008. Precipitous declines in pinto abalone (*Haliotis kamtschatkana kamtschatkana*) abundance in the San Juan Archipelago, Washington, USA, despite statewide fishery closure. *Can. J. Fish. Aquat. Sci.* 65:2703–2711.
- RStudio Team. 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. Available from: <http://www.rstudio.com/>.
- Sagarin, R. D., J. P. Barry, S. E. Gilman & C. H. Baxter. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecol. Monograph* 69: 465-490.
- Schiel, D. R. & M. S. Foster. 2015. The biology and ecology of giant kelp forests. Oakland, CA: University of California Press. 395 pp.
- Seamone, C. B. & E. G. Boulding. 2011. Aggregation of the northern abalone *Haliotis kamtschatkana* with respect to sex and spawning condition. *J. Shellfish Res.* 30: 881-888.
- Shepherd, S. A. 1986a. Studies on southern Australian abalone (genus *Haliotis*). VII. Aggregative behaviour of *H. laevisgata* in relation to spawning. *Mar. Biol.* 90: 231–236.
- _____ 1986b. Movement of the Southern Australian abalone *Haliotis laevisgata* in relation to crevice abundance. *Aust. J. Ecol.* 11:295-302.

- Shepherd, S. A. & P. A. Breen. 1992. Mortality of abalone: its estimation, variability, and causes. In: Shepherd, S. A., M. J. Tegner, S. A. Guzmán del Prío, editors. *Abalone of the world: biology, fisheries, and culture*. Oxford, U.K.: Blackwell Scientific Publications Ltd. Pp. 276-304.
- Shepherd S. A. & L. D. Brown. 1993. What is an abalone stock: Implications for the role of refugia in conservation. *Can. J. Fish. Aquat. Sci.* 50: 2001-2009.
- Shepherd, S. A. & H. M. Laws. 1974. Studies on southern Australian abalone (Genus *Haliotis*). II. Reproduction of five species. *Aust. J. Mar. Fresh. Res.* 25: 49-62.
- Shepherd, S. A. & D. Partington. 1995. Studies on southern Australian abalone (genus *Haliotis*). XVI. Recruitment, habitat and stock relations. *Mar. Fresh. Res.* 46: 669- 680.
- Shepherd, J. G., J. G. Pope & R. D. Cousens. 1982. Variations in fish stocks and hypotheses regarding their links with climate. ICES CM Mini Symposium, Gen:6. Accessed on June 28, 2018. Available from: http://www.ices.dk/sites/pub/CM%20Documents/1982/Gen/1982_Gen6.pdf
- Shears, N. D., R. C. Babcock, C. A. J. Duffy & J. W. Walker. 2004. Validation of qualitative habitat descriptors commonly used to classify subtidal reef assemblages in north-eastern New Zealand. *New Zeal. J. Mar. Fresh. Res.* 38:743-752.
- Sloan, N. A. & P. A. Breen. 1988. Northern abalone, *Haliotis kamtschatkana*, in British Columbia: Fisheries and synopsis of life history information. *Can. Spec. Pub. Fish. Aquat. Sci.* 103:1-46.
- Stekoll, M. S. & T. C. Shirley. 1993. *In situ* spawning behavior of an Alaskan population of pinto abalone *Haliotis kamtschatkana* Jonas, 1845. *Veliger* 36: 95-97.
- Stevick, B. C. 2010. Experimental rearing methods of pinto abalone (*Haliotis kamtschatkana*) and their effect on outplant survival in Washington State. PhD Dissertation. University of Washington, Seattle, WA.
- Stierhoff, K. L., M. Neuman & J. L. Butler. 2012. On the road to extinction? Population declines of the endangered white abalone, *Haliotis sorenseni*. *Biol. Conserv.* 152: 46-52.
- Straus, K. M. 2010. Shellfish aquaculture and conservation of two Puget Sound molluscs: the pinto abalone (*Haliotis kamtschatkana kamtschatkana*) and the Pacific geoduck (*Panopea generosa*). PhD Dissertation. University of Washington, Seattle, WA.

- Supernault, K. J., A. Demsky, A. Campbell, T. J. Ming, K. M. Miller & R. E. Withler 2010. Forensic genetic identification of abalone (*Haliotis* spp.) of the northeastern Pacific Ocean. *Conserv. Genet.* 11:855-865.
- Tegner, M. J., P. A. Breen, C. E. Lennert. 1989. Population biology of red abalone, *Haliotis rufescens*, in Southern California and management of the red and pink, *H. corrugata*, abalone fisheries. California Department of Fish and Game Fish Bulletin, 87:313-339.
- Tegner, M. J. & P. K. Dayton. 1977. Sea urchin recruitment patterns and implications of commercial fishing. *Science, New Series* 196: 324-326.
- Tegner, M. J. & P. K. Dayton. 1987. El Niño effects on southern California kelp forest communities. *Adv. Ecol. Res.* 17:243-279.
- Tegner, M. J. & P. K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. *ICES J. Mar. Sci.* 57:579-589.
- Tegner, M. J., P. L. Haaker, K. L. Riser & L. I. Vilchis. 2001. Climate variability, kelp forests, and the southern California red abalone fishery. *J. Shellfish Res.* 20(2): 755-763.
- Tomascik, T. & H. Holmes. 2003. Distribution and abundance of *Haliotis kamtschatkana* in relation to habitat, competitors and predators in the Broken Group Islands, Pacific Rim National Park Reserve of Canada. *J. Shellfish Res.* 22:831-838.
- Tutschulte, T. C. 1976. The comparative ecology of three sympatric abalones. PhD Dissertation. University of California, San Diego, La Jolla, CA.
- Uki, N. & S. Kikuchi. 1984. Regulation of maturation and spawning of an abalone, *Haliotis* (Gastropoda) by external environmental factors. *Aquaculture* 39: 247-261.
- U.S. Fish and Wildlife Service. 2015. Southern Sea Otter (*Enhydra lutris nereis*) 5-Year Review: Summary and Evaluation [Internet]. Ventura, CA: Ventura Fish and Wildlife Office; [cited 17 Jun 2018]. Available from <https://www.fws.gov/ventura/docs/species/sso/Southern%20Sea%20Otter%205%20Year%20Review.pdf>
- VanBlaricom, G., J. Butler, A. DeVogelaere, R. Gustafson, C. Mobley, M. Neuman, D. V. Richards, S. Rumsey & B. Taylor, B. 2009. Status review report for black abalone (*Haliotis cracherodii* Leach, 1814). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Long Beach, CA.
- Vilchis, L. I., M. J. Tegner, J. D. Moore, C. S. Friedman, K. L. Riser, T. T. Robbins & P. K. Dayton. 2005. Ocean warming effects on growth, reproduction, and survivorship of Southern California abalone. *Ecol. App.* 15:469-480.

- Withler, R. E., A. Campbell, S. Li, K. M. Miller, D. Brouwer & B. G. Lucas. 2001. High levels of genetic variation in northern abalone *Haliotis kamtschatkana* of British Columbia. Ottawa, Canada: Canadian Science Advisory Secretariat. Research document 2001/097 27pp.
- Young, J. S. & J. D. DeMartini. 1970. The reproductive cycle, gonadal histology, and gametogenesis of the red abalone, *Haliotis rufescens* (Swainson). *California Fish and Game* 56(4): 298-309.
- Zacherl, D., S. D. Gaines & S. I. Lonhart. 2003. The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). *J. Biogeogr.* 30:913-924.