

NEGATIVELY CORRELATED ABUNDANCE SUGGESTS COMPETITION
BETWEEN RED ABALONE (*Haliotis rufescens*) AND RED SEA URCHINS
(*Mesocentrotus franciscanus*) INSIDE AND OUTSIDE ESTABLISHED MPAs
CLOSED TO COMMERCIAL SEA URCHIN HARVEST IN NORTHERN
CALIFORNIA

By

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ABSTRACT

NEGATIVELY CORRELATED ABUNDANCE SUGGESTS COMPETITION BETWEEN RED ABALONE (*Haliotis rufescens*) AND RED SEA URCHINS (*Mesocentrotus franciscanus*) INSIDE AND OUTSIDE ESTABLISHED MPAs CLOSED TO COMMERCIAL SEA URCHIN HARVEST IN NORTHERN CALIFORNIA

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Red abalone and sea urchins are both important herbivores that potentially compete with each other for resources like food and space along the California coast. Red abalone supported a socioeconomically important recreational fishery during this study (which was closed in 2018) and red sea urchins support an important commercial fishery. Both red sea urchins and red abalone feed on the same macroalgae (including *Pterygophora californica*, *Laminaria setchellii*, *Stephanocystis osmundacea*, *Costaria costata*, *Alaria marginata*, *Nereocystis leutkeana*), and a low abundance of this food source during the period of this project may have created a highly competitive environment for urchins and abalone. Evidence that suggests competition between red abalone and red sea urchins can be seen within data collected during the years of this study (2014-2016): a significantly higher red sea urchin density, concomitant with a significantly lower red abalone density, was observed within areas closed to commercial sea urchin harvest (in MPAs) compared to nearby reference areas open to sea urchin harvest. In addition, a significant negative relationship was found between red abalone

and red sea urchin abundances when examined at the 60 m² transect level: transects with higher abundances of red sea urchins contained fewer red abalone. Designating MPAs that are closed to sea urchin harvest, in the absence of sea urchin predators such as sunflower stars (*Pycnopodia helianthoides*), sea otters (*Enhydra lutris*), spiny lobster (*Panulirus interruptus*), and predatory fish species, (such as the sheephead (*Semicossyphus pulcher*) found in Southern California), may all have contributed to an increase in red sea urchin abundances and a concomitant decrease in red abalone within the Cabrillo MPA studied in this project.

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INTRODUCTION

Red abalone are an important invertebrate resource that supported a socioeconomically important sport fishery in northern California up until 2018 (when the fishery was closed). They are found on the west coast of North America from southern Oregon to Baja California. Abalone live within a coiled shell with multiple open ports that facilitate water flow over their gills and their large, muscular foot is considered a delicacy by the many people. This marine snail is an herbivore, feeding on a variety of algae including bull kelp (*Nereocystis luetkeana*), stalked kelp (*Pterygophora californica*) and palm kelp (*Laminaria setchellii*) among many other microalgae in both intertidal and subtidal habitats (Leighton, 1966). Abalone utilize a broadcast spawning reproductive strategy dependent on close proximity to neighboring abalone (Babcock and Keesing, 1999). Throughout the red abalone range, from southern Oregon to Central Baja California, densities vary dramatically on both large- and small- geographic scales (Geiger and Owen, 2012; Rogers-Bennett *et al.*, 2004).

Brown macroalgae, a major primary producer in coastal ecosystems, is a key food source for adult abalone. Crustose coralline algae, another major primary producer, has been found to be an important settlement surface for abalone recruits (Day & Branch, 2000, Morse *et al.*, 1979, Morse and Morse, 1984), and is crucial for immediate post-settlement processes and early growth of abalone (Won *et al.*, 2013).

In California, red abalone and other species of abalone supported recreational and commercial fisheries south of San Francisco up until 1996 (Rogers-Bennett *et al.*, 2004).

The fisheries south of San Francisco were closed in 1997 due to low densities of abalone as a result of overfishing, disease and other environmental factors (Dugan and Davis, 1993; Rogers-Bennett *et al.*, 2004). At its height this fishery landed more than 3,000 metric tons (t) of abalone per year (Cox, 1962). Declines in red abalone as well as other abalone species in southern California during the 1980's were likely the result of reduced adult densities that decreased fertilization success, and ultimately led to recruitment failure (Babcock and Keesing, 1999; Rogers-Bennett *et al.*, 2004; Neuman *et al.*, 2010 [for black abalone]). This devastated the abalone fishery south of San Francisco where there were higher harvesting pressures due to the southern California commercial fishery, where SCUBA was used to harvest over 20,000 metric tons (t) of abalone during the 1950s and 1960s (Karpov *et al.*, 2000). Many commercial abalone divers switched to commercial sea urchin harvesting after commercial abalone harvest was banned.

Historically, red abalone support a recreational fishery only north of San Francisco. This was still true during this study because of the large numbers of abalone in some regions of Northern California, however abalone harvesting is closed for the 2018 season due to low densities at California Fish and Wildlife's (CDFW) indicator sites. This decline in red abalone is likely related to a marked decrease in kelp abundance. This is probably the result of a combination of years with anomalous warm ocean conditions (the "warm blob" followed by a strong El Nino), the outbreak of sea star wasting syndrome which greatly decreased the abundance of *Pycnopodia helianthoides* (an important sea urchin predator), and a marked increase in purple sea urchin abundance (Kintisch, 2015; Hewson *et al.*, 2014). During the course of this study abalone

take in Northern California was limited to removal by free diving (breath hold diving) or shore picking, and each sport diver was allowed 3 abalone per day and 12 total abalone per year. However, prior to this study, divers were allowed 4 or even 5 abalone per day with no yearly limit.

Red sea urchins predominantly feed on similar macroalgal food sources as red abalone (Leighton, 1966), and also utilize a broadcast spawning reproductive strategy. Currently Red sea urchins sustain a large and important commercial fishing industry in northern California (particularly in Mendocino County). Commercial take of red sea urchins in California has exceeded 23,000 metric tons (t) in a single year (Kalvass and Hendrix, 1997). The fishery in the Fort Bragg area has been described as a “recruitment” fishery, with fishermen harvesting sea urchins as soon as they reach the legal size of 3.5 inches or 8.89 cm (California Department of Fish and Game, M.R., 2004). Thus it is highly likely that all “open” areas in this study have seen recent harvest of red sea urchins.

Red abalone and red and purple sea urchins (*Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*) have been observed competing for macroalgal food and space along the California coast (Karpov *et al.*, 2001). Urchin overgrazing impacts benthic algal diversity by eliminating fleshy macroalgae while also bioeroding crustose coralline algae (CCA), reducing primary producer biomass (O’Leary & McClanahan, 2010). Red abalone have been previously reported to occur only infrequently with sea urchins in areas with little macroalgae (Karpov *et al.*, 2001). Sea urchin grazing activities that can physically alter coralline algal habitat are common in areas of increased sea

urchin abundance (O’Leary & McClanahan, 2010). Abalone (*Haliotis spp.*) have not been found to physically alter coralline algal habitats. However, decreasing sea urchin densities have been found to cause abalone to shift from exposed to sheltered microhabitats; conversely, changing abalone densities have not been found to have effects on sea urchin behaviors in Tasmania (Strain *et al.*, 2013). Larger size classes of abalone have been seen in areas along the Northern California coast where sea urchins were removed, compared to pre-removal conditions (Karpov *et al.*, 2001).

In part to protect these species and others from overfishing, the Marine Life Protection Act of 1999 mandated the creation of a series of Marine Protected Areas (MPAs) that have only recently been established all along the state of California; these were phased in by region, starting with the Channel Islands in the south, and ending with the northern California region sampled in this study (established in the North Coast Study Region in Dec of 2012). MPAs in nearshore subtidal reefs have been demonstrated to provide multiple benefits, including, but not limited to, conserving biodiversity (Villamor & Becerro, 2012) and providing refuges from fishing pressure on targeted species (Watson *et al.*, 2009). However, in northern California there is a lack of sea urchin predators common in other areas such as sea otters, spiny lobster, and specialized predatory fish species (like *Semicossyphus pulcher*, the California Sheephead) which are capable of reducing sea urchin abundance and sizes (Pinnegar *et al.*, 2000, Hamilton and Caselle, 2014). This lack of sea urchin predators in Northern California may result in differing reserve effects compared to regions such as Southern California where predators are present. Areas with natural predators show a reduction in sea urchin abundance within

MPAs, whereas areas without predators may show an increase in sea urchin abundance within protected areas (Hamilton *et al.*, 2015).

The 40+-year-old Point Cabrillo State Marine Reserve (SMR) and adjacent 25+-year-old Caspar Sea Urchin Closure Area surveyed in this study were the only areas closed to commercial sea urchin harvest in the north coast study region prior to the implementation of more MPAs in December of 2012. This area is also nearly devoid of sea urchin predators, while some southern species are absent altogether, and other local species like sunflower stars (*Pycnopodia helianthoides*) and wolf eels (*Anarrhichthys ocellatus*) are found in very low abundances. Therefore, I hypothesized that red sea urchins would be larger and more abundant, and red abalone less abundant, within these reserves compared to areas open to commercial red sea urchin harvest. I formulated this hypothesis because I expect that since this region has few natural sea urchin predators, the absence of commercial sea urchin harvesting within the MPAs (at Point Cabrillo and Caspar Sea Urchin Closure) may have allowed red sea urchins to proliferate and negatively impacted abalone abundance relative to adjacent areas open to harvest.

METHODS

HSU Rocky Reef Monitoring Project

The HSU Rocky Reef monitoring project was designed to provide baseline monitoring data and characterization of nearshore rocky reefs inside and outside of recently established Marine Protected Areas (MPAs) (Dec, 2012) along the coast of northern California. A modified protocol, originally designed for subtidal monitoring in other MPA regions by the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO), was used for this project. This project characterized densities, percent cover and species diversity of many invertebrates, algae, and fish species inside and outside of MPAs at several sites all along the north coast.

I conducted surveys specifically designed to quantify densities and sizes of red abalone and sea urchins at three sites: The Pt. Cabrillo Marine Reserve and, two adjoining reference sites, Caspar to the north and Russian Gulch to the south of the Point Cabrillo Marine Reserve. These three sites were chosen both because of the higher abundances of sea urchins and red abalone in this region and most importantly, because of the pre-existing reserve status of the Pt. Cabrillo Marine Conservation Area (prior to the implementation of MPAs on the north coast on December 19, 2012). This State Marine Conservation Area was originally established in 1975, and later expanded and incorporated into the statewide MPA network in 2012. This site borders the Caspar sea urchin closure, first created in 1989 and later expanded in 1991. Both of these closed

areas have therefore been closed to commercial take of sea urchins for more than 25 years (long prior to this study).

Sites

Each site was divided into either 2 or 3 replicate cells. A cell is a randomly chosen location, within a given site, within which data was collected on multiple transects located at multiple depths. Replicate cells increased surveyed areas and sample sizes within a site and helped to describe spatial variability at the entire site and not simply at one location within a site. Three replicate depths were targeted within each cell (20 m, 12 m and 4 m). These replicate depths span the majority of the subtidal abalone and sea urchin habitat on the north coast. Each replicate cell was designated by randomly selecting drop points, one for each cell, along the 20 m depth contour within a given site. GPS coordinates of 20 m drop points are mapped in Figure 1 and given in Appendix H. Random drop points for the two shallower depths were made by starting at the randomly selected 20 m drop point and heading in the shoreward direction perpendicular to shore in the boat until the appropriate depth appeared on the sounder. At that point a new drop point was made for that depth zone. Each of the sites and their individual cells are described in Appendix G. Caspar and Point Cabrillo were sampled between May and September in 2014 – 2016 and Russian Gulch was sampled in May and June of 2016 (Figure 1). The Russian Gulch site was added as an additional reference site directly to the south of Point Cabrillo in 2016 (Table 1) to increase sample size and rule out the possibility of abundance and size variations of species being due to increased numbers

and sizes in the southern regions as compared to northern regions. These three sites were chosen because of Pt. Cabrillo's pre-existing marine reserve status, and both the Caspar and Russian Gulch sites were used as reference areas (non-MPA sites where urchin harvesting is ongoing) due to their close proximity to the marine reserve area and the fact that they had similar bottom type and topography. A total of eight replicate cells were sampled within the three main study sites used in this thesis, four replicate cells in areas open to sea urchin harvest and four replicate cells in areas closed to sea urchin harvest (Table 1).

Divers and Equipment

All data was collected by AAUS (American Academy of Underwater Sciences) SCUBA divers off small boats under the auspices of the Humboldt State University Scientific Diving Program. The AAUS divers were required to go through a week long training program prior to each field season where they learned the specific protocols and how to use the specific equipment (slates, tapes and calipers) for this study. Small boat (under 25') use allowed for access to locations with limited or no shore access, and allowed us to easily dive at different locations, greater depths and greater distances off shore than other survey groups (e.g. Reef Check) that conducted research only from shore in nearby areas. Small boat use also allowed researchers to approach the sites in the same way as boat based commercial sea urchin fishermen would. These boat based surveys are likely to cover the same areas as boat based sea urchin fishermen do.

Swath Surveys

Swath surveys conducted to measure the abundance of mobile invertebrates and brown algae were conducted at three replicate depth zones (20 m, 12 m and 4 m) in each replicate cell both inside and outside of MPA sites. These depths were chosen to be within the depth and time limitations of SCUBA sampling to characterize the variability of the entire cell. At each of these depths, two 30 m transects were laid out along the depth contour in opposing directions, yet parallel to the shoreline, whenever the depth contour allowed (Appendix A & B). A diver counted mobile invertebrates including abalone, sea urchins and a select group of sessile invertebrates greater than 2.5 cm in size as well as adult brown macroalgae (stipes > 10 cm long) in the area 1m to either side of these transect lines, covering a total area of 60 m² per transect. Stipes were only counted if they had at least one blade, stipes with no blades were considered dead and not counted. If a count of more than 30 was reached for a given species within the first 10 m section of a transect, and the density of that organism appeared to be uniform all along the transect, then that species was sub-sampled. Sub-sampling was denoted by recording the distances traveled (within that 10m section) down to 1/10th of a meter, and recording the number of individuals observed over that entire sub-area on the data sheet (Appendix C & D). Each of the three 10 m sections within each transect were sub-sampled separately in order to accurately characterize each section and account for differences in densities between 10 m transect segments. Using this method, the estimated number of individuals was calculated for each 10 m section, and the three 10 m sections were added

together to create an estimated count for the entire 60 m² area. It took a pair of SCUBA divers approximately 45 minutes underwater to complete the two 30 m long transects deployed at each depth, and each depth zone was completed on a single dive by a pair of SCUBA divers.

Abalone/Urchin Size Surveys

Separate dives of similar length were made by a pair of divers to conduct abalone/urchin size surveys. Special interest was given to these species because of their socioeconomic importance and the pre-existing protection status within the Pt. Cabrillo marine conservation area. These surveys were conducted at two depths (12 m and 4 m) at each site near, but not overlapping, the transects deployed during the swath surveys described above (See Appendix B). Similar to the swath surveys described above, two 30 m long transects were laid out along each depth contour in opposing directions, parallel to the shoreline (when the depth contour allowed), as long as they did not overlap the swath survey areas. A diver counted all the abalone and all the sea urchins in the area 1 m to either side of the transect line, covering an area of 60 m² per transect (without sub-sampling). A subset of each species was sized; for each 10 m section along the 30 m transect, the first 30 individuals of each species were sized to the nearest centimeter with calipers, while all other individuals in that section were simply counted. Both swath and abalone/urchin surveys were conducted at each cell sampled in 2014 and 2015 using the data sheet in Appendix E. In 2016, only abalone/urchin size swaths and algal swath protocols, including observations of the sunflower star, were conducted at 2 of the 3 cells

within each site. The third cell within each site was not be sampled in 2016 due to budget limitations. These data were recorded on the abalone/urchin size swath data sheet and a modified algal swath data sheet in Appendix F. Over the three years, employing these two protocols (Swath and Size/Abundance transects) at all depths, a total of 134 transects were sampled covering an area of 8,040 m² (Table 2).

Data Analysis

Data from all surveys were analyzed and graphed using R statistical software (R Core Team 2017). Normality was checked using a Shapiro test to make sure assumptions for each test were met. Brown algal stipe counts from five species (*Pterygophora californica*, *Laminaria setchellii*, *Stephanocystis osmundacea*, *Costaria costata*, *Alaria marginata*) within each transect were summed before analysis, yielding a total brown macroalgal abundance per transect. *Nereocystis leutkeana* was analyzed separately due to its larger biomass when compared to the other species brown algae, as well as its morphology which makes it more likely to be fed upon when it is adrift and not when it is attached to rock. Effects of year, depth zone and protection level (in- or outside- of urchin harvesting closed areas) were tested using a three-way analysis of variance (ANOVA) on abundances, where all transects at a given depth were averaged within a cell for a given year. Tukey's HSD (honest significant difference) test was used to test all possible pairwise comparisons. T-tests were performed to look for differences in size of a given species between open and closed (MPA) areas. For comparisons of red sea urchin and red abalone densities at the transect level, linear regression was used on natural log-

transformed data after it was checked for linearity. In order to transform transects with zero observations, one was added to all red abalone observations prior to natural log transformation.

TABLES

Table 1. Study site, cell, harvesting status, and sampling frequency.

Cells from north to south	Open to all take	Closed to urchin harvest only	Closed to all take	Sampled in 2014	Sampled in 2015	Sampled in 2016
Caspar 1	X			X	X	
Caspar 2	X			X	X	X
Caspar 3		X		X	X	X
Pt. Cabrillo 1			X	X	X	
Pt. Cabrillo 2			X		X	X
Pt. Cabrillo 3			X	X	X	X
Russian Gulch 1	X					X
Russian Gulch 2	X					X

Table 2. Benthic sampling design showing number of transects completed at each site, cell and depth.

Cells from north to south	Ab/urchin 4 m Transects	Ab/urchin 12 m Transects	Swath 4 m Transects	Swath 12 m Transects	Swath 20 m Transects	Total # of 60 m ² Transects
Caspar 1	4	4	4	4	4	20
Caspar 2	6	6	4	4	4	24
Caspar 3	6	6	4	4	4	24
Pt. Cabrillo 1	4	4	4	4	4	20
Pt. Cabrillo 2	4	4	2	2	2	14
Pt. Cabrillo 3	6	6	4	4	4	24
Russian Gulch 1	2	2	-	-	-	4
Russian Gulch 2	2	2	-	-	-	4
Total	34	34	22	22	22	134

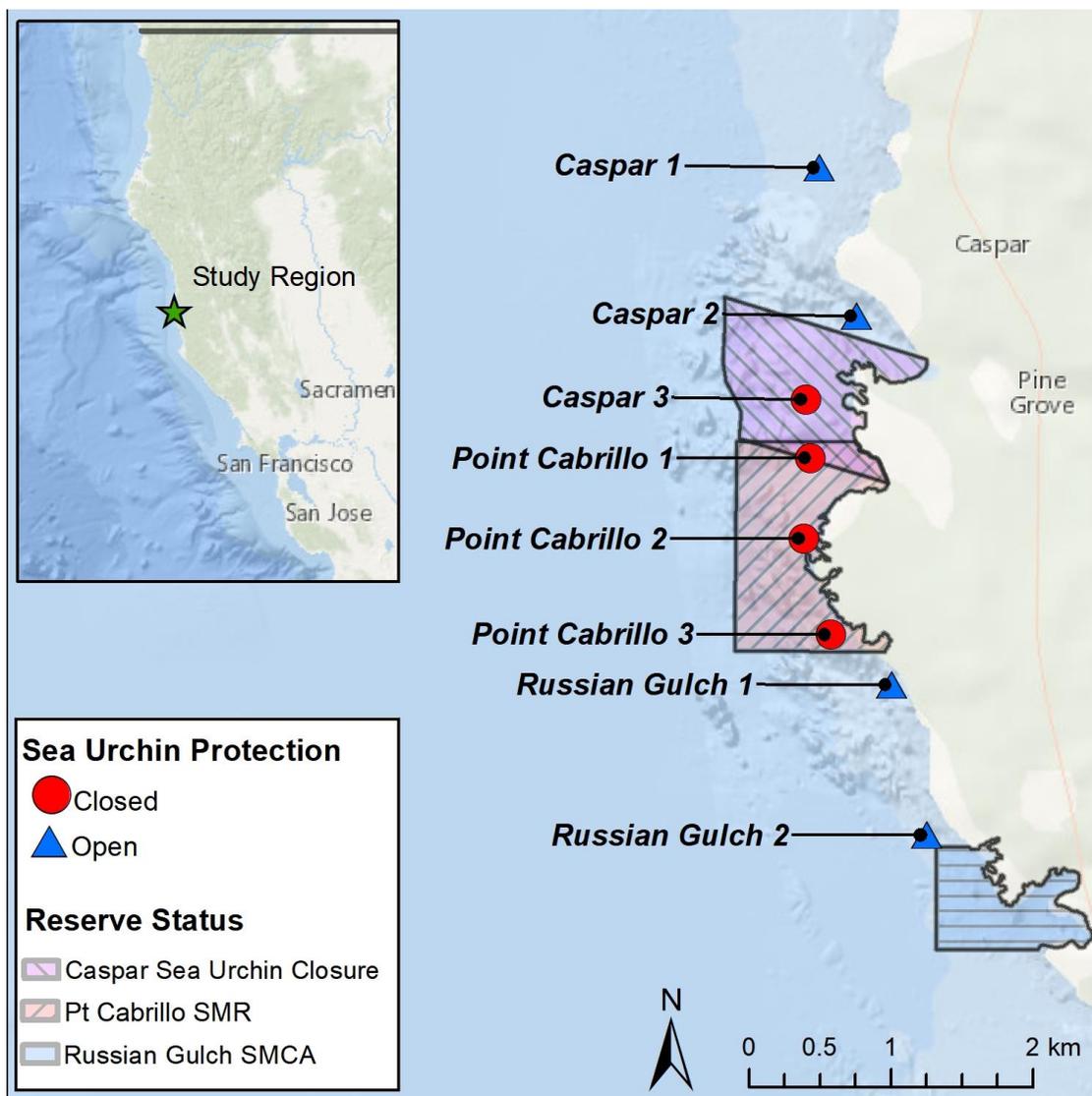


Figure 1. Map of study region encompassing three study sites and eight cells denoted by a symbol at the deepest depth stratum sampled for the given cell, outside or within reserves. Red circles denote cells where sea urchin harvest is prohibited and blue triangles represent cells where sea urchin harvest is legal. Prior to 2012 the Pt. Cabrillo SMR area on this map that is not overlapping the Caspar Sea Urchin closure area (established in 1991) was a SMCA (established in 1975). Mapped in ArcGIS.

RESULTS

Three-Way ANOVA's

No significant year effect was found for red abalone or red sea urchins (Tables 3-4 & Figures 2-3). Significantly more purple sea urchins were observed over time (Table 5 & Figure 4) and significantly fewer brown algae were observed over time (Table 6 & Figure 5). There were significant effects of depth for red abalone, red sea urchins and brown algae (Tables 3, 4 & 6, Figures 6, 7 & 9) but not for purple sea urchins (Table 5 & Figure 8). There were significant relationships between protection levels in red abalone, red sea urchins (Tables 3-4, Figures 6-7) but not for purple sea urchins or brown algae (Tables 5-6 & Figure 8-9). Red sea urchins showed a significant interaction effect between depth and protection level (Table 4, Figure 7). No significant year, depth or protection level effects were found for bull kelp (Table 7). The only significant interaction effect was observed between depth and protection level for red sea urchins (Table 4).

Table 3. Three way ANOVA testing effects of year, depth zone, protection level, and all interactions between factors for red abalone.

Model r^2	Factors	d.f.	F-ratio	P-value
A. Red abalone density				
0.58	Year	2, 28	0.82	0.45
	Depth	2, 28	10.408	< 0.001
	Prot. Level	1, 28	8.89	< 0.01
	Year * Depth	3, 28	0.15	0.93
	Year * Prot. Level	2, 28	0.18	0.84
	Depth * Prot. level	2, 28	2.92	0.07
	Year * Depth * Prot. Level	3, 28	0.26	0.85

Years included in analysis are 2014-2016. Depths included in analysis are 4 m, 12m, and 20m. Statistically significant *P*-values are in bold text. Prot. level, protection level.

Table 4. Three way ANOVA testing effects of year, depth zone, protection level, and all interactions between factors for red sea urchins.

Model r^2	Factors	d.f.	F-ratio	P-value
B. Red sea urchin density				
0.69	Year	2, 28	2.04	0.15
	Depth	2, 28	8.71	< 0.01
	Prot. Level	1, 28	27.99	< 0.001
	Year * Depth	3, 28	0.37	0.78
	Year * Prot. Level	2, 28	0.82	0.45
	Depth * Prot. level	2, 28	4.79	0.02
	Year * Depth * Prot. Level	3, 28	0.04	0.99

Years included in analysis are 2014-2016. Depths included in analysis are 4 m, 12m, and 20m. Statistically significant *P*-values are in bold text. Prot. level, protection level.

Table 5. Three way ANOVA testing effects of year, depth zone, protection level, and all interactions between factors for purple sea urchins.

Model r^2	Factors	d.f.	F-ratio	P-value
C. Purple sea urchin density				
0.45	Year	2, 28	5.90	< 0.01
	Depth	2, 28	2.67	0.09
	Prot. Level	1, 28	0.03	0.87
	Year * Depth	3, 28	1.45	0.25
	Year * Prot. Level	2, 28	0.17	0.85
	Depth * Prot. level	2, 28	0.00	1.00
	Year * Depth * Prot. Level	3, 28	0.35	0.79

Years included in analysis are 2014-2016. Depths included in analysis are 4 m, 12m, and 20m. Statistically significant *P*-values are in bold text. Prot. level, protection level.

Table 6. Three way ANOVA testing effects of year, depth zone, protection level, and all interactions between factors for brown macroalgae (excluding bull kelp).

Model r^2	Factors	d.f.	F-ratio	P-value
D. Brown algae density				
0.49	Year	2, 26	3.83	< 0.05
	Depth	2, 26	3.67	< 0.05
	Prot. Level	1, 26	1.04	0.32
	Year * Depth	3, 26	2.21	0.11
	Year * Prot. Level	2, 26	0.58	0.57
	Depth * Prot. level	2, 26	0.23	0.80
	Year * Depth * Prot. Level	3, 26	0.09	0.97

Brown algae includes five species (*Pterygophora californica*, *Laminaria setchellii*, *Stephanocystis osmundacea*, *Costaria costata*, *Alaria marginata*).

Years included in analysis are 2014-2016. Depths included in analysis are 4 m, 12m, and 20m. Statistically significant *P*-values are in bold text. Prot. level, protection level.

Table 7. Three way ANOVA testing effects of year, depth zone, protection level, and all interactions between factors for bull kelp.

Model r^2	Factors	d.f.	F-ratio	P-value
E. Bull kelp density				
0.31	Year	2, 26	0.79	0.46
	Depth	2, 26	0.80	0.46
	Prot. Level	1, 26	1.29	0.27
	Year * Depth	3, 26	0.55	0.65
	Year * Prot. Level	2, 26	0.97	0.39
	Depth * Prot. level	2, 26	0.87	0.43
	Year * Depth * Prot. Level	3, 26	0.71	0.56

Years included in analysis are 2014-2016. Depths included in analysis are 4 m, 12m, and 20m. Statistically significant *P*-values are in bold text. Prot. level, protection level.

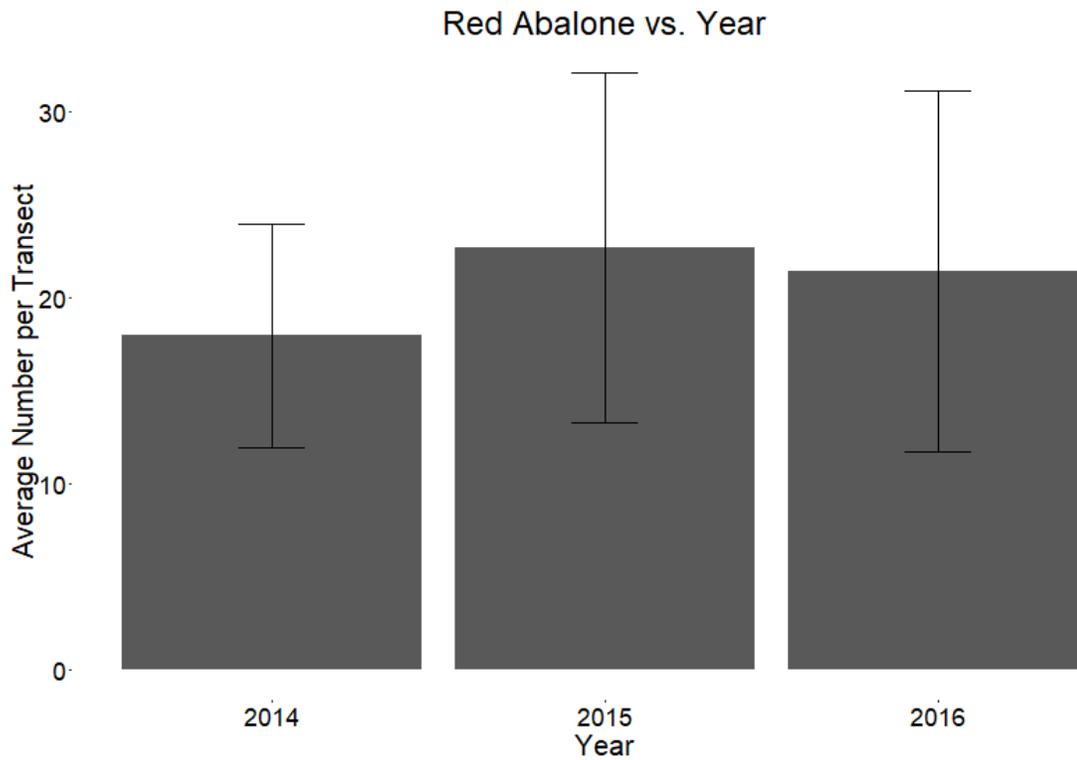


Figure 2. Average red abalone numbers versus year from both swath and abalone/urchin size surveys at all depths combined. No significant relationship observed. Error bars represent \pm one standard error.

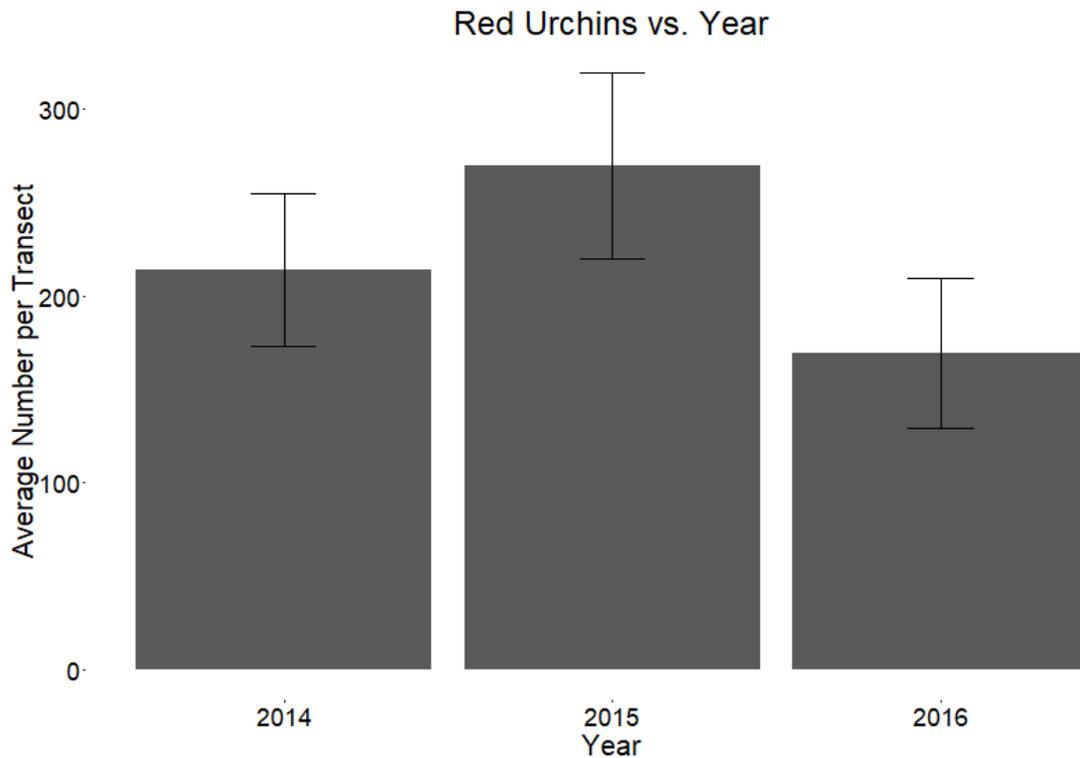


Figure 3. Average red sea urchin numbers versus year from both swath and abalone/urchin size surveys with at all depths combined. No significant relationship observed. Error bars represent \pm one standard error.

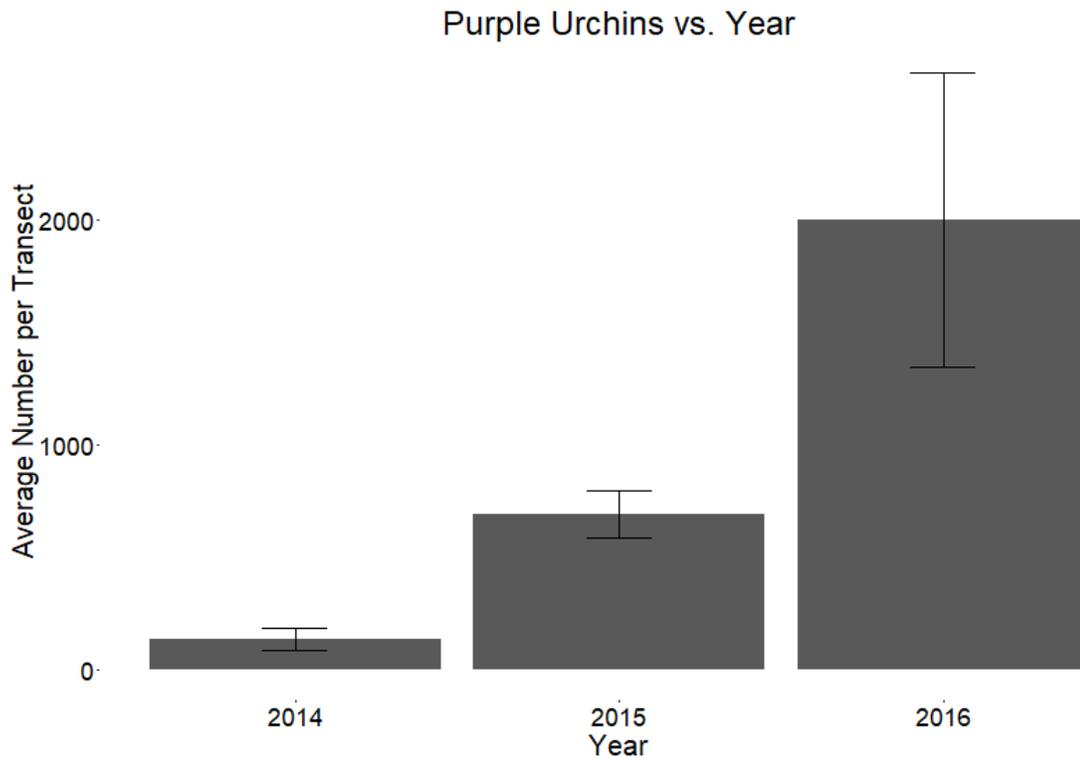


Figure 4. Average purple sea urchin numbers versus year from both swath and abalone/urchin size surveys with all depths combined. Error bars represent \pm one standard error. There were significant differences among years ($p < 0.01$).

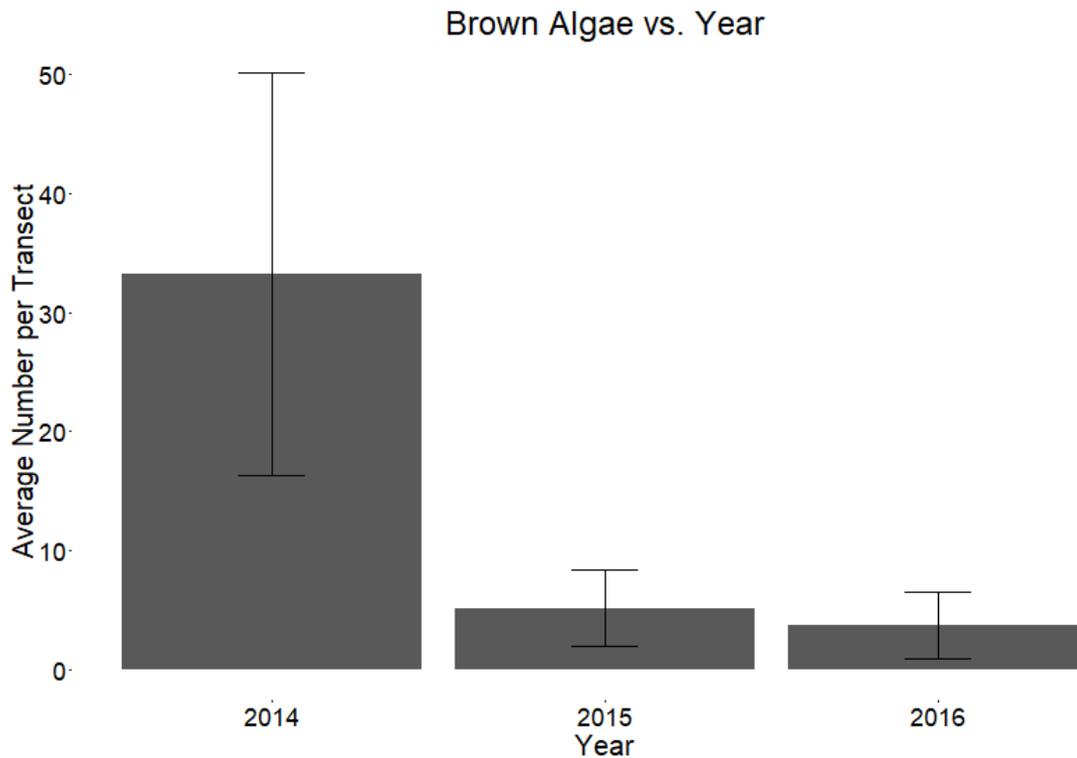


Figure 5. Average brown algal numbers (not including bull kelp) versus year from both swath and abalone/urchin size surveys with at all depths combined. Error bars represent \pm one standard error. There were significant differences among years ($p < 0.05$).

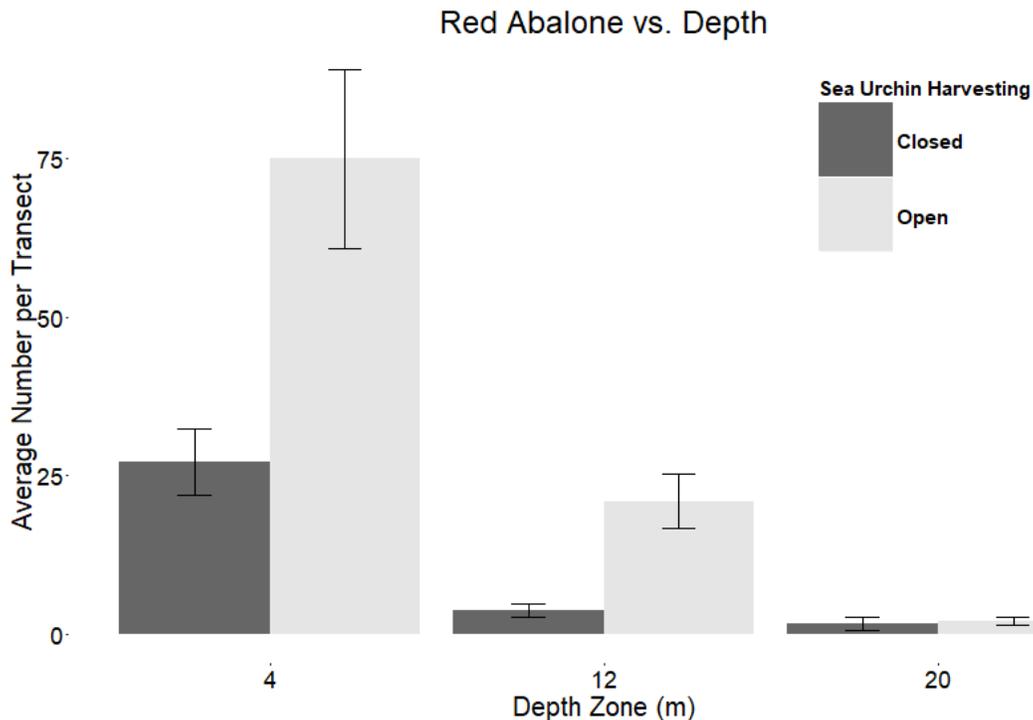


Figure 6. Average red abalone numbers at three depth zones (4 m, 12 m, 20 m) in areas open to harvest (right bars, light gray) versus those closed to harvest (left bars, dark gray) within MPAs. Data are from all years (2014-2016) and both swath and abalone/urchin size surveys. Error bars represent \pm one standard error. There were significant differences among depths ($p < 0.001$). There were significant differences among protection level ($p < 0.01$). There were no significant interactions between depth and protection level ($p > 0.05$).

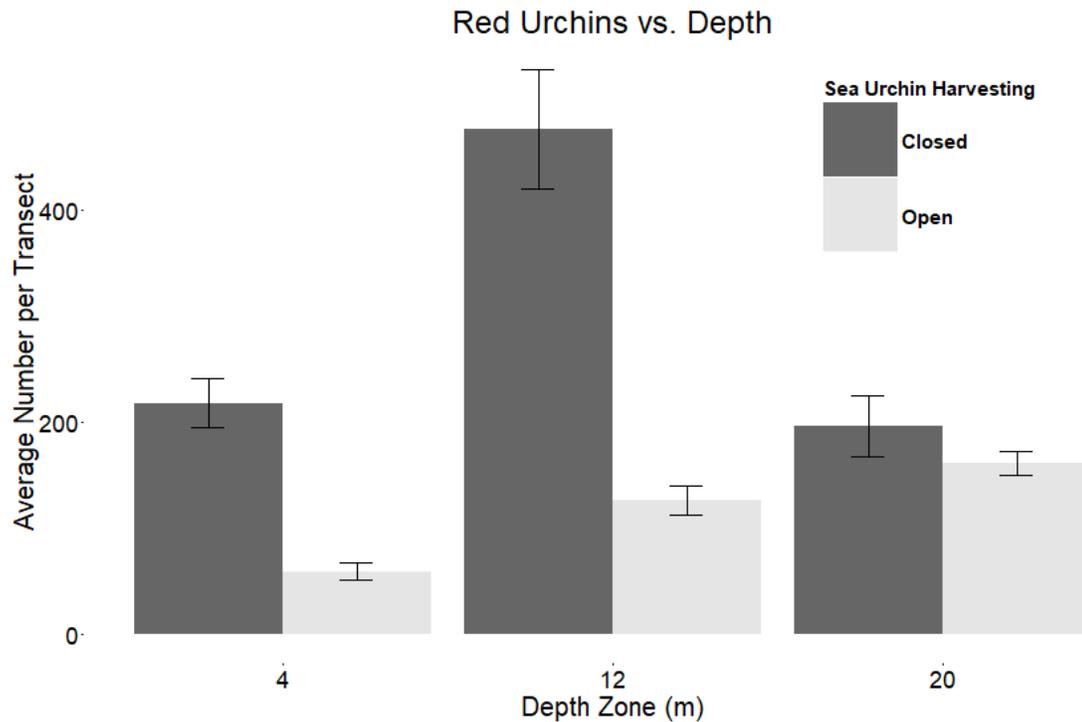


Figure 7. Average red sea urchin numbers at three depth zones (4 m, 12 m, 20 m) in areas open to harvest (right bars, light gray) versus those closed to harvest (left bars, dark gray) within MPAs. Data is from all years (2014-2016) and both swath and abalone/urchin size surveys. Error bars represent \pm one standard error. There was a significant interaction between depth and protection level ($p < 0.05$).

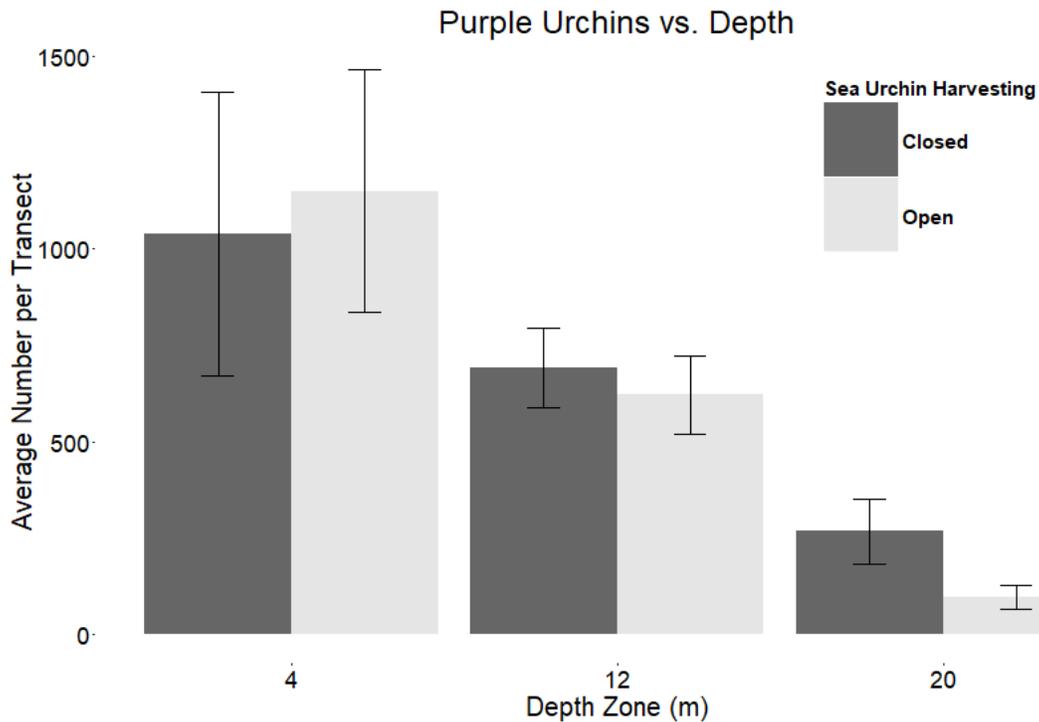


Figure 8. Average purple sea urchin numbers at three depth zones (4 m, 12 m, 20 m) in areas open to harvest (right bars, light gray) versus those closed to harvest (left bars, dark gray) within MPAs. Data is from all years (2014-2016) and both swath and abalone/urchin size surveys. Error bars represent \pm one standard error. There were no significant interactions between depth and protection level ($p > 0.05$).

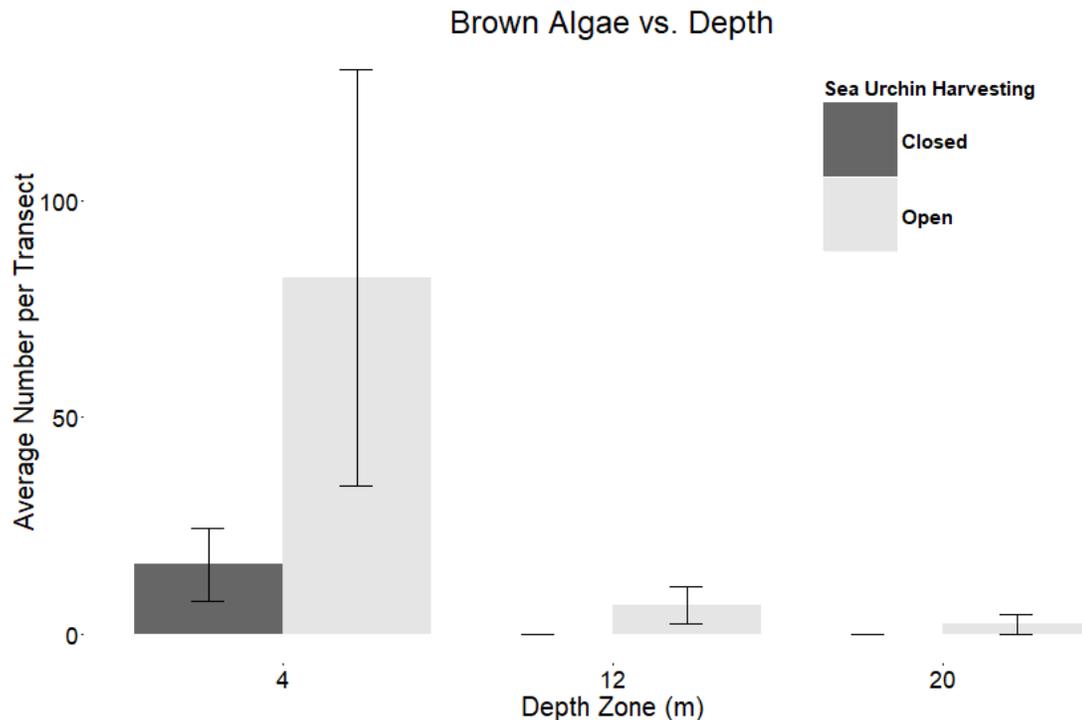


Figure 9. Average brown algal numbers (not including bull kelp) at three depth zones (4 m, 12 m, 20 m) in areas open to harvest (right bars, light gray) versus those closed to harvest (left bars, dark gray) within MPAs. Data is from all years (2014-2016) and both swath and abalone/urchin size surveys. Error bars represent \pm one standard error. There were significant differences among depths ($p < 0.05$). There were no significant interactions between depth and protection level ($p > 0.05$).

Size

No significant difference in abalone size was observed between areas open to sea urchin harvest versus closed areas ($t = 0.34729$, $p = 0.73$). Similarly, there was no significant difference for average purple sea urchin sizes between areas open to sea urchin harvest and areas closed to sea urchin harvest. The average purple sea urchin size only varied by 0.09 cm between open and closed cells ($t = 1.95$, $p = 0.051$). However, a significant difference was observed for the average size of red sea urchins in areas open to sea urchin harvest versus those closed to sea urchin harvest: larger red sea urchins were present in areas closed to harvest. Red sea urchins were on average 9.48 cm in size within closed areas (MPAs), and 8.07 cm in size within areas open to their harvest, a difference of 1.41 cm (± 0.2 cm) on average ($t = 14.62$, $p < 0.0001$; Figure 10).

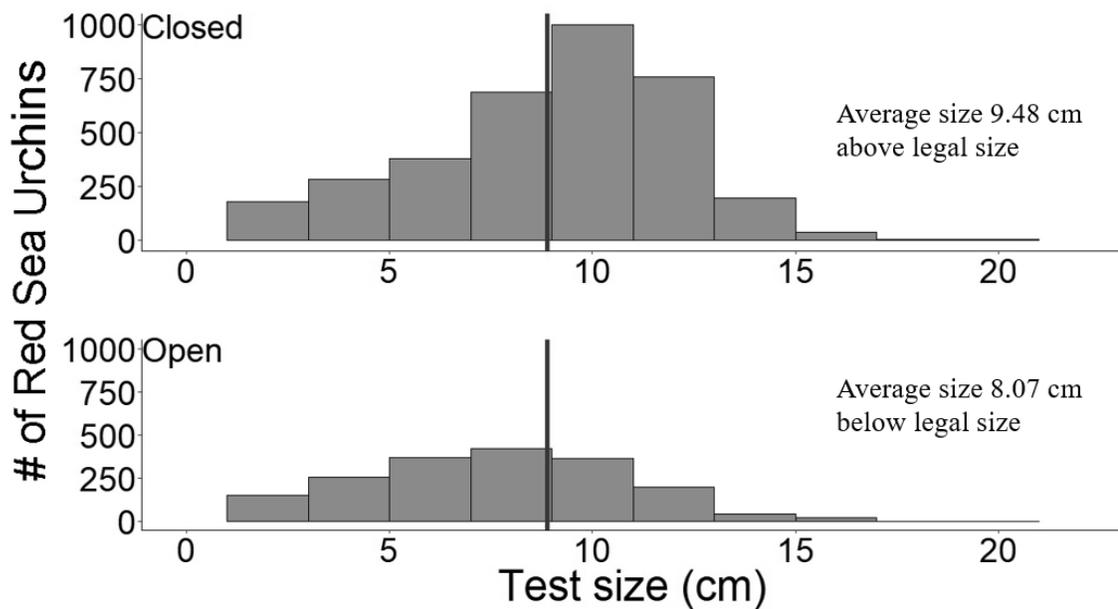


Figure 10. Distribution of red sea urchin test size in cm. Top graph is of test sizes from red urchins within closed areas and bottom graph is for red urchins within open areas. Data is from abalone/urchin size surveys in all years (2014-2016) at all depths. Vertical line indicates the minimum legal commercial take (test) size of 3.5 inches (8.89 cm).

Density-effect

A negative relationship was found between the density of red abalone and red sea urchin abundances at the transect level. In areas of high red sea urchin abundance there were often few or no red abalone, whereas in areas of low red sea urchin abundance there were generally more abalone ($R^2 = 0.2$, $p < 0.001$; Figure 11). A similar negative relationship was found between the density of red abalone and red sea urchin abundances when observed at the transect level when the data were analyzed separately by depth zone for 2 of the 3 depths: within the 4 m and 12 m depths, but not at the 20 m depth, fewer abalone were seen on transects with more red urchins (Figures 12-14). No significant relationship was found between the density of red abalone and that of purple sea urchins when observed at the transect level ($R^2 = 0.2$, $p = 0.12$; Figure 15).

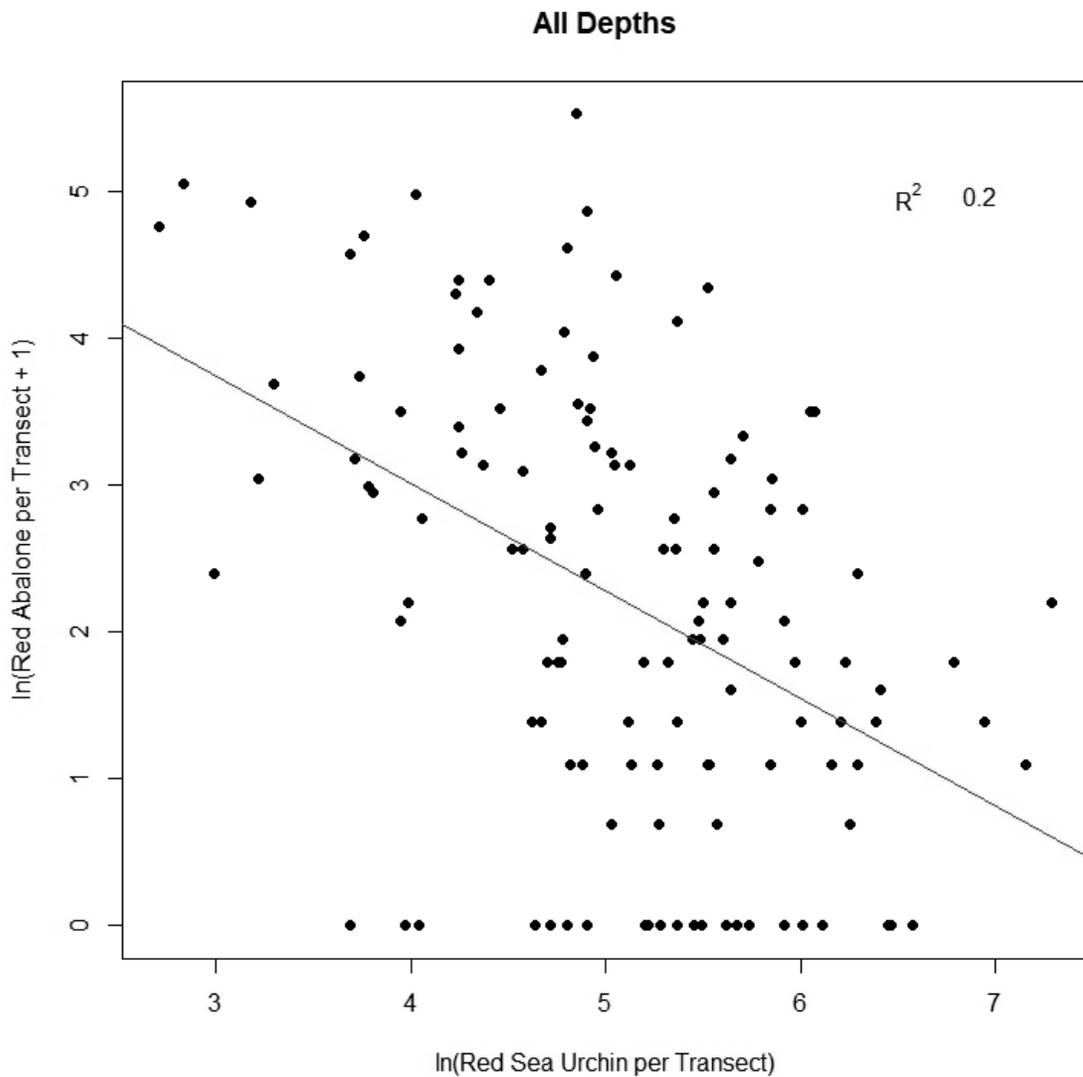


Figure 11. Log_e-transformed red sea urchin numbers per 60 m² transect vs. Log_e-transformed red abalone numbers per 60 m² transects (from the same transect). Data was obtained from all swath and abalone/urchin size surveys at all cells and all depths over all 3 years. Each dot represents an individual transect ($R^2 = 0.2$, $p < 0.001$).

$$(\ln(\text{red abalone} + 1)) = -0.73 (\ln(\text{red sea urchin})) + 5.98$$

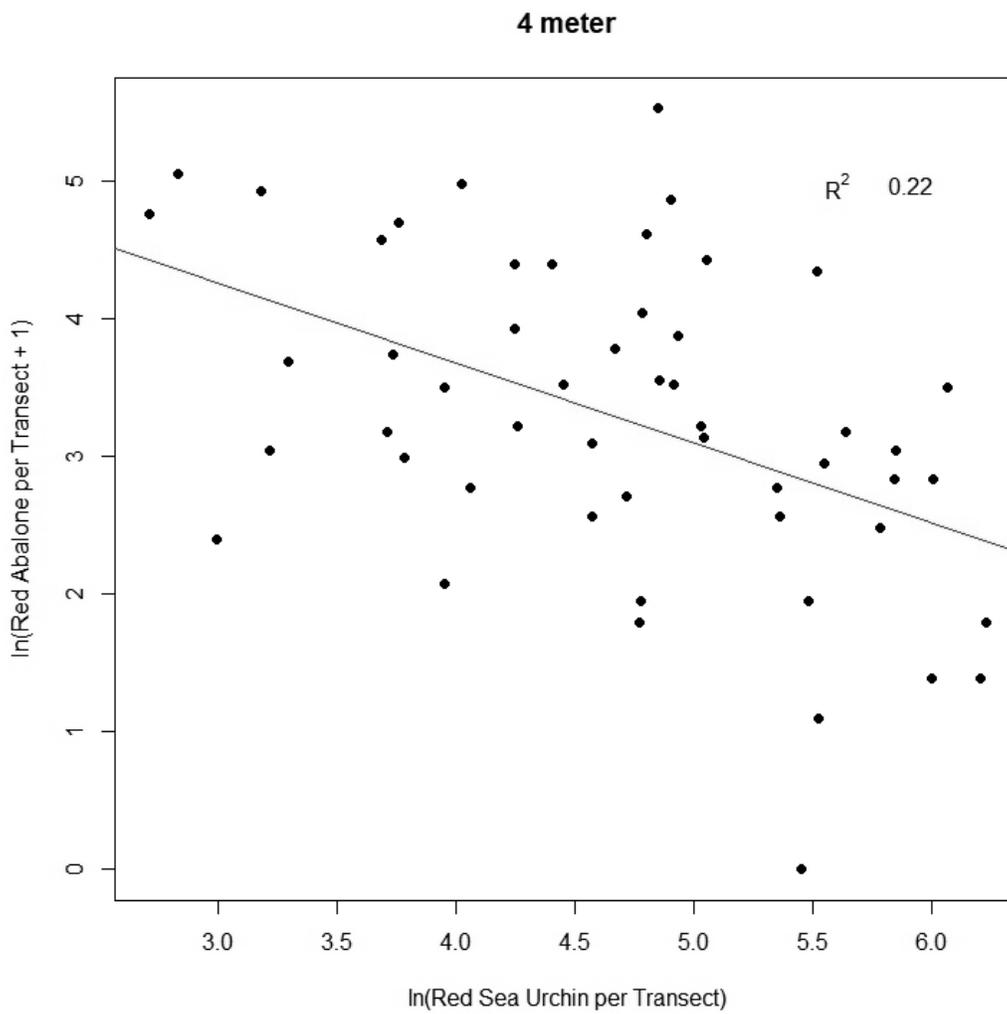


Figure 12. Log_e -transformed red sea urchin numbers per 60 m^2 transect vs. Log_e -transformed red abalone numbers per 60 m^2 transects (from the same transect). Data was obtained from all swath and abalone/urchin size surveys at all cells for the 4 m depth strata over all 3 years. Each dot represents an individual transect ($R^2 = 0.22$, $p < 0.001$).

$$(\ln(\text{red abalone} + 1)) = -0.58 (\ln(\text{red sea urchin})) + 6.00$$

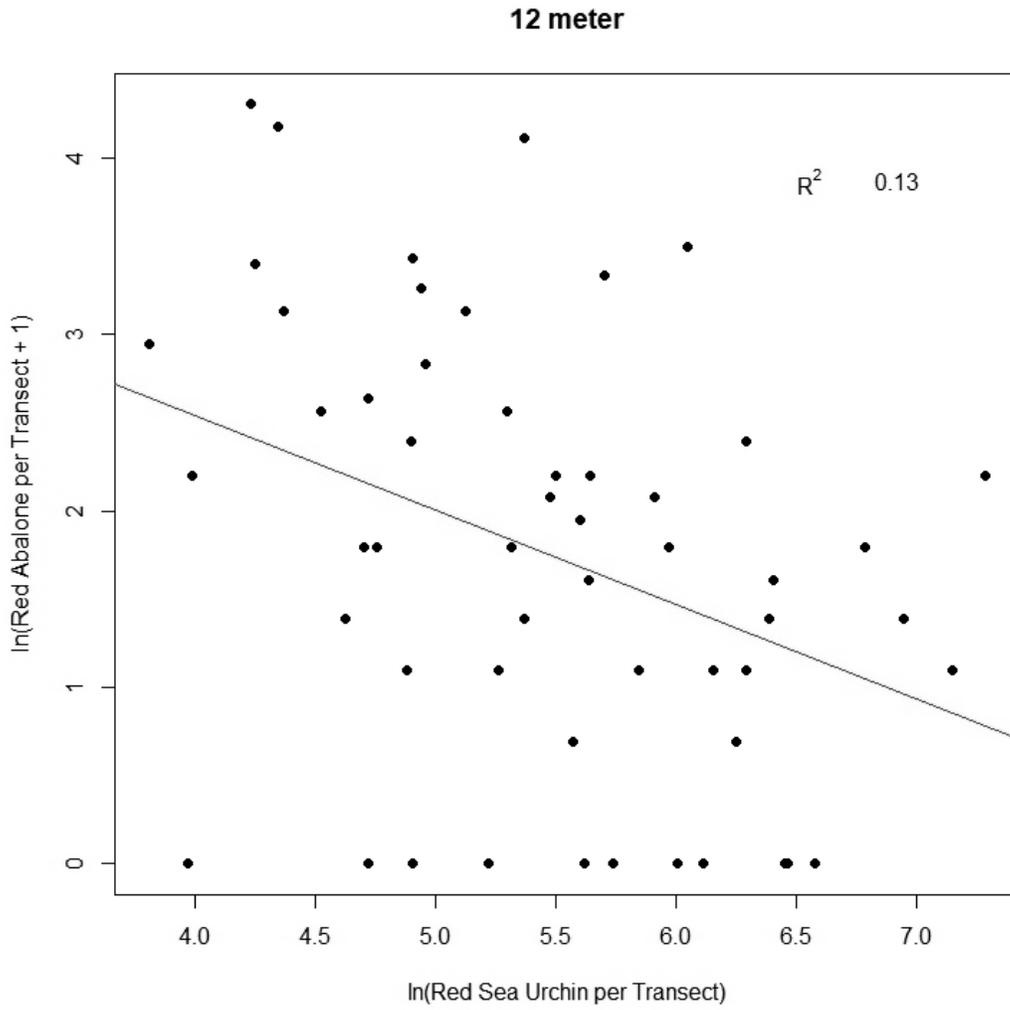


Figure 13. Log_e -transformed red sea urchin numbers per 60 m^2 transect vs. Log_e -transformed red abalone numbers per 60 m^2 transect (from the same transect). Data was obtained from all swath and abalone/urchin size surveys at all cells for the 12 m depth strata over all 3 years. Each dot represents an individual transect ($R^2 = 0.13$, $p = 0.006$).
 $(\ln(\text{red abalone} + 1)) = -0.54 (\ln(\text{red sea urchin})) + 4.68$

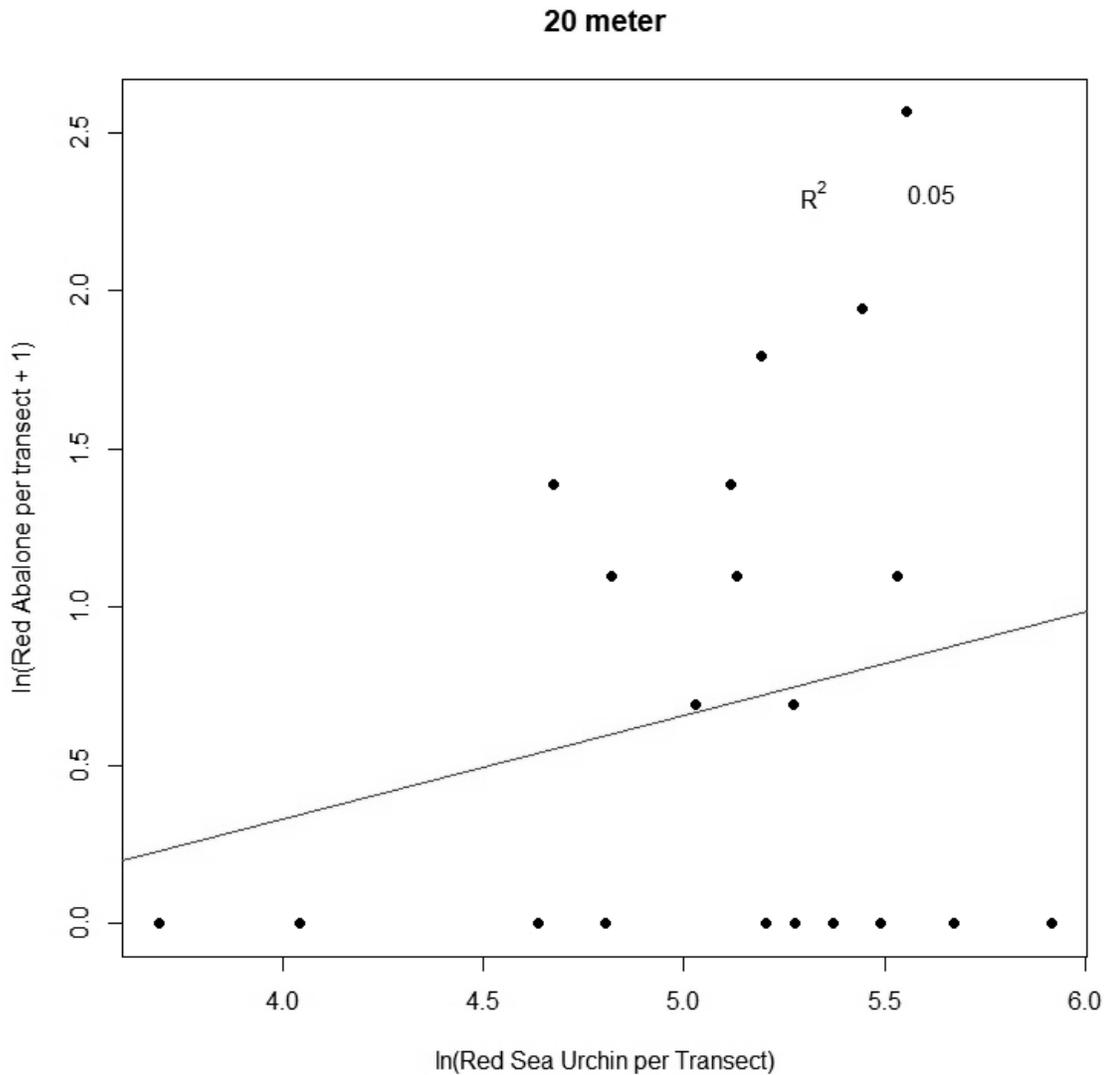


Figure 14. Log_e -transformed red sea urchin numbers per 60 m^2 transect vs. Log_e -transformed red abalone numbers per 60 m^2 transect (from the same transect). Data was obtained from all swath and abalone/urchin size surveys at all cells for the 20 m depth strata over all 3 years. Each dot represents an individual transect. No significant relationship observed ($R^2 = 0.05$, $p = 0.36$).

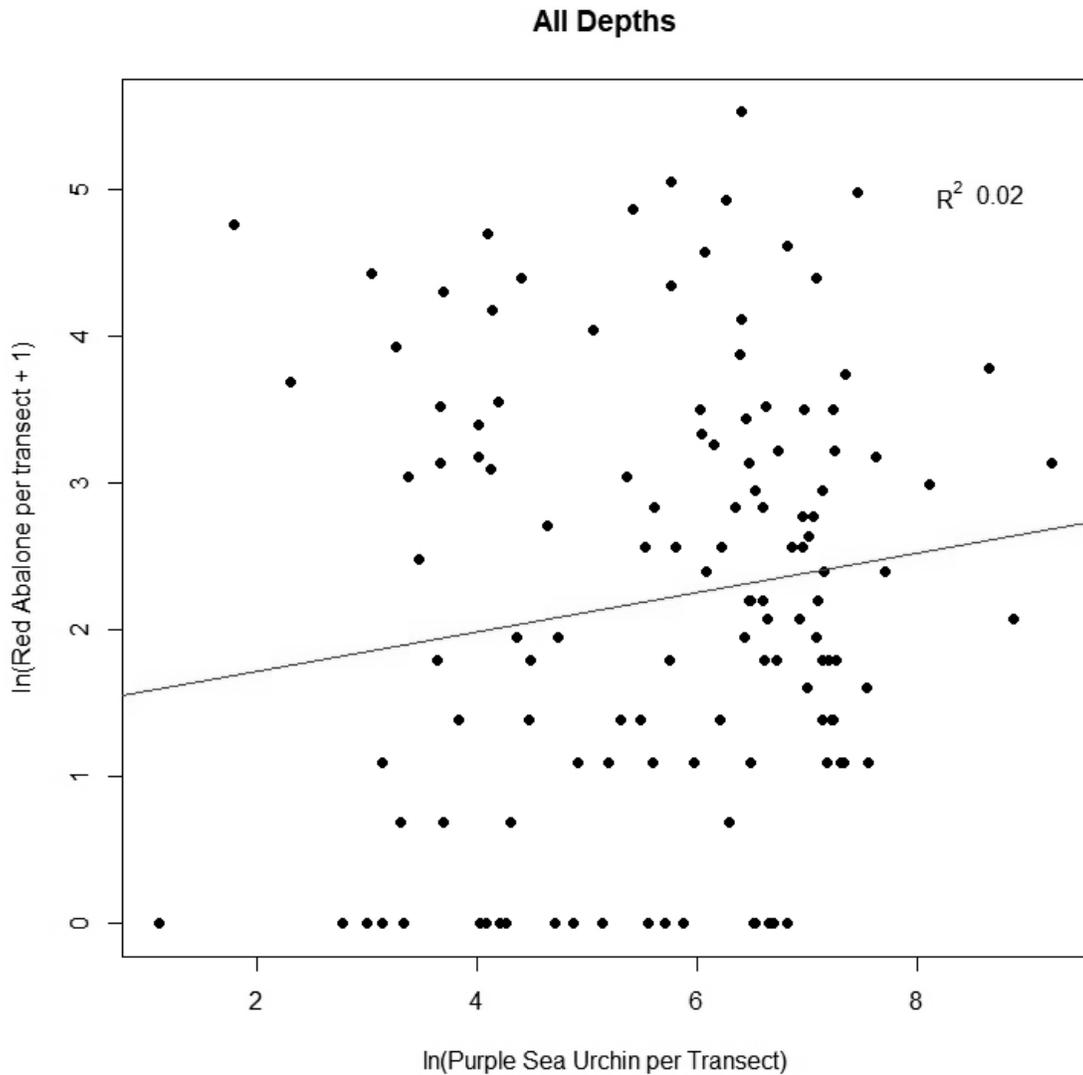


Figure 15. Log_e -transformed purple sea urchin numbers per 60 m^2 transect vs. Log_e -transformed red abalone numbers per 60 m^2 transect (from the same transect). Data was obtained from all swath and abalone/urchin size surveys at all cells and all depths over all 3 years. Each dot represents an individual transect. No significant relationship observed. ($R^2 = 0.02$, $p = 0.12$)

Predators

Only one sunflower star was seen in 2014, six in 2015 and none in 2016 across all closed and open areas combined, however. These numbers are likely to be much lower than what would have been obtained pre-2014 (before SSWD).

DISCUSSION

Red abalone and red sea urchins are highly abundant in and around the Pt. Cabrillo area when compared to other areas within the northern California study region (NCSR). This area, as a whole, exhibits the ideal habitat and oceanographic conditions necessary for these species. At these sites, no significant changes in the abundance of red abalone and red sea urchins were observed through time, but there was a significant increase in purple sea urchins. In addition, there was a significant reduction in brown algal abundance through time, a trend that was likely driven (at least in part) by the increased numbers of purple sea urchins.

There were significant effects of depth on the abundance of red abalone, red sea urchins and brown algae, but not for purple sea urchins. Red abalone were more abundant at the shallow depth stratum (4m) relative to the deeper strata (12m and 20m) where urchin harvesters more often work (to remove them). In addition, a significant difference was found in the average size of red sea urchins in areas open to sea urchin harvest, relative to closed areas (MPA's), in the direction expected: larger red sea urchins were present in areas closed to harvest.

While red urchins were more abundant in MPA's closed to their harvest, the opposite was true for red abalone, which were more abundant in open areas where red sea urchins are still harvested. In addition, a negative relationship was found between the density of red abalone and that of red sea urchin abundances when observed at the transect level. In areas of higher red sea urchin abundance there were often few or no red

abalone. No significant relationship was found between the density of red abalone and that of purple sea urchins when observed at the transect level. The sunflower star was one of very few predators of abalone and sea urchins observed during this study, albeit infrequently, probably due to the recent occurrence of sea star wasting disease (Hewson *et al.*, 2014). The sunflower star has been described as the most important sea urchin predator in some southern California areas (Lafferty and Kushner, 2000).

The higher abundance of red sea urchins in areas closed to sea urchin harvesting (e.g. MPAs) is likely due to the absence of commercial harvest, along with the absence of sea urchin predators in general along the northern California coast during this study (such as sea otters or sunflower stars). It is likely that all open areas were commercially harvested in this recruitment fishery. Similar increased densities of red urchins within MPAs have been observed in southern California (Shears *et al.* 2013). In the presence of predators such as sea otters, spiny lobster, and California sheephead, it is likely that red sea urchin abundances inside and outside the reserve would be reversed (or similar to one another), with more red urchins found outside of protected areas. This could, in turn, increase the abundance of macroalgae, as seen in southern California (Lafferty, 2004) protected areas, and free up algal foods and space for red abalone. Hence in southern California, one would therefore expect the relative abundance of red abalone within MPAs to increase. This is because in a reserve scenario where predatory species are present, their abundances would be predicted to be higher within reserves. These predators would therefore be likely to have a greater impact on the red sea urchin population within reserves when compared to areas open to harvest by humans, lowering

the number of red sea urchins in the reserve and, in turn, competition for algal food and space between red sea urchins and red abalone.

The lack of a significant difference in purple sea urchin abundances between areas open to sea urchin harvest and MPAs that were closed to harvest was expected, due to the fact that purple sea urchins are not a commercially targeted species. Purple sea urchins lack the size necessary for a cost-effective yield in this fishery. Despite their small size, they remain an important competitor in this system and their extremely high abundances in the study areas likely reduced the abundance of brown macroalgae available for red abalone. The uniform abundance of purple sea urchins in this area may lower the overall carrying capacity for red abalone and red sea urchins. The dramatic increase in the abundance of purple urchins seen over the course of this study likely contributed to the decline in brown algae, and possibly also red abalone, towards the end of this research, perhaps causing the 2018 sport fishery closure. These changes may also be due, at least in part, to the near absence of sunflower stars at these sites.

Overgrazing by red and purple sea urchins has likely led to decreases in brown algal abundance inside areas closed to red sea urchin harvest (e.g. MPAs). In contrast, commercial sea urchin harvest has reduced the number of red sea urchins in open areas. This (harvesting) has likely lead to a reduction in grazing in areas open to red urchin harvest, resulting in trends of higher brown algal abundances and significantly more red abalone numbers in non-protected areas. This trend of more brown algae in open areas may have been more apparent in the past, and it is quite possible that past competition could have heavily influenced the trends observed in this study. Because bull kelp was

not included with brown algal abundances in analyses, any potential differences in abundance of this annual kelp between cells or years cannot be driving these trends.

The significantly lower abundance of red abalone within closed areas when compared to open areas seen in this study is likely due to increased competition with red sea urchins for algal resources and space. This outcome is contradictory to what one might otherwise expect (more abalone in areas where they cannot be harvested) within the relatively narrow geographic range of this study where ocean conditions are relatively the same in open and closed areas. Red sea urchins are one of the major herbivores present in this ecosystem, are capable of competing with red abalone and have markedly different abundances inside MPAs (closed areas) versus areas open to their harvest, and are thus the most likely contributor to the observed trends.

Although the abundance of these species varies with depth, the trend of increased red sea urchin density concomitant with a decrease in red abalone density observed within areas closed to commercial sea urchin harvest compared to similar areas open to sea urchin harvest still exists at 2 of the 3 depths, with the 20 m depth strata having very low abundances of all these species in all areas. It is therefore unlikely that the negative relationship between red sea urchins and red abalone is an artifact created by differences in depth preferences for red abalone versus red sea urchins.

The lack of a significant size difference between abalone inside closed areas (MPAs) versus areas open to red sea urchin harvest is contradictory to the trend expected in my hypothesis (larger abalone inside the reserve). This may be a result of increased competition with red sea urchins within MPAs, which could lead to slower red abalone

growth rates and smaller sizes in closed areas (where resources are scarce due to competition) or perhaps competition drives larger individuals out of the area. More research is needed to determine the exact drivers behind this observation.

The significant size difference between red sea urchins inside versus outside Marine Protected Areas (MPAs) is likely due to take of larger individuals by commercial sea urchin fishermen. Urchin fishermen can legally take red sea urchins with a minimum test diameter of 3.5 inches or 8.9 cm. The average size in open areas is below the legal size and average size in closed areas is above the minimum legal size from these normally distributed sizes. Thus, fishing has likely reduced the average size in areas open to harvest because red urchins are harvested as soon as they reach legal size. The nearly significant size difference seen between purple sea urchins inside versus outside MPAs is likely an artifact of the large sample size ($n=5,622$) for purple sea urchins. This species is not targeted by fishermen and the difference in size between open and closed areas is very small (less than 1mm), far less than the 1cm precision of the survey methods used.

The negative relationship found in this study between red abalone and red sea urchin abundances could be due to competition for resources (algae and space) at this local scale. In areas with high red sea urchin abundances, there were fewer red abalone relative to areas with low red sea urchin abundances. This relationship is also still present when looking at both the 4m and 12m depth strata individually, thus it is not likely an artifact of differing depth preferences between these species. The lack of a significant trend at the 20 m depth stratum is likely to due to the low densities and lower sample sizes at this depth. None of the transects in this study were devoid of red sea urchins.

This is likely a tribute to the ability of this species to outcompete red abalone and sustain themselves for long periods of time by moving to food resources (Mattison *et al.*, 1976), as well as their ability to live in a wide array of microhabitats including those with high or low relief, high or low wave action, and on a variety of substrates (rock, bolder, and cobble habitats) -- even those with sand or without places to hide. A number of transects (21) were devoid of red abalone. This could be due to the inability of this species to compete with red sea urchins in areas where they are abundant or these transects are located on poor red abalone habitats. In those areas where both species exist, it is likely that competition is playing a role in reducing the abundance of red abalone.

Significant year-to-year variation was seen in this study only for purple sea urchins and brown algae, with purple sea urchins increasingly dramatically in the final year of this study and brown algae decreasing in the final year of this study, likely due to feeding by urchins. The recent reduction in red abalone densities along the Mendocino and Sonoma coasts may reflect the fact that red abalone are more sensitive to reductions in food (brown algae) than red sea urchins are. The negative relationship between red sea urchins and red abalone, seen at the transect level both when all transects are combined and for two of the three depth strata (4 meters and 12 meters depth but not 20 m) when analyzed separately, support (but do not prove) the hypothesis that these two species are competing with one another, at least during this period of low food abundance seen during this study.

These results are also not an artifact created by variations in yearly abundance of all urchins, nor does it appear to be an artifact of variability between cells because all

cells tend to follow this same relationship (the more red sea urchins, the fewer red abalone). In terms of site locations, we chose the same number of “calm” cells and “rough” (or exposed) cells in both open and closed areas, hence the trends seen in this study are unlikely to be due to wave exposure. Red algae and drift algae were rare in both open and closed areas of this study. Therefore, the relationship between red sea urchins and red abalone is likely due to competition between these species resulting from the effects of commercial sea urchin harvesting (the main difference between areas open and closed to harvest), and not due to differences in exposure to wave action or availability of red algae and/or drift algae between MPAs and non-protected areas.

CONCLUSIONS AND RECOMMENDATIONS

In this study I found fewer red abalone within areas closed to red sea urchin harvest, relative to areas open to harvesting. This difference may be due to competition between red abalone and red sea urchins for brown algal resources and/or space. The lack of macroinvertebrate predators capable of mediating sea urchin abundances at local scales within the region (as well as inside of MPAs) is a likely contributor to the patterns found in this study. In the presence of macroinvertebrate (sea urchin) predators, increased abalone abundances would be expected inside MPAs, where there would be more predators (in no-take areas) to consume sea urchins. Conclusions from studies like this, drawn from connections between long-established closed areas and directly adjacent sites along the north coast of California, may be able to inform the future expectations of subtidal rocky reef community structure within recently established MPA reserves in the north coast region. This is a case study of only one such area, and comparable results might be expected in areas with similar oceanographic conditions (and with similar histories of sea urchin harvesting with very few predators).

More work is needed to determine whether these same changes will occur at other sites along the northern California coast due to the highly variable oceanographic conditions and varying sea urchin harvesting pressures (and predator abundances) across the north coast study region (NCSR). Similarly, more work is needed to determine if the decreased abalone abundances within the Cabrillo MPA is due to direct interspecific

competition between red abalone and red sea urchins, in the form of behavioral changes in abalone (moving out of MPAs) and/or indirect interspecific competition between abalone and sea urchins in the form of decreased food availability for abalone.

In an attempt to better understand this complicated and poorly studied subtidal northern California ecosystem, I recommend that sampling and analyses similar to those performed in this study be repeated in the future, inside and outside of all northern California MPAs and SMCAs, after sufficient time has passed for populations of these slow growing animals to have adjusted to the creation of these new MPAs (in 2012). In particular, if the new MPAs exhibit patterns similar to those seen at Cabrillo (larger and more numerous red sea urchins, reduced red abalone abundances), this would further support the hypothesis that abalone density has decreased as a result of negative interactions with red sea urchins that have grown bigger and more abundant, due to a release from predation (by urchin divers). In addition, urchin removal experiments should be conducted to further confirm whether competition between red sea urchins and red abalone is driving the changes seen within this study.

REFERENCES

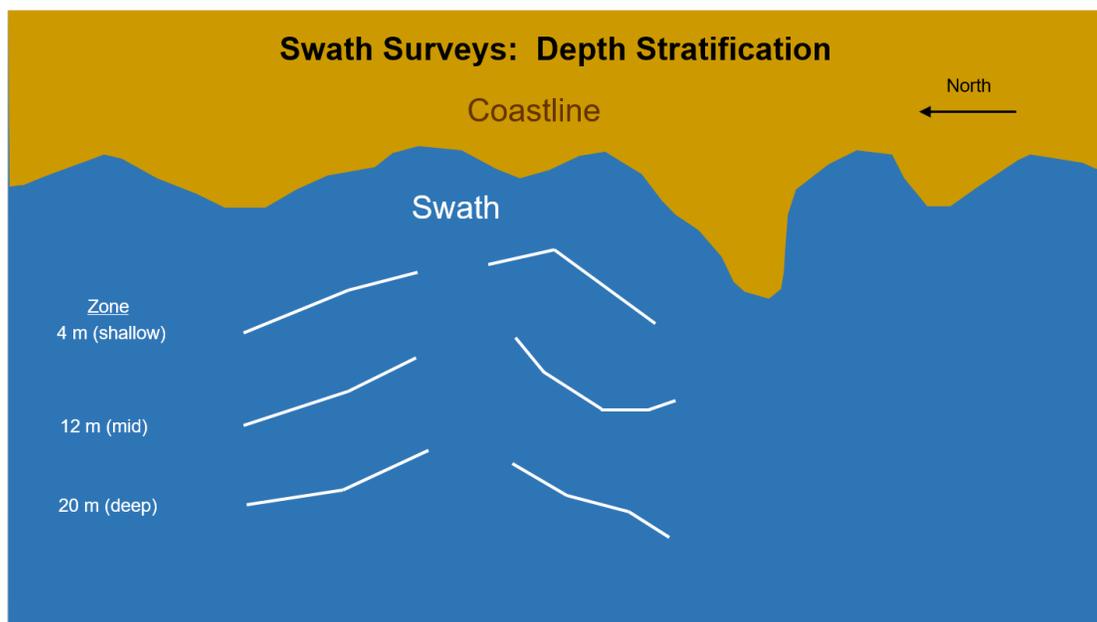
- Babcock, R. & J. Keesing. 1999. "Fertilization biology of the abalone *Haliotis laevis*: Laboratory and field studies." *Can. J. Fish. Aquat. Sci.* 56:1668-1678
- California Department of Fish and Game, M.R., 2002. Draft Abalone Recovery and Management Plan. In: California Department of Fish and Game, M.R. (Ed.), California Department of Fish and Game, Marine Region, Sacramento, CA. C
- California Department of Fish and Game, M.R., 2004. Annual Status of the Fisheries report through 2003, California Department of Fish and Game, Marine Region, Sacramento, CA. C
- Day, E., and G. M. Branch. "Relationships between recruits of abalone *Haliotis midae*, encrusting corallines and the sea urchin *Parechinus angulosus*." *South African Journal of Marine Science* 22.1 (2000): 137-144.
- Dugan, J.E. & G. E. Davis. 1993. "Applications of marine refugia to coastal fisheries management." *Can J. Fish. Aquat. Sci.* 50:2029-2042
- Geiger, Danel L., and Buzz Owen. *Abalone Worldwide Haliotidae*. Hackenheim: Conch, 2012.
- Hamilton, Scott L., and Jennifer E. Caselle. "Exploitation and recovery of a sea urchin predator has implications for the resilience of southern California kelp forests." *Proceedings of the Royal Society of London B: Biological Sciences* 282.1799 (2015): 20141817.

- Hewson, Ian, et al. "Densovirus associated with sea-star wasting disease and mass mortality." *Proceedings of the National Academy of Sciences* 111.48 (2014): 17278-17283.
- Kalvass, Peter E., and Jon M. Hendrix. "The California red sea urchin, *Strongylocentrotus franciscanus*, fishery: catch, effort, and management trends." *Marine Fisheries Review* 59.2 (1997): 1-17.
- Karpov, K. A., Tegner, M. J., Rogers-Bennett, L., Kalvass, P. E., & Taniguchi, I. K. (2001). Interactions among red abalones and sea urchins in fished and reserve sites of northern California: implications of competition to management. *Journal of Shellfish Research*, 20(2), 743-754.
- Karpov, K., et al. "Serial depletion and the collapse of the California abalone (*Haliotis* spp.) fishery." *Canadian Special Publication of Fisheries and Aquatic Sciences* (2000): 11-24.
- Kintisch, Eli. "'The Blob' invades Pacific, flummoxing climate experts." (2015): 17-18.
- Lafferty, Kevin D. "Fishing for lobsters indirectly increases epidemics in sea urchins." *Ecological Applications* 14.5 (2004): 1566-1573.
- Lafferty, Kevin D., and D. Kushner. "Population regulation of the purple sea urchin, *Strongylocentrotus purpuratus*, at the California Channel Islands." *Fifth California Islands Symposium*. Vol. 99. Minerals Management Service, 2000.
- Leighton, David L. "Studies of food preference in algivorous invertebrates of southern California kelp beds." (1966).

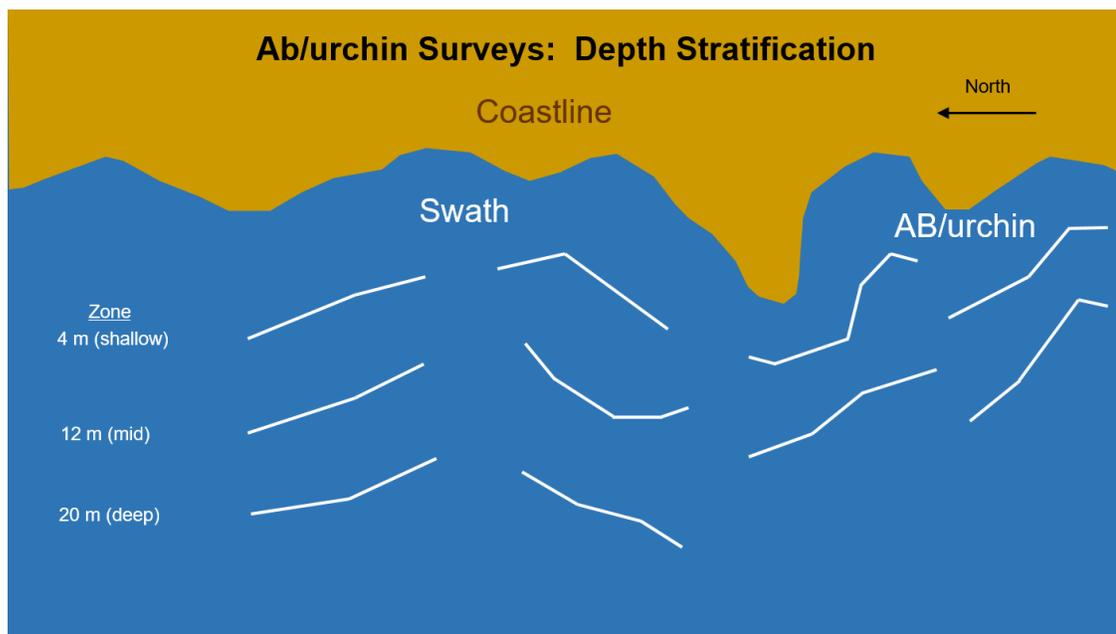
- Mattison, J. E., et al. "Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest." *Marine Biology* 39.1 (1976): 25-30.
- Morse, A. N. C. and D. E. Morse (1984) - Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surfaces of crustose red algae. *J. expl mar. Bioi. Ecol.* 75(3): 191-215.
- Morse, D. E., Hooker, N., Duncan, H. and L.1Ensen (1979) - Y-aminobutyric acid, a neurotransmitter, induces plank Downloaded by [75.111.62.132] at 11:07 27 February 2016 144 South African Journal of Marine Science 22 2000 tonic abalone larvae to settle and begin metamorphosis. *Science*. N.Y. 204: 407-410.
- Neuman, Melissa, Brian Tissot, and Glenn Vanblaricom. "Overall status and threats assessment of black abalone (*Haliotis cracherodii* Leach, 1814) populations in California." *Journal of Shellfish Research* 29.3 (2010): 577-586.
- O'Leary, J. K., & McClanahan, T. R. (2010). Trophic cascades result in large-scale coralline algae loss through differential grazer effects. *Ecology*, 91(12), 3584-3597.
- Pinnegar, J. K., Polunin, N. V. C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M. L., & Pipitone, C. (2000). Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation*, 27(02), 179-200.

- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rogers-Bennett, Laura, Brian L. Allen, and Gary E. Davis. "Measuring abalone (*Haliotis* spp.) recruitment in California to examine recruitment overfishing and recovery criteria." *Journal of Shellfish Research* 23.4 (2004).
- Shears, N. T., Kushner, D. J., Katz, S. L., & Gaines, S. D. (2012). Reconciling conflict between the direct and indirect effects of marine reserve protection. *Environmental Conservation*, 39(03), 225-236.
- Strain, Elisabeth MA, Craig R. Johnson, and Russell J. Thomson. "Effects of a range-expanding sea urchin on behaviour of commercially fished abalone." *PloS one* 8.9 (2013): e73477.
- Villamor, A., & Becerro, M. A. (2012). Species, trophic, and functional diversity in marine protected and non-protected areas. *Journal of Sea Research*, 73, 109-116.
- Watson, D., Anderson, M., Kendrick, G., Nardi, K., & Harvey, E. (2009). Effects of protection from fishing on the lengths of targeted and non-targeted fish species at the Houtman Abrolhos Islands, Western Australia.
- Won, Nam-II, et al. "Trophic structure in natural habitats of the abalone *Haliotis discus hannai* with distinct algal vegetation of kelp and crustose coralline algae: implication of ontogenetic niche shifts." *Fisheries science* 79.1 (2013): 87-97.

APPENDICES



Appendix A. Layout of swath transects at associated depth zones within a site.



Appendix B. Layout of size transects in association with swath surveys at a given cell.

SITE:		CELL: 1 2 3			TRANSECT #: 1 2	
TARG. DEPTH: 4 12 20		ACT. DEPTH:			HEADING OUT:	
OBSERVER:		BUDDY:			DATE:	
All spp. > 2.5 cm dia		0-10 m	10-20 m	20-30 m		
S e a s t a r s	<i>Pateria miniata</i> (Bat Star)					
	<i>Dermasterias imbricata</i> (Leather Star)					
	<i>Henricia leviuscula</i> (Blood Star)					
	<i>Orthasterias koehleri</i> (Rainbow Star)					
	<i>Solaster dawsoni</i>					
	<i>Solaster stimpsoni</i> striped					
	<i>Pisaster brevispinus</i> (Pink Thick Large)					
	<i>Pisaster giganteus</i> (Circles of Blue)					
	<i>Pisaster ochraceus</i> (Central Pentagon)					
	<i>Pycnopodia helianthoid</i> Sunflower					
A m e n o n i a s	<i>Urticina lofotensis</i> (Spotted Column)					
	<i>Urticina crassicornis</i> red-green stripe					
	<i>Urticina piscivora</i> (No Spots)					
	Metridium species (Normally All White)					
	<i>Anthoplura sola</i> red bands, solitary					
U r c h i n s	<i>Strongylocentrotus purpuratus</i> Purple Urchin					
	<i>Strongylocentrotus franciscanu</i> Red Urchin					
C u c u m b i a	<i>Cucumaria miniata</i> (Orange Filter)					
	<i>Parastichopus californicus</i> (Large Spines)					
C r a b s	Cancer spp (Classic Crab Shape)					
	<i>Pugettia producta</i> Keel Crab					
	<i>Pugettia richii</i> (Carapace "Spines")					
	<i>L. crispatus</i> / <i>S. acutifrons</i> Clypeus "Decorations"					
	<i>Mimulus foliatus</i> (Squarish Carapace, Red)					
M o l l u s c a	<i>Cryptochiton stelleri</i> Gumbood Chiton					
	<i>Crassidoma giganteum</i> Rock Scallop					
	<i>Haliotis</i> - ID species Abalone					
	<i>Diodora aspera</i> key hole limpet					
	<i>Lithopoma gibberosum</i> Red Turban Snail					
	<i>Ceratostoma foliatum</i> Leaf Hornmouth					
O t h e r	<i>Tetuya aurantia</i> Puff Ball					
	<i>Styela montereyensis</i> Stalked Turiccate					
	<i>Balanus nubilus</i>					
Other Urticina		<i>Anth. xanthogrammica</i>	<i>Craniella</i> (gray puffball)			
Cancer magister		<i>Lopholithodes</i> sp.	<i>Stylasterias forreri</i> (velcro star)			

Appendix C. Swath data sheet.

SWATH ALGAE DATASHEET (NCSR rev. 6/5/14)

SITE: _____ DATE: _____ HEADING OUT: _____ OBSERVER: _____
 TRANSECT #: 1 | 2 ACT. DEPTH: _____ BUDDY: _____
 CELL: 1 2 3 TARG. DEPTH: 4 | 12 | 20

>30 cm stipe length	0-10 m	10-20 m	20-30 m
Nereocystis			
Macrocystis			
Cytoseira > 6 cm dia)			
Pterygophora			
Laminaria setchellii			
Costaria costata			
Alaria marginata			
Pteurophycus sp.			
Undaria pinnatifida			

SITE: _____ DATE: _____ HEADING OUT: _____ OBSERVER: _____
 TRANSECT #: 1 | 2 ACT. DEPTH: _____ BUDDY: _____
 CELL: 1 2 3 TARG. DEPTH: 4 | 12 | 20

>30 cm stipe length	0-10 m	10-20 m	20-30 m
Nereocystis			
Macrocystis			
Cytoseira > 6 cm dia)			
Pterygophora			
Laminaria setchellii			
Costaria costata			
Alaria marginata			
Pteurophycus sp.			
Undaria pinnatifida			

Appendix D. Swath algae data sheet

NCSR AB-URCHIN / HSU / rev. June 2014														
SITE:		CELL: 1 2 3				TARG. DEPTH: 4 12				ACT. DEPTH:				
TRANSECT #: 3 4		DATE:				BUDDY:				HEADING OUT:				
OBSERVER:														
		0-10 m				10-20 m				20-30 m				
RED URCHIN														
PURPLE URCHIN														
RED ABALONE														
PINTO ABALONE														
FLAT ABALONE														

Appendix E. Abalone/urchin size data

Algae

Observer: Site: Cell: 1 2 3 Date: Heading:
 Buddy: Targ. Depth: 4 12 Act. depth: Transect#: 1 2

>30 cm stipe length	0-10m	10-20m	20-30m																											
Nereocystis																														
Macrocystis																														
Cystoseira (>6cm dia)																														
Pterygophora																														
Laminaria setchellii																														
Costaria costata																														
Alaria marginata																														
Pleurophycus sp.																														
<i>Pycnopodia Helianthoides</i>																														
UPC																														
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
Red Algae = R				Brown Algae = B				Drift Algae = D				Crustose Coralline algae = C				Articulated Coralline Algae = A				Invert = I		Bare Rock = X		Bare Sand = S						
Off Transect Red Abalone																														
Start Time:				End Time:				Depth range:																						
Hidden abalone = H				Twisting abalone = T				Lollipop abalone = L				Dead Algae = D				Dead Algae with abalone = LD														

Appendix F. Modified swath algae data sheet for 2016.

Appendix G. Site Descriptions

Caspar

Caspar cell 1 is in the waters off Jug Handle State Park on the south side of the cove to the south of the trailhead at the Jug Handle parking lot near Highway 1. This cell is open to all recreational and commercial take of marine life and is exposed to prevailing northwest swells with 12 m and 4 m depth zones to the southeast of the 20 m drop point. Much of the bottom is bedrock covered by boulder with some high relief pinnacles and slopes to depths greater than 20 m near shore. Caspar cell 2 is south of Caspar cell 1 in the waters of the north side of Caspar cove, south of Pacifica Drive. This cell is open to all recreational and commercial take of marine life and is leeward of prevailing northwest swells with 12 m and 4 m depth zones to the northeast of the 20 m drop point. Much of the bottom is boulder and is devoid of high relief pinnacles and slopes more gradually than Caspar cell 1 to depths greater than 20 m near center of the cove. Caspar cell 3 is south of Caspar cell 2 in the waters south of Caspar cove, west of South Caspar Drive between Headlands Drive and Otter Point Circle. This cell is within the Caspar Sea Urchin Closure Area and is open to recreational and commercial take of marine life except for the commercial take of sea urchins in water shallower than 120 ft. The 20 m depth zone is exposed to prevailing northwest swells with the 4m depth zone in the protected cove to the east. The 12 m depth zone is in the connecting boulder and cobble covered wash channel created by exposed rocks. The cell slopes to depths greater than 20m near shore similar to Caspar cell 1.

Point Cabrillo

Point Cabrillo cell 1 is south of Caspar cell 3 in the waters of Frolic Cove, west of Greenling Circle. This cell is within the current boundary of Point Cabrillo SMR established in 2012 and is closed to all recreational and commercial take of marine life and rides the east/west boundary line of the preexisting Caspar Sea Urchin Closer Area established in 1991 and Point Cabrillo SMCA established in 1975. This cell is leeward of prevailing northwest swells with 12 m and 4 m depth zones in the cove to the southeast of the 20 m drop point. Much of the bottom is boulder and bedrock with a gradually sloping bottom. Point Cabrillo cell 2 is south of Point Cabrillo cell 1 in the waters northwest of Point Cabrillo light station off Lighthouse Road. This cell is within the current boundary of Point Cabrillo SMR and is closed to all recreational and commercial take of marine life. It is exposed to prevailing northwest swells with 12 m and 4 m depth zones in the channel to the south of the 20 m drop point. Much of the bottom is bedrock covered by boulder with high relief walls along exposed rocks and slopes to depths greater than 20 m near shore. Point Cabrillo cell 3 is south of Point Cabrillo cell 2 in the waters southwest of the south trail in Point Cabrillo Light Station State Historic Park. This cell is within the current boundary of Point Cabrillo SMR and is closed to all recreational and commercial take of marine life and the 20 m and 12 m depth zones are exposed to prevailing northwest swells with the 4 m depth zones in the protected cove on the leeward side of a wash rock to the east of the 20 m drop point. Much of the bottom is bedrock covered by

boulder with high relief walls along exposed and submerged rocks and slopes to depths greater than 20 m near shore.

Russian Gulch

Russian Gulch cell 1 is south of Point Cabrillo Cell 3 in the waters west of Overton Drive. This cell is open to all recreational and commercial take of marine life and is exposed to a prevailing northwest swells with 4 m depth zones to the east of the 12 m drop point. Much of the bottom is bedrock covered by boulder with some coble patches and a few high relief pinnacles. The cell slopes to depths greater than 20 m near shore. Russian Gulch cell 2 is south of Russian Gulch cell 1 in the waters northwest of the northwest point of the Russian Gulch SMCA, west of Cypress Drive. This cell is open to all recreational and commercial take of marine life and is exposed to prevailing northwest swells with the 4 m depth zones on a plateau to the east of the 12 m drop point that lies on the upper edge of a vertical subsurface wall. The bottom is bedrock and drops off quickly to depths greater than 20 m near shore. (Figure 1)

Appendix H. Cell position at the 20 m depth strata

Cells from north to south	Latitude	Longitude
Caspar 1	39.22.445"N	123.49.607"W
Caspar 2	39.21.880"N	123.49.417"W
Caspar 3	39.21.561"N	123.49.662"W
Pt. Cabrillo 1	39.21.337"N	123.49.636"W
Pt. Cabrillo 2	39 21.030"N	123 49.665"W
Pt. Cabrillo 3	39.20.667"N	123.49.530"W
Russian Gulch 1	39.20.477"N	123.49.230"W
Russian Gulch 2	39.19.904"N	123.49.050"W