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Lottia Gigantea Size and Density Differences in Rocky Intertidal Communities near Monterey Bay, California

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LOTTIA GIGANTEA SIZE AND DENSITY DIFFERENCES IN ROCKY INTERTIDAL COMMUNITIES NEAR MONTEREY BAY, CALIFORNIA

A Thesis
Presented to the
Faculty of the
Division of Science and Environmental Policy
California State University Monterey Bay

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
in
Coastal and Watershed Science and Policy

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by
Shae Mitchell
Spring 2011

CALIFORNIA STATE UNIVERSITY MONTEREY BAY

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LOTTIA GIGANTEA SIZE AND DENSITY DIFFERENCES IN ROCKY
INTERTIDAL COMMUNITIES NEAR MONTEREY BAY, CALIFORNIA

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ABSTRACT

Lottia gigantea Size and Density Differences in Rocky Intertidal
Communities Near Monterey Bay, California
by
Shae Mitchell
Master of Science in Coastal and Watershed Science and Policy
California State University Monterey Bay, 2011

Owl limpets (*Lottia gigantea*) are ecologically important grazers that live on exposed rocky intertidal shores of the west coast of North America. *Lottia gigantea* are a major competitor for space and are considered a co-competitive dominant with California mussels (*Mytilus californianus*) in mid to high rocky intertidal areas from Baja California to Washington. In recent years *Lottia gigantea* have been impacted by human access via visitation and harvesting. Owl limpet size and density have been correlated with human access, where higher access leads to reduced size and density.

Human visitation may have different effects on owl limpets in central California. For instance, human activities may directly and indirectly alter owl limpet population growth via trampling of limpets and other species. Trampling may also open space in rocky intertidal areas by clearing macroalgae. If space is not a limiting factor in owl limpet populations, then there should be a decrease in intraspecific competition for space, in turn leading to density dependent population growth.

The goal of this study was to investigate the relationship between humans and their potential impact on owl limpet populations. The underlying objectives were to determine any differences in owl limpet size, density, and species diversity associated with differing levels of human access. Site-level differences of accessibility were used to infer how owl limpet density and size distribution have been affected by human access. Sampling was conducted at four sites between Point Lobos, California and southern Monterey Bay, California. Two sites had high human access while the remaining two sites were categorized as having low human access. From July 2009 to September 2010 owl limpets in 10 permanent 1 m^2 square plots were counted and measured at each of the four sites. Species diversity and visitor use were also measured during the study.

A mixed effects model was used to analyze owl limpet size data while a negative binomial general linear model was used to analyze owl limpet density data. Species diversity was calculated from high-resolution digital photos. Contrary to previously published findings, this study found owl limpets were larger and less dense in high access sites and smaller and more dense at low access sites. There was also more open rock and lower species diversity at high access sites. Owl limpets are important ecosystem engineers modifying rocky intertidal habitat, which is an important and rare habitat within Monterey Bay National Marine Sanctuary (MBNMS). Therefore, understanding owl limpet dynamics and human access in MBNMS may assist management and conservation of rocky intertidal habitats.

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CHAPTER 1

INTRODUCTION

BACKGROUND

Owl limpets (*Lottia gigantea*) are ecologically important grazers that live on exposed rocky intertidal coasts (Stimson 1970; Wright and Lindberg 1982; Lindberg et al. 1987). *Lottia gigantea* are a major competitor for space and are considered a co-competitive dominant with California mussels, *Mytilus californianus* (Lindberg et al. 1987; Pombo and Escofet 1996; Denny et al. 2006), in mid to high rocky intertidal areas from Baja California to Washington (Abbott and Haderlie 1980; Kido and Murray 2003) where they feed on microalgae patches (Stimson 1970; Wright 1989), typically moving short distances (<0.5 m) when submerged. When owl limpets are removed through predation or harvesting, the abundance of macroalgae in intertidal communities can dramatically increase (Wooton 1992; Lindberg et al. 1998). *Lottia gigantea* also modify rocky intertidal habitat and are therefore considered ecosystem engineers. Owl limpets make modifications by clearing patches around their home scars (Stimson 1970) and adding physical structure since their shells often act as a substrate for other organisms, including smaller limpets (Gutíerrez et al. 2003).

Lottia gigantea also provide important services to humans and coastal ecosystems in the form of provisioning and cultural services (Millenium Ecosystem Assessment 2005; Daily et al. 2009). Provisioning services, such as food for human consumption, are provided by owl limpets since they taste similar to abalone and have been consumed by west coast native populations for thousands of years (Vedder and Norris 1963; Lindberg et al. 1998). Owl limpets may also provide cultural services, which include aesthetic and recreational values associated with humans visiting rocky intertidal habitats. Millions of tourists are attracted to beaches and coasts every year and these areas drive coastal economies (Miller and Auyong 1991). Owl limpets are important species contributing to the biological diversity of the rocky intertidal habitats, and their removal could result in a reduction of aesthetic or recreational value.

HISTORICAL HUMAN IMPACTS

While the ecosystem services provided by *L. gigantea* may be beneficial to humans, owl limpets can be negatively impacted by human activity in rocky intertidal communities (Lindberg et al. 1987; Addessi 1994; Murray et al. 1999; Sagarin et al. 2007; Smith et al. 2008). Rocky intertidal areas are susceptible to human activities such as trampling and harvesting because there is often a lack of enforcement, access is easy, and there is limited education of visitors on regulations and stewardship within the intertidal environment (Murray et al. 1999; Hall et al. 2002; Tenera Environmental 2003; Sagarin et al. 2007). Intertidal communities with high visitation can have more bare rock and fewer species than in areas of low visitation (Brosnan 1994; Fletcher and Flid 1996; Van De Werfhorst and Pearse 2007). Human trampling can also reduce the density and cover of mussel bed communities (Smith and Murray 2005; Smith et al. 2008). Mussel beds are important communities providing food, shelter and space (Smith et al. 2008). One explanation for the decline in owl limpet size in areas of high human visitation is that people are likely to harvest larger individuals for food, which can influence rates of reproduction since owl limpets are protandrous (born male but switch to female with increasing age and size) and larger individuals have a higher reproductive output (Wright and Lindberg 1982; Lindberg et al. 1987). During low tides, owl limpets remain in one spot, often in easy to view spaces such as large vertical rock faces, making them easily accessible (Denny and Blanchette 2000; Miller et al. 2009). The removal of large herbivores, such as owl limpets, can in turn increase the abundance of macroalgae and can change species structure and composition in intertidal communities (Lindberg et al. 1998; Addessi 1994; Kido and Murray 2003).

Previous studies have shown a negative correlation between the size and density of rocky intertidal invertebrates and human visitation (Addessi 1994; Kido and Murray 2003; Roy et al. 2003; Smith and Murray 2005; Sagarin et al. 2007; Smith et al. 2008; Ramírez et al. 2009). For example, Addessi (1994) measured the density of 10 invertebrate species on the coast of San Diego, California and found that all species had lower density at sites that were highly visited. Similarly, Kido and Murray (2003) observed size structures of *L. gigantea* at sites with differing human visitation and found mean shell length was negatively correlated with number of visitors and collectors, suggesting collectors remove larger limpets at sites in southern California. Roy et al. (2003) found similar results when they compared museum samples of rocky intertidal gastropods to samples from mainland southern California sites, indicating that human visitation and activities have led to decreased body sizes of the gastropods including *L. gigantea*. Smith and Murray (2005) experimented with trampling and collection of mussels (*M. californianus*) from mussel bed communities and found that human visitation and collecting can reduce mussel cover, density and size. Similarly, Smith et al. (2008) found smaller mussel populations at highly visited sites than at rarely visited sites. Sagarin et al. (2007) conducted an analogous study comparing owl limpets at sites with differing human visitation and found larger limpets at low vulnerability sites versus high vulnerability sites in southern California. Ramírez et al. (2009) studied the size and density of five different gastropods at sites with varying vulnerability to human activities and reported both smaller sizes (for 4 of 5 species) and lower densities at the higher vulnerability sites.

CURRENT POLICIES IN MONTEREY BAY

Marine Protected Areas (MPAs) are spatial management tools that provide protection to marine resources in a specified area. The biological goal of MPAs is to increase size and density of exploited species, conserve biological diversity, and protect species of particular interest (Palumbi 2001). MPAs are one way to limit harvesting and increase protection to rocky intertidal areas (Smith et al. 2008). The establishment of MPAs can limit the number of human activities, depending on the management goals. In California there are three common types of marine MPAs implemented by the state: reserves, conservation areas, and parks. For example, in California state marine reserves "it is unlawful to injure, damage, take or possess any living, geological or cultural marine resource, except under a permit or specific authorization from the managing agency for research, restoration or monitoring purposes" (McArdle 1997). By contrast, in state marine conservation areas "it is unlawful to injure, damage, take or posses any specified living, geological or cultural marine resources for certain commercial, recreational, or a combination of commercial and recreational purposes" but "research, education and recreational activities, and certain commercial and recreational harvest of marine resources may be permitted" (McArdle 1997). In addition to state MPAs, the Federal government also has MPAs in central California. National Marine Sanctuaries are Federal MPAs, allowing most human activities (e.g., commercial and recreational fishing, tourism) while restricting a few, such as oil drilling, mineral exploration and dumping.

Harvesting of owl limpets is legal in California except in state marine reserves, state marine parks and state marine conservation areas ((14 Cal. Code of Regs. 29.05(b) (1)). There is currently no size limit or bag limit in areas where harvesting of owl limpets is legal ((14 Cal. Code of Regs. 29.05(b) (1)). In Monterey Bay there are multiple regulations protecting rocky intertidal areas from human impacts including those under the Marine Life Protection Act (MLPA) and the National Marine Sanctuaries Act (NMSA). The goals of the MLPA include protecting natural diversity and abundance of marine life and function of marine ecosystems, sustaining, conserving and protecting marine life populations, improving recreational and educational opportunities provided by marine ecosystems with minimal disturbance, and management and enforcement based on scientific findings (State of California 1999). The MLPA's goals are implemented and enforced by the California Department of Fish and Game within established Marine Protected Areas in California. NMSA's goals are to designate areas of special national significance (due to conservation, scientific, recreational or aesthetic qualities, communities of living marine resources or human-use values) as national marine sanctuaries, providing authority for conservation and management of these areas, enhancing public awareness of the marine environment, and promoting scientific research and long-term monitoring of the resources of these marine areas (16 USC 1431 et seq). Monterey Bay National Marine Sanctuary (MBNMS) was designated by Congress through the NMSA in 1992 and spans nearly 300 miles of the central California coastline and encompasses 6,094 square miles of ocean from Marin County to Cambria (NOAA 2008). MBNMS prohibits drilling, dredging and alteration of the habitat within the sanctuary's boundaries, which include the deep ocean to the mean high water mark (Title 15 CFR 922.132).

POTENTIAL HUMAN IMPACTS IN MONTEREY BAY

Human impacts may be different in Monterey Bay since there are more regulations set to protect rocky intertidal communities. Human activity may have a different effect on owl limpet density and size distribution than what has been observed in previous studies in southern California, where harvesting was prevalent (Addessi 1994; Kido and Murray 2003; Roy et al. 2003; Smith and Murray 2005; Sagarin et al. 2007; Smith et al. 2008; Ramírez et al. 2009). Trampling in rocky intertidal ecosystems can decrease macroalgae cover (Brosnan 1994; Fletcher and Flid 1996; Van De Werfhorst and Pearse 2007) and mussel bed cover (Smith and Murray 2005; Smith et al. 2008). Owl limpets are often found within mussel bed habitat (Lindberg et al. 1987; Pombo and Escofet 1996; Kido and Murray 2003; Denny et al. 2006) and therefore a reduction in mussel bed cover could potentially result in an increase in owl limpet size.

Since trampling can decrease the percent cover of both mussel bed and macroalgae, there would likely be more open space associated with rocky intertidal communities susceptible to human activities. If we assume that space is not a limiting factor at sites with high human access but may be limiting at low access sites, intraspecific competition leading to density dependent population growth is possible in owl limpet populations (Creese and Underwood 1982; Dungan 1986; Wright 1989; Boaventura et al. 2003; Huchette et al. 2003). For example, Crease and Underwood (1982) studied size and density of the limpet *Cellana tramoserica* (also a grazer) based on exclusion experiments in which the density of the limpets was altered. They found reduced growth due to intraspecific competition at increased densities. Dungan (1986) also investigated competitive interactions between the limpet, *Collisella strongiona*, the alga, *Ralfsia* spp., and a barnacle *Chthamalus*. In his study Dungan (1986) observed interspecific competition as grazing by the limpet limited algal abundance and indirectly increased barnacle abundance due to opening of space. High percent cover of barnacles in turn led to lower algal and limpet abundance. Wright (1989) investigated density dependent growth in *L. gigantea* by observing the size at which limpets change sex given different densities. Wright (1989) observed that at low densities, limpets were able to grow larger and demonstrated a propensity to change sexes more often than at high densities. Boaventura et al. (2003) studied intraspecific competition in different sizes of the limpet *Patella depressa*. They found that limpets at low densities were larger, had higher growth rates, and on average weighed more. Furthermore they also observed that larger limpets favored areas where limpet population sizes were low due to their higher energetic requirements. Huchette et al. (2003) also observed density dependent growth in the blacklip abalone *Haliotis rubra* as a result of intraspecific competition for preferred shelter space.

Limpet size and density may also be correlated with habitat type in terms of available space (Kido and Murray 2003; Gilman 2005). Kido and Murray (2003) found lower density and higher frequency of larger owl limpets on open-rock surfaces compared with patch habitats within California mussel (*M. californianus*) beds where limpets were confined to their specific grazing patch. Gilman (2005) found that the mean size of the limpet *Collisella scabra* was negatively correlated with its density in all habitats; size was positively correlated with open rock habitat and negatively correlated in turf grass habitat similar to the open rock and mussel bed habitat.

STUDY OBJECTIVES

As the human population grows and visitation rates increase in Monterey County, concerns about the effectiveness of existing regulations to protect the rocky intertidal exist (Murray et al. 1999; Tenera Environmental 2003; Smith et al. 2008). The goal of this study was to investigate the relationship between humans and owl limpet populations within Point Lobos, California and southern Monterey Bay, California. The specific objectives were to determine any differences in owl limpet size, density, and species diversity between sites with either high or low levels of human access. Describing the nature of human-induced impacts on owl limpet populations due to accessibility provides important information to improve resource management of rocky intertidal areas within Monterey Bay National Marine Sanctuary (MBNMS). The data provided by this study may also provide insight on MPA effects on rocky intertidal areas and could be used to improve state regulations. Owl limpets are ecosystem engineers that modify rocky intertidal habitat (Stimson 1970; Gutíerrez et al. 2003). The removal of owl limpets from the rocky intertidal reduces the extent of small-scale patches, and may allow a few species of macroalgae to dominate, ultimately reducing the diversity of the community

(Wooton 1992; Lindberg et al. 1998). Connell (1978) and Sousa (1979) suggested that communities with low disturbance will proceed toward a low-diversity equilibrium, but that intermediate disturbance would result in higher diversity. Loss of owl limpets may indirectly result in a reduction in species diversity or change in species composition in rocky intertidal communities.

RESEARCH QUESTIONS

Postulate I: There is a difference in owl limpet mean size between rocky intertidal areas with high human access versus areas with low human access. Specifically the following pair of hypotheses was tested:

H_0: $S_l = S_h$

H_1: $S_l \neq S_h$

Where, H_0 is the null hypothesis, H_1 is an alternative hypothesis, S is owl limpet size, l is low access, and h is high access.

Postulate II: There is a difference in owl limpet density between rocky intertidal areas with high human access and low human access. Specifically the following pair of hypotheses was tested:

H_0: $D_l = D_h$

H_1: $D_l \neq D_h$

Where, H_0 is the null hypothesis, H_1 is an alternative hypothesis, D is owl limpet density, l is low access, and h is high access.

Postulate III: There is a difference in species diversity between rocky intertidal areas with high human access and low human access. Specifically the following pair of hypotheses was tested:

H_0: $H'_l = H'_h$

H_1: $H'_l \neq H'_h$

Where, H_0 is the null hypothesis, H_1 is an alternative hypothesis, H' is species diversity, l is low access, and h is high access.

Postulate IV: There is a difference in number of visitors between rocky intertidal areas with high human access and low human access. Specifically the following pair of hypotheses was tested:

H_0: $N_l = N_h$

H_1: $N_l \neq N_h$

Where, H_0 is the null hypothesis, H_1 is an alternative hypothesis, N is the number of visitors, l is low access, and h is high access.

Postulate V: Visitors exhibit different behavior between rocky intertidal areas with high human access and low human access. Specifically the following pair of hypotheses was tested:

H_0: $B_a = B_p$

H_1: $B_a \neq B_p$

Where, H_0 is the null hypothesis, H_1 is an alternative hypothesis, B is visitor behavior, a is active behavior, and p is passive behavior.

CHAPTER 2

METHODS

STUDY SITE

This study was conducted at four sites along the west coast of California within Monterey Bay National Marine Sanctuary (MBNMS). All sites were categorized as having high or low access, which was determined based on the amount of human visitation and accessibility to the sites. Low access sites have both low visitation and limited public access, whereas high access sites have both high visitation and extensive public access. Two sites were located in southern Monterey Bay (north sites) and two sites were located at Point Lobos State Natural Reserve (south sites). The northern and southern sites each consisted of one high access and one low access site. The northern sites were Hopkins Marine Life Refuge (low access) (36°37'N, 121°54'W) and Lovers Point (high access) (36°37'N, 121°54'W) while the southern sites were Sea Lion Point (low access) (36°31'N, 121°57'W) and Sand Hill Cove (high access) (36°30'N, 121°56'W) (Figure 1). The intertidal zone at the northern sites consists of granodiorite rock formations with steep walls and tidepools at the base leading toward the ocean. The intertidal zone at the south sites consists of sandstone benches that extend toward the ocean. At both north and south sites, the intertidal zones can be categorized by barnacles (*Balanus glandula*) and red algae (*Endocladia muricata*) and (*Mastocarpus* spp.) in the high intertidal zone, California mussels (*M. californianus*) in the mid-intertidal zone, and surfgrass (*Phyllospadix* spp.) in the low intertidal zone. Tides in Monterey Bay area are mixed semidiurnal with a maximum amplitude of 2.5 meters.

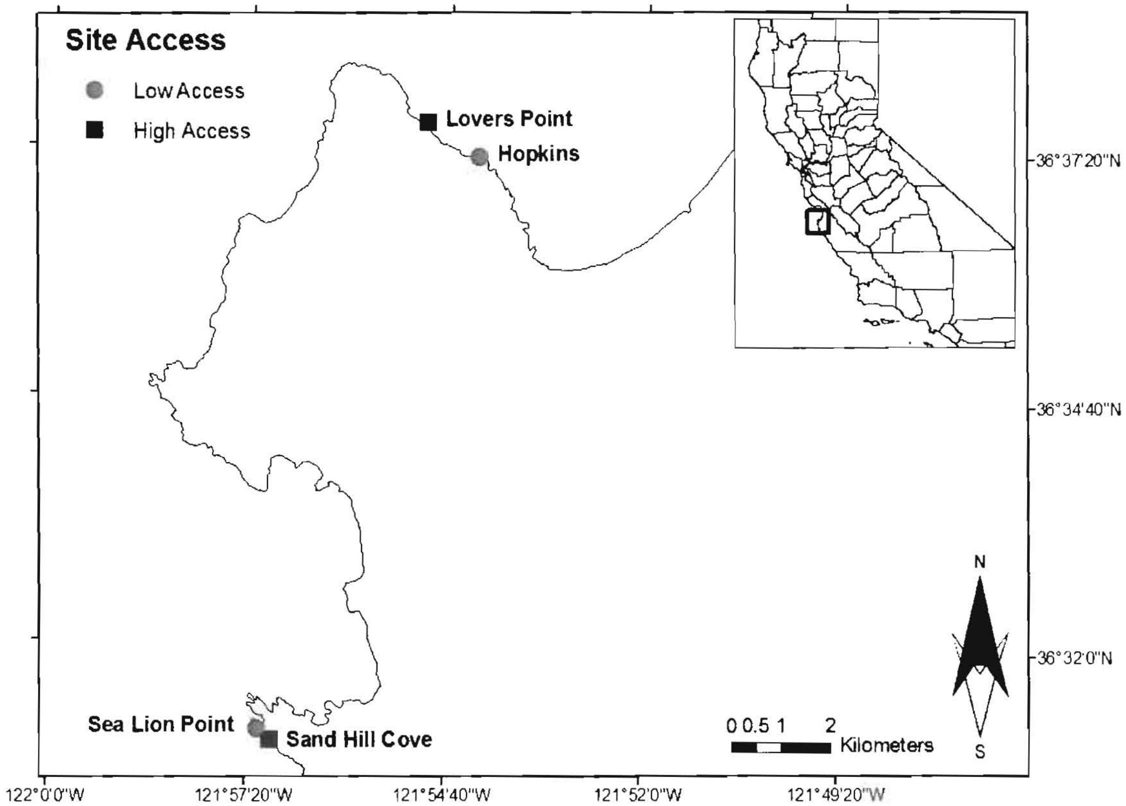


Figure 1: Site map showing all four study sites with level of human access (high or low).

Site pairs (north or south) were chosen based on their close proximity to each other as well as their similar oceanographic conditions. Sites with low access were categorized by barriers, steep cliffs, gates, and/or legal enforcement (Sagarin et al. 2007). Sites with high access lacked barriers and were in close proximity to other recreational areas or urban areas, trails or parking lots (Sagarin et al. 2007). All sites are associated with a marine protected area (MPA), specifically State Marine Reserves (SMRs) (Table 1). SMRs are a type of no-take MPA, where no commercial or recreational take of any species is allowed (McArdle 1997). Owl limpets are considered a no-take species in all study sites as they are within SMRs ((14 Cal. Code of Regs. 29.05(b)(1)).

Table 1: Study site characteristics.

Study Site	Site Pair (North/South)	Access (low/high)[1]	Protection	Dominant Habitat Type[2]	Latitude (N) Longitude (W)	Aspect	Angle	Geologic Substrate
Hopkins	North	Low	Lovers Point SMR- no take of any species, gated-access for research only	Open Rock / Mussel Bed	36N 37' 8.15" 121W 54' 18.88"	360°N	Vertical Rock Wall	Granodiorite
Lovers Point	North	High	Lovers Point SMR- no take of any species, close to parking lot, open to public with stairs, tourist attraction	Open Rock	36N 37' 6.22" 121W 54' 58.61"	350°N	Vertical Rock Wall	Granodiorite
Sea Lion Point	South	Low	Point Lobos SMR- no take of any species, no public access, research only	Mussel Bed	36N 31' 4.07" 121W 57' 11.17"	87°E	Horizontal Surface	Sandstone
Sand Hill Cove	South	High	Point Lobos SMR- no take of any species, close to parking lot and trail, open to public	Open Rock/ Mussel Bed	36N 30' 5.91" 121W 56' 55.09"	268°W	Horizontal Surface and Vertical Rock Wall	Sandstone

[1] Access is characterized by both amount of human visitation and accessibility to each site. Low access sites have low visitation and limited public access, while high access sites have higher visitation and extensive public access.

[2] Dominant habitat types as described in Kido and Murray (2003).

SAMPLING DESIGN

OWL LIMPET SIZE AND DENSITY

In order to determine if there were significant differences in owl limpet size and density between low and high access sites, owl limpet surveys were conducted. Surveys were conducted at all four study sites (Hopkins, Lovers Point, Sea Lion Point, and Sand Hill Cove). The sites were chosen based on the presence of owl limpets in the mid to high rocky intertidal zone and the associated human access. The study duration was from July 2009 through July 2010; data from Lovers Point were collected between November 2009 and October 2010. Data were collected at all sites during spring, summer and fall seasons during low tide sets. At each site, fixed benchmarks (permanent markers) consisting of metal bolts were placed in areas that were level and slightly above the survey sites, to estimate the relative position of each plot relative to Mean Lower Low Water (MLLW). The bolts remained at each site for the extent of the study. A TopCon GTS 230-W Wireless Total Station was placed over the benchmark at the start of each survey and used to measure distance in meters from Mean Lower Low Water (MLLW) to ensure measurements were being collected at similar tidal heights.

At each site, ten one-meter square fixed plots were sampled. Plots were selected based on the presence of owl limpets. The plots were marked by a center bolt to demarcate the center of the grazing patch along a transect of 15 meters (15 meters was the maximum extent of owl limpet habitat at all sites). The non-overlapping plots were separated by at least one meter from center bolt to center bolt and within a ±1 meter vertical distance from center bolt to center bolt to reduce differences due to distance from MLLW (Figure 2).

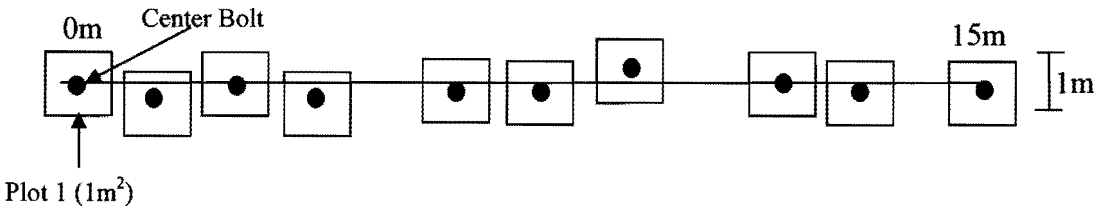


Figure 2: Sampling design, 15 meter transect with ten 1 meter square plots.

Permanent stainless steel bolts marked the beginning and end of each transect. All bolt positions were recorded using a hand-held GPS unit to determine the latitude and longitude. A TopCon Total Station (surveyor) was also used to determine the distance from MLLW for every center bolt. The Total Station provides data in the form of x, y, and z coordinates. These data can be put into ESRI® ArcGIS to map the exact location of each plot relative to MLLW to ensure plots were at similar tidal heights across sites to reduce confounding factors such as variation in immersion times. In order to estimate if limpets were moving between plots, owl limpets were tagged *in situ* with a 2 mm numbered plastic Bee Tag (beeworks.com) following methods in Stewart (2007) and using Zap Cyanoacrylate glue as the adhesive. The tags were glued on the owl limpet's shell just beneath the apex, but varied in location based on how much of the limpet was exposed from rock crevices. The impact of tags on owl limpet predation and health is unknown. The tags can last for months to years before detaching from the limpet's shell (Stewart 2007). Each month, owl limpets in each plot were counted and measured using calipers to the nearest millimeter of shell length along the sagittal plane. Owl limpets <25 mm in sagittal length were not recorded due to difficulty in distinguishing them from other, smaller limpet species. These exclusions follow procedures set by LiMPETS (Long-term Monitoring Program and Experiential Training for Students) (http://limpetsmonitoring.org), a program within MBNMS. Measurements of each limpet's distance relative to MLLW were recorded using the Total Station for every tagged owl limpet.

SPECIES DIVERSITY

Digital photos using were taken of every plot using a Nikon D40X 12 Megapixel Digital Camera in order to calculate species diversity. Digital photos were taken of each plot four times at various intervals during the 13-month study, generating a total of 160 photos. Photos were taken at different times of the year to account for seasonal changes in the composition of the benthic community in each plot (Table 2).

Table 2: Photo plot sampling calendar, sites per month. Months of December and January were not sampled due to high swells.

Month	Sites			
Fall 2009 (Jul-Nov)	Lovers Point	Hopkins	Sea Lion Point	Sand Hill Cove
Winter 2010 (Feb-Mar)	Lovers Point	Hopkins	Sea Lion Point	Sand Hill Cove
Spring 2010 (Apr-May)	Lovers Point	Hopkins	Sea Lion Point	Sand Hill Cove
Summer 2010 (Jul-Sep)	Lovers Point	Hopkins	Sea Lion Point	Sand Hill Cove

The photos were taken 1.7 meters above (perpendicular to) the plot following methods from Blakeway et al. (2004) and Robles et al. (2010). The photos from each plot were georeferenced in ESRI® ArcMap using the georeferencing tool and associated x, y, and z points from the total station. Once the photos were georeferenced, a 1 m^2 grid with cells scaled to 0.043 meters (average limpet size) was placed over each photo (Figure 3).

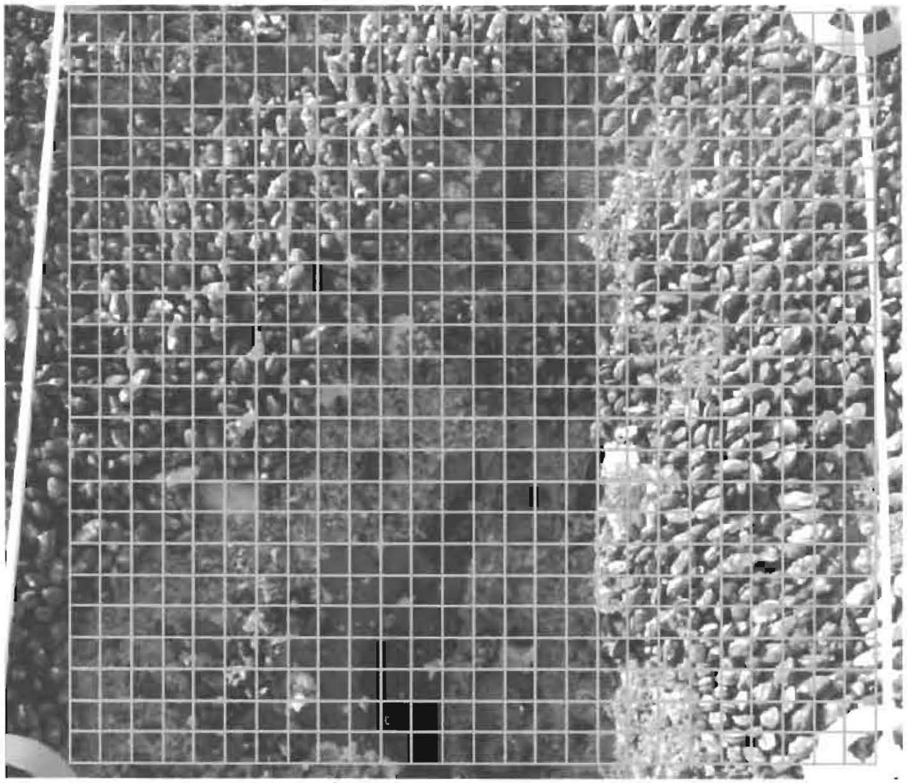


Figure 3: Example of a 1 m^2 photo plot at Sea Lion Point, which has been georeferenced in ESRI® ArcMap using the georeferencing tool with a grid overlay. Cells were 0.043 meters (average limpet size) on each side.

In each photo, species were assigned to each cell in the grid within the attribute table in ArcMap. Numeric codes were assigned to each species and used in the attribute table. Since the attribute table in ArcMap allows no more than one value per cell, the code for a species occupying ≥50 percent of the cell was assigned. Species diversity was classified only in a two-dimensional surface area of each photo. In order to minimize scoring discrepancies, five 0.25 m^2 quadrats encompassing similar species as in the photo plots were ground-truthed in the field by marking each species with a piece of colored tape corresponding to the species' name. The quadrats were then photographed without the colored tape and categorized in ArcMap the same way as the photo plots. The error of categorizing species was less than five percent. Previous studies have shown no significant difference in determining species percent cover using digital photos versus field methods (Dethier et al. 2003; Pech et al. 2004; Drummond and Connell 2005). Estimates of percent cover using digital photos have benefits including serving as a historical record and being more time efficient when weather or tides could be time limiting in the field (Whorff and Griffing 1992; Drummond and Connell 2005). Species diversity is useful to know because it may help to explain variation in limpet size and density differences or conversely how variation in limpet size and density may explain variation in intertidal species diversity.

The Shannon-Wiener Diversity Index (Shannon and Weaver 1963) was used to calculate species diversity for each photo. This diversity index was chosen because of its usefulness for determining species diversity within a community and its use in related studies (Seapy and Littler 1982; Gray 2000).

The following equation was used to determine species diversity:

$$H' = -\sum_{i=1}^{n} p_i \ln p_i$$

where H' is the maximum diversity (Shannon-Wiener Diversity Index), n is the number of species, and p_i is the relative proportion of each species.

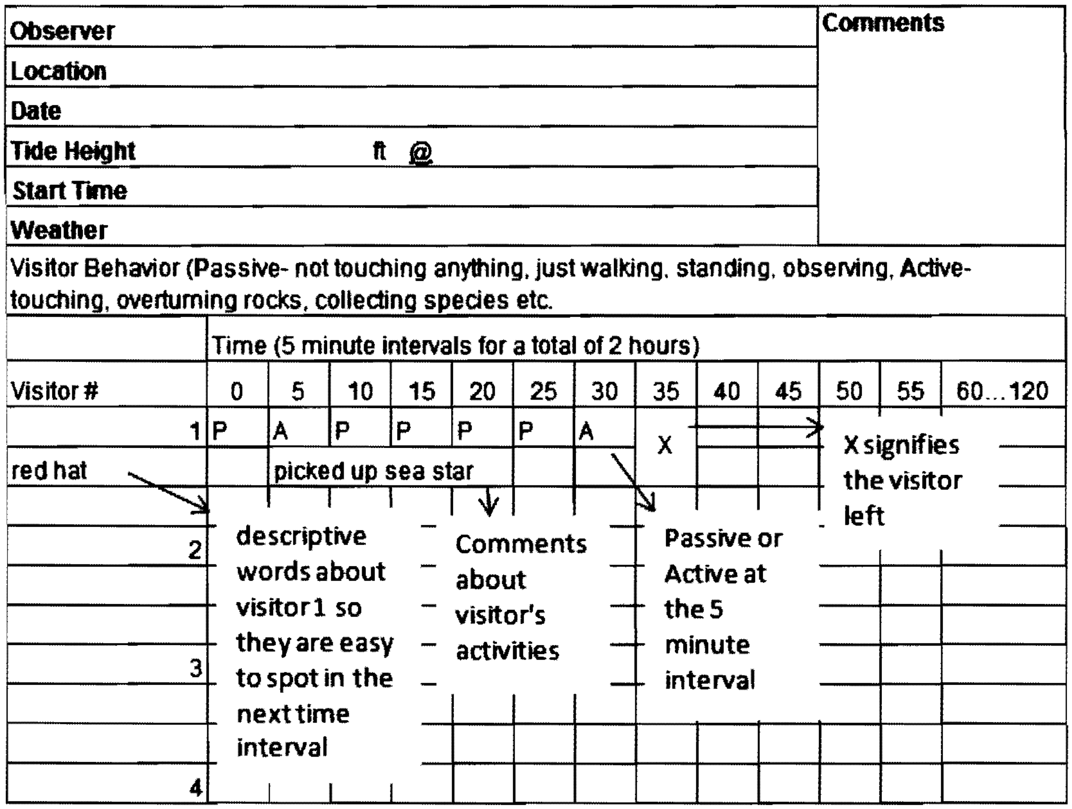
In each photo, the owl limpet's grazing patch accounted for a percentage of the total photo area. In order to understand the relationship between grazing patch size and owl limpet size and density, grazing patch size was also categorized for each photo only when the presence of an owl limpet could be associated with the open rock area. Other open rock lacking an associated owl limpet was excluded from the grazing patch category. Grazing patch size can be used to estimate how limpet size and density vary given differing amounts of available space (Kido and Murray 2003). Grazing patch size differences between sites may also be used to estimate the degree of density dependence within the owl limpet population.

VISITOR USE

Access categories (low or high) for the sites were determined by observing visitors at each site approximately once per month from June 2009 to July 2010 for a total of 11 sample dates (but only 6 dates from November 2009 to September 2010 for Lovers Point because it was added as a site later in the study). The days selected encompassed both weekdays and weekends, including some major holidays where high visitation was expected as well as during times when lower visitation was expected. Nine observations occurred on the last Saturday of the month and two on the last Wednesday in the summer months of July 2009 and August 2009. At Lovers Point, all observations were done on the last Saturday of each month. The last Saturday and last Wednesday were chosen for consistency in observation days for each month. Surveys of visitor behavior coincided with the observations of number of visitors. The observation times were based on the low tide and began one hour before low tide and continued for one hour after low tide for a total of two hours. In the case of the lowest low tide occurring before sunrise, the observations were made during the second low tide of the day since Monterey Bay experiences mixed semidiurnal tides.

Visitor behavior was classified as either passive or active following the methods used by Tenera Environmental (2003). Passive behaviors were those in which visitors were walking, kneeling, and visually observing without touching species or overturning rocks. Active behaviors were those in which visitors were touching or handling species, overturning rocks, or collecting organisms (taking them from the rocky intertidal). If visitors collected species, the species were recorded if identifiable. However, if people were collecting for fishing bait or consumption, they are likely to fish at the lowest tides and were likely underrepresented during this study because the lowest tides are often before sunrise.

Trained volunteers from the Marine Landscape Ecology Lab at California State University Monterey Bay assisted in counting visitors, performing owl limpet surveys, and observing visitor behavior. Observations occurred simultaneously at all sites. Volunteers occupied a location where they could observe the entire site, but not influence visitor activities. For each site, volunteers counted and observed each visitor in terms of behavior. Visitor behavior was recorded every five minutes using the scan sampling method (Altmann 1974) to monitor changes in activities. Volunteers recorded their observations on a datasheet (Figure 4).



Observer
Location
Date
Tide Height ft @
Start Time
Weather
Comments

Visitor Behavior (Passive- not touching anything, just walking, standing, observing, Active- touching, overturning rocks, collecting species etc.

Time (5 minute intervals for a total of 2 hours)

Visitor #	0	5	10	15	20	25	30	35	40	45	50	55	60...120
1	P	A	P	P	P	P	A	X					
red hat		picked up sea star											
2													
3													
4													

descriptive words about visitor 1 so they are easy to spot in the next time interval

Comments about visitor's activities

Passive or Active at the 5 minute interval

X signifies the visitor left

Figure 4: Sample visitor observation sheet showing a 2 hour observation time (120 minutes), behavior categories, and visitor characteristics.

STATISTICAL ANALYSES

OWL LIMPET SIZE

A mixed effects model was used to analyze if there was a difference in owl limpet size between high and low access sites. Individual limpets were the sample unit. Limpet size was the dependent/response variable noted as Size. Access was the fixed effect, either low or high, because there were physical boundaries in which human access was controlled. The random effect was SitePlot, which includes the limpets in a given plot per site (example- limpets in plot 1 of Sea Lion Point) (Figure 5). SitePlot was a random effect because individual limpets were not fully independent of each other within each plot and the effect of the plot was unpredictable. Two pairs of data were analyzed separately, the north pair of sites (Hopkins and Lovers Point) and the south pair of sites (Sea Lion Point, Sand Hill Cove). Size data were analyzed for three separate dates, seasonally. The three dates included September 2009 (Fall), February 2010 (Winter) and July 2010 (Summer). Three dates were chosen in order to obtain seasonal replication.

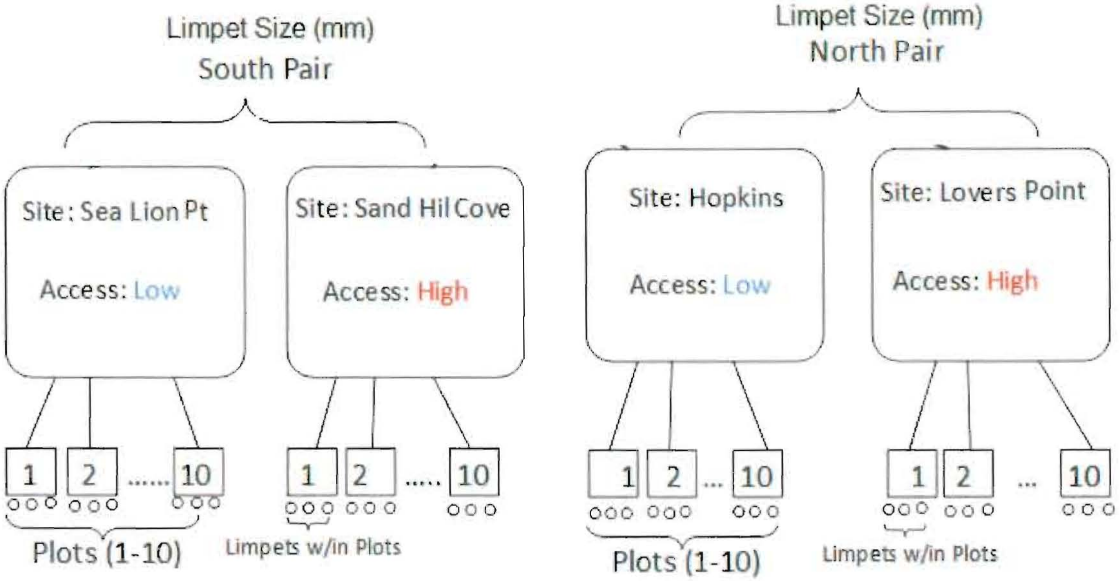


Figure 5: Set-up of the limpet data, size measurements were taken at 2 different site pairs (low and high vulnerability) for 4 total sites, 10 1m^2 plots were sampled, individual limpets were the sample unit.

The linear mixed effects model (as a random intercept model due the idea that the intercept of Size as a function of Access can change per Plot and per Pair) was used to find the difference in owl limpet size between sites with different levels of Access using the following model:

$$S_{i,j,k} = \beta A_i + c_{i,j} + \varepsilon_{i,j,k}$$

where $S_{i,j,k}$ is the size (mm) of the k-th limpet in plot j at site i, A_i is an indicator variable denoting the level of access at site i, β is a fitted coefficient representing the effect of access on limpet size, $c_{i,j}$ is the random effect of membership in plot j at site i, and $\varepsilon_{i,j,k}$ is the residual error, which was assumed to be normally distributed.

The model was run in the statistical program R using the following code:

```
lme_NS<-lme(Size~ Access, random = ~1|SitePlot )
```

OWL LIMPET DENSITY

In order to analyze if there was a difference in owl limpet density between high and low access sites within a region, a negative binomial generalized linear model (GLM) was performed. This model was chosen because the data were count data of positive integers, which could have variance not dependent on the mean. Each plot in a site served as the sample unit for a total of 10 plots. One independent variable, Access was used in the model. Access was the classification of each site, either low or high access based on barriers that allow or restrict human use, which was expected to have the greatest effect. Limpet density was the dependent/response variable noted as density (Figure 6). The two pairs of data were analyzed separately, the north pair of sites (Hopkins and Lovers Point) and the south pair of sites (Sea Lion Point, Sand Hill Cove). Density data were analyzed for three separate dates, seasonally. The three dates included September 2009 (Fall), February 2010 (Winter) and July 2010 (Summer). Three dates were chosen in order to obtain seasonal replication.

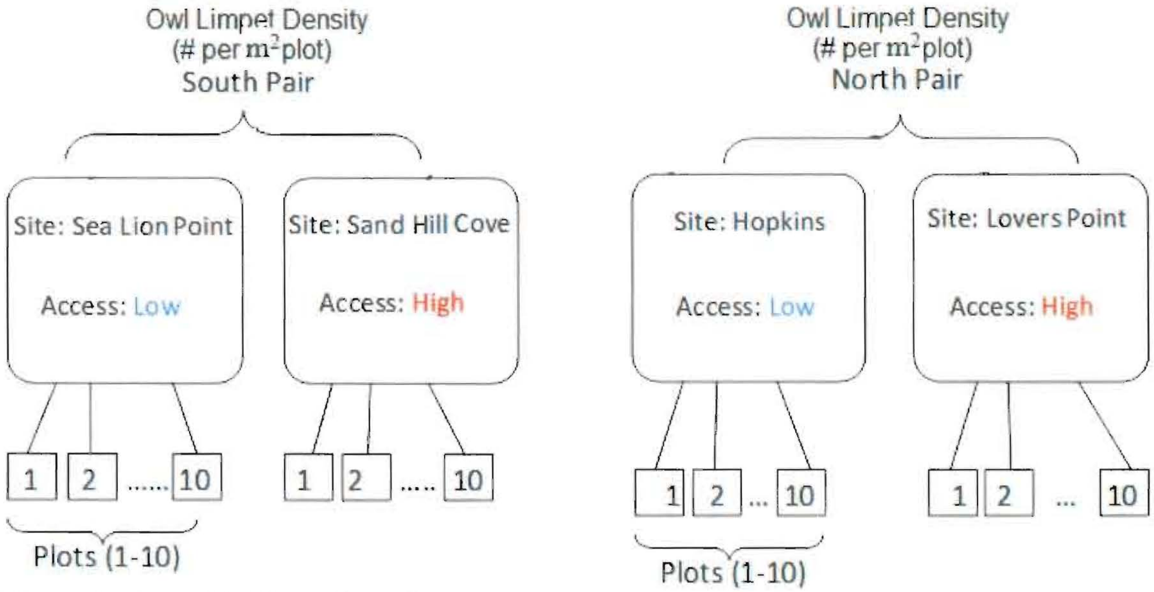


Figure 6: Set-up of the limpet data, density measurements (counts) were taken at 2 different site pairs (low and high access) for 4 total sites, 10 $1m^2$ plots were sampled, plot was the sample unit.

I modeled variation in owl limpet density, $Y_{i,j}$, in plot j at site i, as a function of level of access, $A_{i,j}$ (either low (1) or high (0)), using a linear model with negative-binomial variance:

$$f_{Y_{i,j}}\left(y|\mu_{i,j},\theta\right) = \mathrm{NB}\left(y|\mu_{i,j},\theta\right) = \frac{\Gamma(\theta + y)}{\Gamma(\theta)y!}\frac{{\mu_{i,j}}^{y}\theta^{\theta}}{\left(\mu_{i,j} + \theta\right)^{\theta+y}}$$

$$\mu_{i,j} = \beta_0 + \beta_A A_{i,j}$$

where $\mu_{i,j}$ is a linear model for the mean density, β_0 and β_A are fitted coefficients representing the mean density with access, and the effect of lack of access on the density, $f_{Y_{i,j}}(y|\mu_{i,j},\theta)$ is the probability mass function for $Y_{i,j}$, θ is a dispersion parameter, and $\Gamma(.)$ is the gamma function. This model leads to:

$$\mathrm{E}(Y_{i,j}) = \mu_{i,j}$$

$$\mathrm{var}(Y_{i,j}) = \mu_{i,j} + \mu_{i,j}{}^2/\theta$$

where $\mathrm{E}(Y_{i,j})$ denotes the expected value of $Y_{i,j}$, and $\mathrm{var}(Y_{i,j})$ denotes the variance of $Y_{i,j}$, where the variance increases with the mean and can be larger than the mean (Venables & Ripley 2002).

The model was run in the statistical program R using the following code:

```
Glm_NB<-glm.nb(Density~Access, link= “identity”, data=d)
```

SPECIES DIVERSITY

A two-tailed *t*-test was used to determine if there was a difference in species diversity between high and low access sites. The dependent/response variable was species diversity (H’), the independent variable was access (high or low) and the sampling unit was the plot. A separate *t*-test was analyzed for both the north and south pair of sites in September 2009 (Fall), February 2010 (Winter), and July 2010 (Summer) sites.

The test was run in the statistical program R using the following code:

```
t.test (Diversity~Access)
```

A Wilcoxon (Mann-Whitney’s U) test was used to test for a difference in grazing patch size (m^2) between high and low access sites. Grazing patch was not normally distributed (Shapiro test, $p<0.001$). The dependent/response variable was patch size, the independent variable was access (high or low) and the sampling unit was the plot. A separate Wilcoxon test was analyzed for both the north and south pair of sites in September 2009 (Fall), February 2010 (Winter), and July 2010 (Summer).

The test was run in the statistical program R using the following code:

```
wilcox.test(Patch~Access)
```

A linear regression was used to determine if there was a relationship between species diversity (H') and owl limpet density using data from all study dates from Fall 2009 to Summer 2010.

The test was run in the statistical program R using the following equation:

```
fit<-lm(Density~Diversity)
```

A Wilcoxon test was also used to determine if there was a relationship between grazing patch size and owl limpet size using data from all study dates from Fall 2009 to Summer 2010.

The test was run in the statistical program R using the following equation:

```
wilcox.test(Size~Patch)
```

VISITOR USE

A negative binomial generalized linear model was used to test the assumption that there was a difference in number of visitors between high and low access sites. It was chosen because the data were count data of positive integers, which could have variance not dependent on the mean and data were right skewed. Number of visitors was the dependent/response variable, access was the independent variable and site was the sampling unit. Area (m^2) was estimated for each site from Google Earth™ (Table 3). Visitors were observed throughout the entire site, not only at limpet transect locations, to estimate overall access of the site as a whole.

Table 3: Estimated area (m^2) of sites for visitor observations.

Site	Access	Area (m^2)
Hopkins	Low	2600
Lovers Point	High	2200
Sea Lion Point	Low	1700
Sand Hill Cove	High	4500

Visitor use, $V_{i,k}$, at each site i, was modeled using a linear model with negative binomial variation in the same way as limpet density (see above), with mean visitor use, μ_i, modeled as:

$$\mu_i = \beta_o + \beta_A A_i$$

where β_0 and β_A are fitted coefficients representing mean visitation without access, and the effect of access respectively, and A_i is an indicator variable denoting site access.

The test was run in the statistical program R using the following code:

```
Glm_NB<-glm.nb(Visitors~ Access, link=”identity”, data=d)
```

A Pearson's Chi-square test was used to determine if there is an association between site access and the frequency of observed visitor behaviors. Each visitor was classified as either passive or active based on their behavior over the whole study period. They were classified as active if they spent 10 percent or more of their time in active behavior and passive if they spent less than 10 percent of their time in active behavior. The 10 percent cut off was chosen because it was able to give a cautious estimate of all active behavior as those behaviors are likely more destructive to some extent. The chi-square test was a two by two contingency table with total number of active and passive visitors at high and low access sites during the entire study (Table 4). The expected values were calculated in R.

Table 4: Chi-square contingency table with total number of visitors per behavior.

Access	Passive	Active
High	389	139
Low	26	5

The test was run in the statistical program R using the following code:

```
x2<-chisq.test(C, correct=F)
```

CHAPTER 3

RESULTS

OWL LIMPET SIZE

Limpet size was 7 to 7.7 mm or 13% to 16% greater at Lovers Point (high access) vs. Hopkins (low access) on all three sampling dates (Figure 7, Table 5). Limpet size was 4.6 to 11.8 mm or 10% to 22% greater at Sand Hill Cove (high access) vs. Sea Lion Point (low access) on one of the sampling dates in Fall 2009 (Figure 7, Table 6). The results of the mixed effects model indicate that the factor of 'Access' was statistically significant in both north and south site pairs; since Access is related to human use, it suggests that human activity somehow increased limpet size. The random effect due to occurrence within a specific plot had a standard deviation of between 2.3 and 3.2 mm in north sites and 1.4 to 5.3 mm in south sites (Tables 7 and 8). Since this was of comparable magnitude to the sizes of the fixed effect (Access), it confirms that a mixed effects model was necessary in order to not inflate the apparent size of the fixed effect.

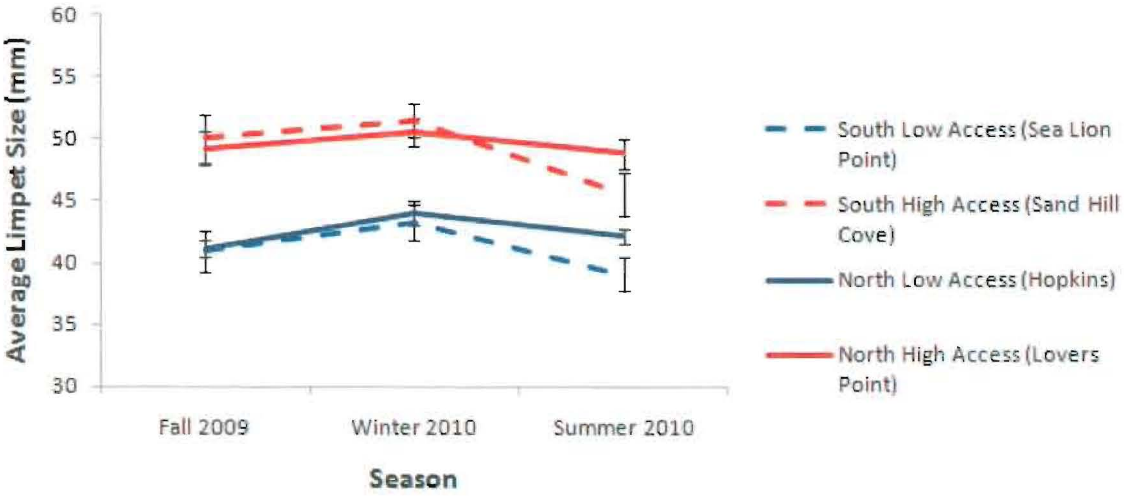


Figure 7: Average limpet size (mm, with standard error) in low (Hopkins and Sea Lion Point) and high (Lovers Point and Sand Hill Cove) access sites over the three study dates from Fall 2009 to Summer 2010.

Table 5: Summary of the mixed effects model results for limpet size in mm with Access as the fixed effect in the north sites (Hopkins and Lovers Point) over the three dates. The Access term refers to low access in reference to high access. In this table owl limpets decreased in size in low access sites.

		Value	Std Error	DF	*T*	*P*	
Fall 2009	(Intercept)	49.09	1.80	175	27.31	5.44E-65	
	Low Access	-7.66	2.15	18	-3.56	2.22E-03	**
Winter 2010	(Intercept)	50.90	1.92	93	26.46	4.50E-45	
	Low Access	-6.95	2.34	17	-2.97	8.53E-03	**
Summer 2010	(Intercept)	48.97	1.75	183	27.93	6.59E-68	
	Low Access	-6.97	1.99	17	-3.51	2.70E-03	**

Significance levels: **P*<0.05, ***P*<0.01, ****P*<0.001

Table 6: Summary of the mixed effects model results for limpet size in mm with Access as the fixed effect in the south sites (Sea Lion Point and Sand Hill Cove) over the three dates. The Access term refers to low access in reference to high access. In this table owl limpets decreased in size in low access sites.

		Value	Std Error	DF	*T*	*P*	
Fall 2009	(Intercept)	50.69	2.75	54	18.46	5.48E-25	
	Low Access	-11.81	3.58	15	-3.29	4.91E-03	**
Winter 2010	(Intercept)	51.62	1.77	52	29.13	7.07E-34	
	Low Access	-8.16	2.39	15	-3.41	3.84E-03	**
Summer 2010	(Intercept)	45.55	1.66	59	27.48	2.55E-35	
	Low Access	-4.66	2.32	15	2.00	4.30E-02	*

Significance levels: **P*<0.05, ***P*<0.01, ****P*<0.001

Table 7: Summary of the mixed effects model results for limpet size in mm of SitePlot, the random effect, in the north sites (Hopkins and Lovers Point) over the three dates. Intercept is the STDEV.

		(Intercept)	Residual
Fall 2009	StdDev SitePlot	3.00	7.90
Winter 2010	StdDev SitePlot	3.23	7.44
Summer 2010	StdDev SitePlot	2.29	7.63

Table 8: Summary of the mixed effects model results for limpet size in mm of SitePlot, the random effect, in the south sites (Sea Lion Point and Sand Hill Cove) over the three dates. Intercept is the STDEV.

		(Intercept)	Residual
Fall 2009	StdDev SitePlot	5.32	9.55
Winter 2010	StdDev SitePlot	2.41	8.27
Summer 2010	StdDev SitePlot	1.37	9.58

Size-frequency histograms depict a higher number of small limpets at the low access sites and fewer large limpets at high access sites for the entire repeated measures dataset (Figure 8). Maximum owl limpet size was 72 mm, found at Sand Hill Cove.

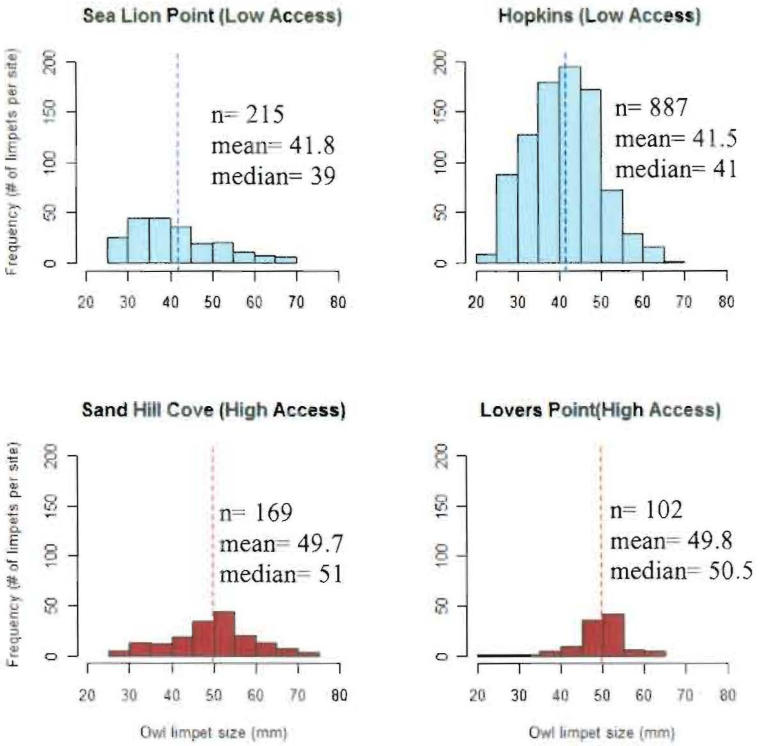


Figure 8: Owl limpet size-frequency histograms per site for the course of the study with mean size displayed as the dashed line. These may not represent individual limpets, but repeated measures of the same limpets during the study.

Q-Q plots verify that the residuals were normally distributed for all three sampling dates for the north and south sites (Figure 9).

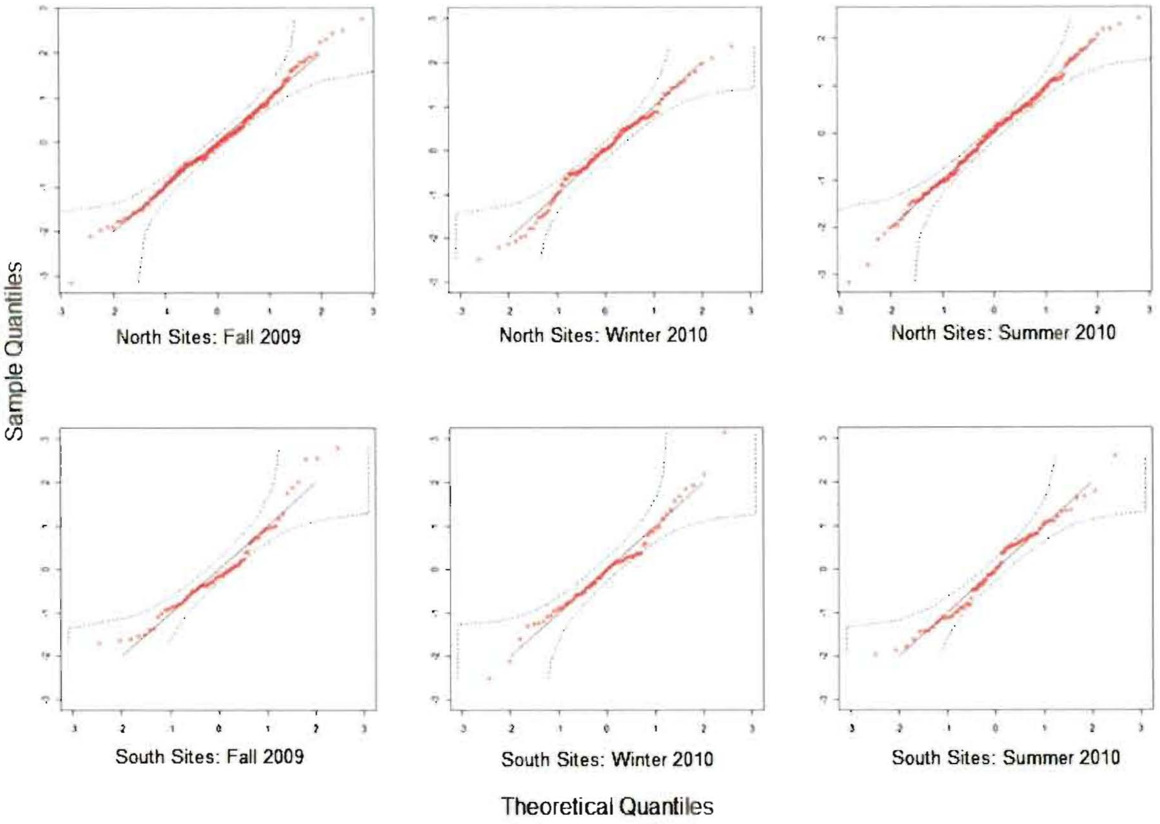
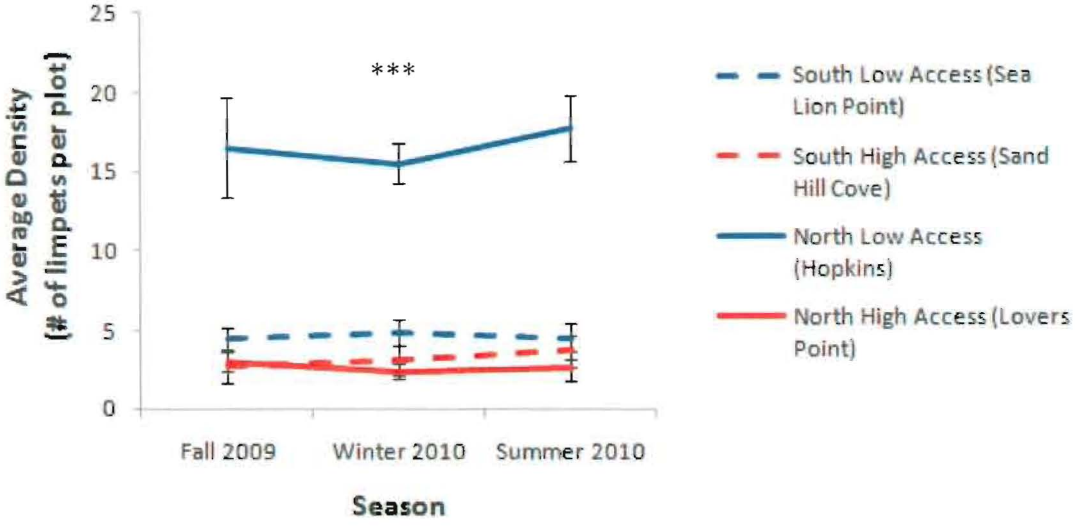


Figure 9: Q-Q plot of residuals for the size data with 95% confidence interval. The dotted lines represent a graphical equivalent of the Kolomogorov-Smirnov test for normality.

OWL LIMPET DENSITY

The results of the negative binomial GLM indicate that there was a statistically significant difference between the low access site (Hopkins), which had on average 13.1 to 15.1 more limpets per m^2 than the high access site (Lovers Point) on all three sampling dates (Figure 10, Table 9). There was not a statistically significant difference between the low access site (Sea Lion Point) and the high access site (Sand Hill Cove) in Fall 2009, however Sea Lion Point had on average 1 to 1.8 more limpets per m^2 than Sand Hill Cove (Figure 10, Table 10).



***$P < 0.001$ **P 0.001-0.02 *P 0.02-0.05

Figure 10: Plot of mean limpet density (number of limpets per m^2) in north (Hopkins and Lovers Point) and south (Sea Lion Point and Sand Hill Cove) sites with standard error bars over the three study dates from Fall 2009 to Summer 2010.

Table 9: Summary of the negative binomial GLM results for limpet density for the north sites (Hopkins and Lovers Point) on the three dates. The Access term refers to low access in reference to high access. In this table owl limpet density increased in low access sites.

		Estimate	Std Error	Z	*P*	
Fall 2009	(Intercept)	3.0	0.72	4.16	3.24E-05	
	Low Access	13.5	2.98	4.53	5.76E-06	***
Winter 2009	(Intercept)	2.4	0.49	4.90	9.64E-07	
	Low Access	13.1	1.34	9.79	<2e-16	***
Summer 2010	(Intercept)	2.6	0.55	4.70	2.63E-06	
	Low Access	15.1	2.06	7.35	2.02E-13	***

Significance levels: *$P<0.05$, **$P<0.01$, ***$P<0.001$

Table 10: Summary of the negative binomial GLM results for limpet density for the south sites (Sea Lion Point and Sand Hill Cove) on the three dates. The Access term refers to low access in reference to high access. In this table owl limpet density increased in low access sites.

		Estimate	Std Error	Z	*P*
Fall 2009	(Intercept)	2.7	0.56	4.83	1.36E-06
	Low Access	1.8	0.94	1.92	5.50E-02
Winter 2009	(Intercept)	3.1	0.60	5.15	2.65E-07
	Low Access	1.8	1.07	1.67	9.58E-02
Summer 2010	(Intercept)	3.7	0.75	4.93	8.27E-07
	Low Access	0.9	1.18	0.72	4.69E-01

Significance levels: *$P<0.05$, **$P<0.01$, ***$P<0.001$

Density frequency histograms depict higher frequency of denser limpet populations at low access sites (Figure 11).

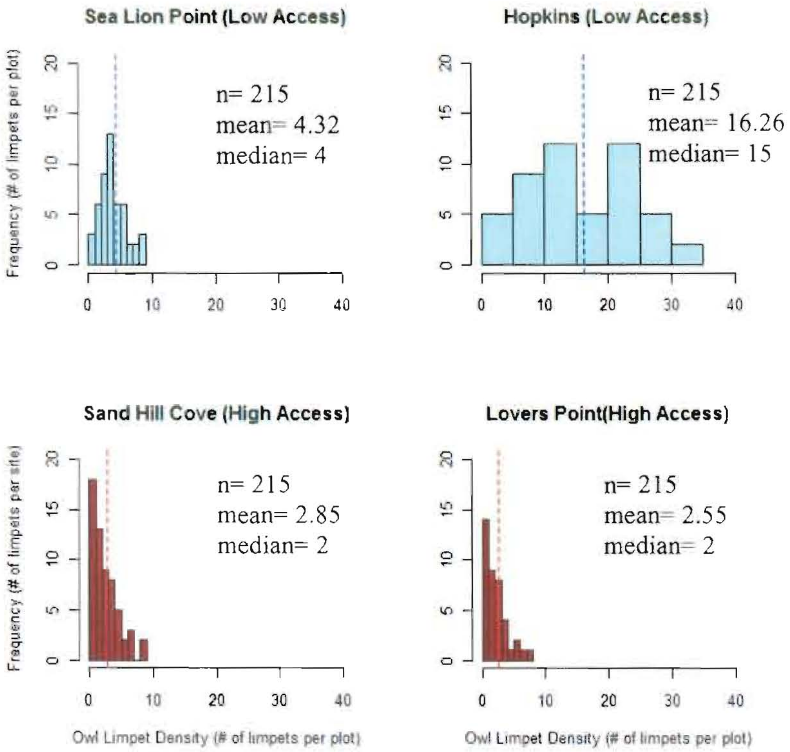


Figure 11: Owl limpet density frequency histograms per site for the course of the study with mean density displayed as the dashed line.

Q-Q plots verify that there was no substantial departure from the assumption that variation in limpet density was negative-binomially distributed (Figure 12).

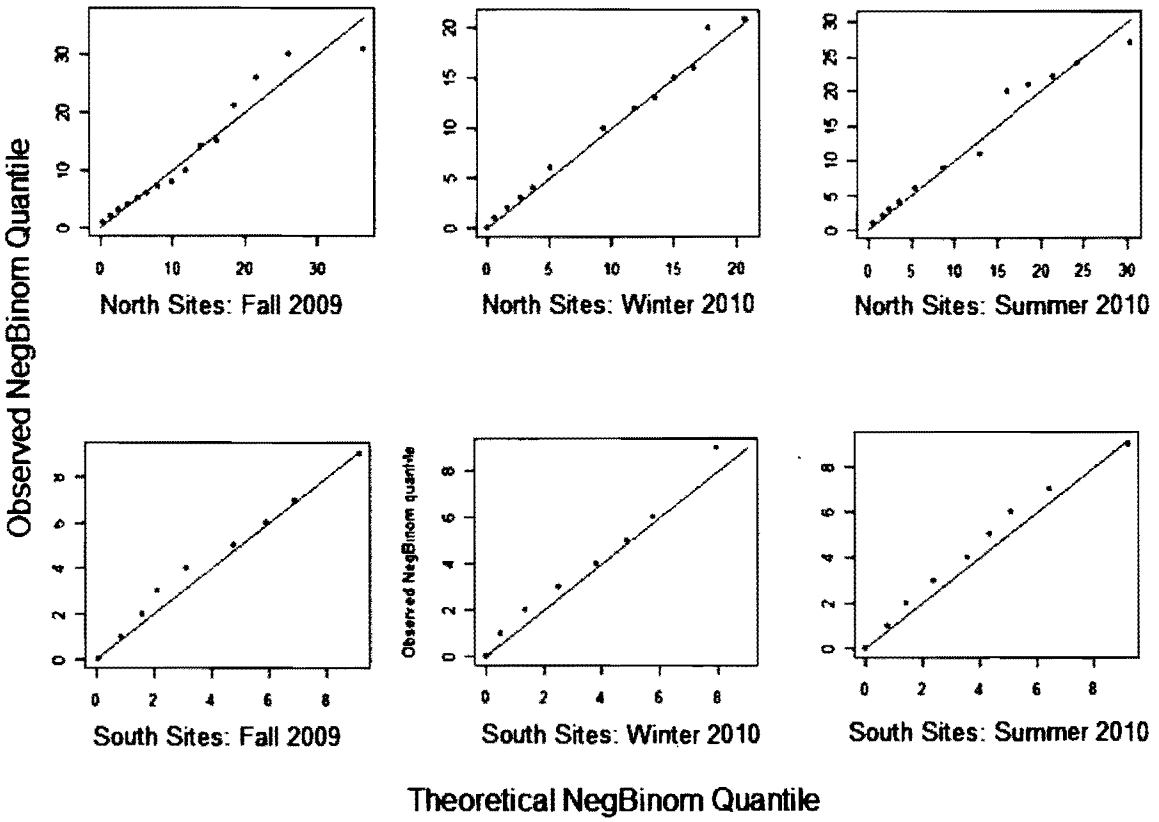


Figure 12: Negative-binomial Q-Q plots of residuals for the density data, verifying no substantial departure from the assumption of negative-binomial variation in limpet density.

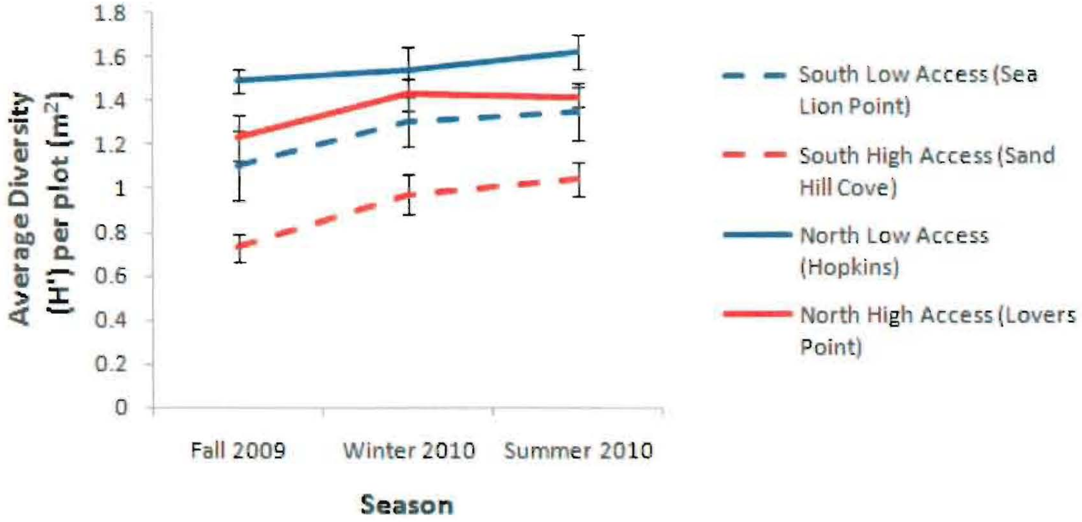
SPECIES DIVERSITY

There was a total of 32 species observed in the photo plots between all four sites (Table 11).

Table 11: Species lists for each site over all four sampling dates with numerical code used in ArcMap.

Code	Sea Lion Point	Sand Hill Cove	Hopkins	Lovers Point
22	*Anthopleura* spp.	*Anthopleura* spp.		*Anthopleura* spp.
9	*Balanus glandula*	*Balanus glandula*	*Balanus glandula*	*Balanus glandula*
25	*Chlorostoma* spp.	*Chlorostoma* spp.	*Chlorostoma* spp.	*Chlorostoma* spp.
8	*Chthamalus* spp.	*Chthamalus* spp.	*Chthamalus* spp.	*Chthamalus* spp.
23	*Codium fragile*			
1	*Corallina* spp.	*Corallina* spp.	*Corallina* spp.	*Corallina* spp.
20	*Egregia menziesii*		*Egregia menziesii*	*Egregia menziesii*
6	*Endocladia muricata*	*Endocladia muricata*	*Endocladia muricata*	*Endocladia muricata*
19	*Enteromorpha* spp.	*Enteromorpha* spp.	*Enteromorpha* spp.	*Enteromorpha* spp.
28	*Fucus gardneri*	*Fucus gardneri*	*Fucus gardneri*	*Fucus gardneri*
16	*Gelidium* spp.		*Gelidium* spp.	*Gelidium* spp.
21	*Haliotis cracherodii*			
38	*Laminaria setchellii*			*Laminaria setchellii*
11	*Lottia digitalis*	*Lottia digitalis*	*Lottia digitalis*	*Lottia digitalis*
17	*Lottia gigantea*	*Lottia gigantea*	*Lottia gigantea*	*Lottia gigantea*
4	*Lottia pelta*	*Lottia pelta*	*Lottia pelta*	*Lottia pelta*
10	*Lottia scabra*	*Lottia scabra*	*Lottia scabra*	*Lottia scabra*
37	*Lottia* spp.		*Lottia* spp.	*Lottia* spp.
7	*Mastocarpus* spp.	*Mastocarpus* spp.	*Mastocarpus* spp.	*Mastocarpus* spp.
3	*Mazzaella splendens*	*Mazzaella splendens*	*Mazzaella splendens*	*Mazzaella splendens*
34		*Mopalia* spp.	*Mopalia* spp.	*Mopalia* spp.
2	*Mytilus californianus*	*Mytilus californianus*	*Mytilus californianus*	*Mytilus californianus*
13	*Nucella emarginata*	*Nucella emarginata*	*Nucella emarginata*	*Nucella emarginata*
27	*Nutallina* spp.	*Nutallina* spp.	*Nutallina* spp.	*Nutallina* spp.
35				*Pachygrapsus crassipes*
30	*Phyllospadix* spp.			
18	*Pisaster*			
5	*Pollicipes polymerus*	*Pollicipes polymerus*	*Pollicipes polymerus*	*Pollicipes polymerus*
39	*Porphyra* spp.	*Porphyra* spp.	*Porphyra* spp.	*Porphyra* spp.
24	*Serpulorbis squamigerus*			
14	*Tetraclites rubescens*	*Tetraclites rubescens*	*Tetraclites rubescens*	*Tetraclites rubescens*
32	*Ulva* spp.	*Ulva* spp.		

The mean species diversity (H') at northern sites was 0.11 to 0.25 higer in the low access site (Hopkins) than the high access site (Lovers Point) on each sampling date (Figure 13). The mean species diversity (H') at southern sites was 0.31 to 0.37 higher in the low access site (Sea Lion Point) than the high access site (Sand Hill Cove) on each sampling date (Figure 13). The results of the *t*-test indicate there was a statistically significant difference between species diversity (H') as a function of access, during both the Fall 2009 and Summer 2010 sampling dates in the north sites (Table 12) but only during the Winter 2009 sampling date in the south sites (Table 13). However, the diversity was always greater at both low access sites than the high access sites (Figure 13).



****P* <0.001 ***P* 0.001-0.02 **P* 0.02-0.05

Figure 13: Average species diversity (H') per plot (m^2) at low (Sea Lion Point and Hopkins) and high (Sand Hill Cove and Lovers Point) access sites with standard error over three study dates from Fall 2009 to Summer 2010.

Table 12: Results of the *t*-test with Diversity by Access for the north sites (Hopkins and Lovers Point) over the three dates.

		t (estimate)	df	*P*	
Fall 2009	Low Access	-2.20	11.92	0.049	*
Winter 2009	Low Access	-0.84	15.66	0.410	
Summer 2010	Low Access	-2.31	13.87	0.037	*

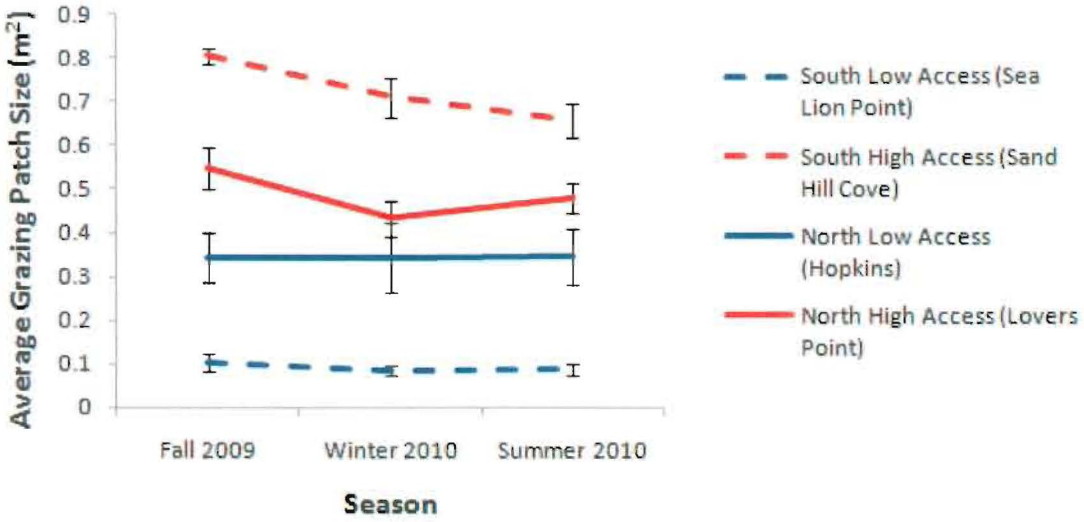
Significance levels: *ns* no significance, **P*<0.05, ***P*<0.01, ****P*<0.001

Table 13: Results of the *t*-test with Diversity by Access for the south sites (Sea Lion Point and Sand Hill Cove) over the three dates.

		t (estimate)	df	*P*	
Fall 2009	Low Access	-2.15	9.18	0.058	
Winter 2009	Low Access	-2.31	13.90	0.037	*
Summer 2010	Low Access	-2.04	12.84	0.062	

Significance levels: *ns* no significance, **P*<0.05, ***P*<0.01, ****P*<0.001

Average grazing patch size (m^2) was 0.10 m^2 to 0.20 m^2 or 10% to 20% greater at the north high access site (Lovers Point) vs. the north low access site (Hopkins) (Figure 14; Table 14). Average grazing patch size (m^2) was 0.57 m^2 to 0.70 m^2 or 57% to 70% greater at the south high access site (Sand Hill Cove) vs. the south low access site (Sea Lion Point) (Figure 14; Table 15). The results of the Wilcoxon rank sum test indicate there was a statistically significant difference between grazing patch size (m^2) as a function of Access on the Fall 2009 date for the north sites and on all three sampling dates for the south sites (Tables 14 and 15). Tagged limpets remained in the same grazing patch throughout the study.



****P* <0.001 ***P* 0.001-0.02 **P* 0.02-0.05

Figure 14: Average grazing patch size (m^2) at low (Sea Lion Point and Hopkins) and high (Sand Hill Cove and Lovers Point) access sites with standard error.

Table 14: Results of the Wilcoxon rank sum test for patch size with continuity correction for north sites (Hopkins and Lovers Point) over the three dates.

		W	*P*	
Fall 2009	Low Access	69.5	0.049	*
Winter 2009	Low Access	55.0	0.44	
Summer 2010	Low Access	56.5	0.15	

Significance levels: **P*<0.05, ***P*<0.01, ****P*<0.001

Table 15: Results of the Wilcoxon rank sum test for patch size with continuity correction for south sites (Sea Lion Point and Sand Hill Cove) over the three dates.

		W	P	
Fall 2009	Low Access	72	6.11E-04	***
Winter 2009	Low Access	72	6.11E-04	***
Summer 2010	Low Access	72	6.02E-04	***

Significance levels: *$P<0.05$, **$P<0.01$, ***$P<0.001$

The results of the linear regression suggest that species diversity explains about 8% of the variation in limpet density data (Table 16 and Figure 15).

Table 16: Results of linear regression between species diversity (H') and density (limpets per m^2).

	Estimate	SE	t	P	
(Intercept)	-0.1	2.1	-5.00e-02	0.9583	
Diversity	5.6	1.6	3.6	0.00048	***

Significance levels: *$P<0.05$, **$P<0.01$, ***$P<0.001$

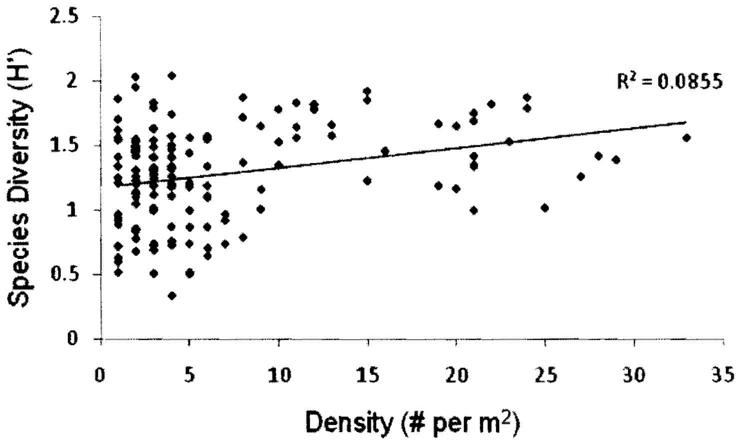


Figure 15: Linear regression between species diversity (H') and density (limpets per m^2), $R^2 = 0.0855$.

The results of the Wilcoxon Rank Sum test show that patch size was correlated to limpet size (Table 17 and Figure 16).

Table 17: Results of Wilcoxon Rank Sum test between grazing patch size (m^2) and limpet size (mm).

	W	P	
Patch	19321	2.20E-16	***

Significance levels: *$P<0.05$, **$P<0.01$, ***$P<0.001$

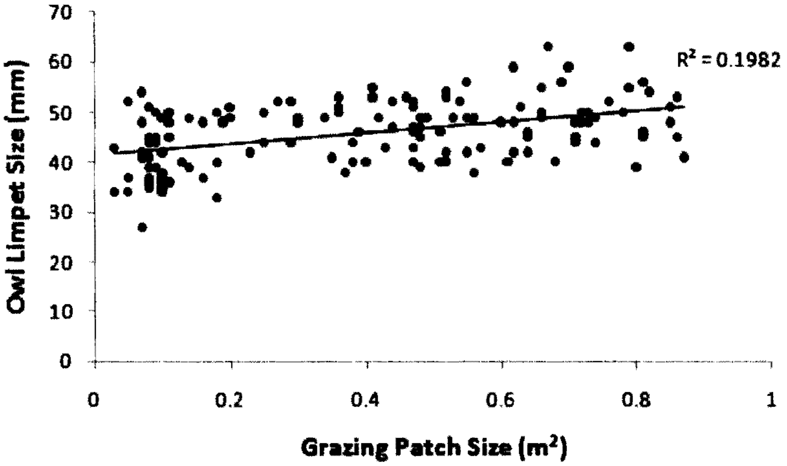
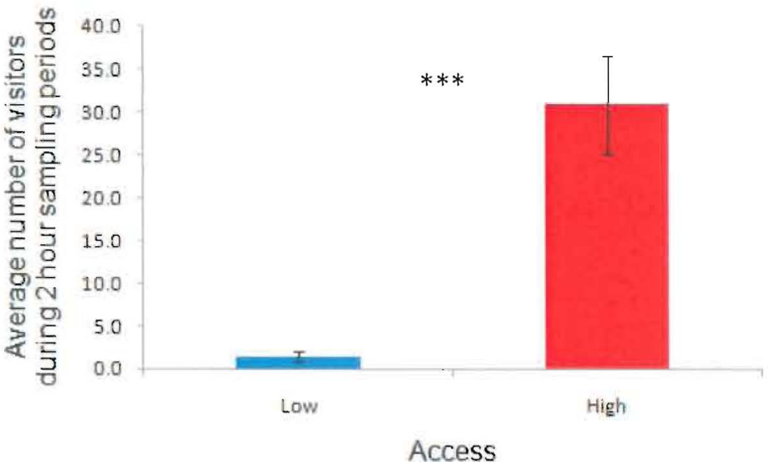


Figure 16: Linear regression between grazing patch size (m^2) and limpet size (mm), $R^2 = 0.1982$.

VISITOR USE

On average there were about 30 more visitors per day at high access sites than low access sites (Figure 17). The results of the negative binomial indicate there was a statistically significant difference in number of visitors between high and low access sites (Table 18). The mean number of visitors at high access sites was 31 visitors and 1.4 visitors at low access sites.



***P <0.001 **P 0.001-0.02 *P 0.02-0.05

Figure 17: Average number of visitors at low (Hopkins and Sea Lion Point) and high (Lovers Point and Sand Hill Cove) access sites from June 2009 to July 2010 over 11 days (6 for Lovers Point) during 2 hour sampling periods with standard error.

Table 18: Summary of the negative binomial test for effect of Access on number of visitors.

	Estimate	Std Error	Z	P-value	
(Intercept)	30.9	8.5	3.6	3.02e-04	***
Low Access	-29.5	8.6	-3.4	5.72e-04	***

Significance levels: *P<0.05, **P<0.01, ***P<0.001

Number of visitors varied over the course of the year (Figure 18). The high access sites, Lovers Point and Sand Hill Cove, had more visitors than the low access sites on every sampling date.

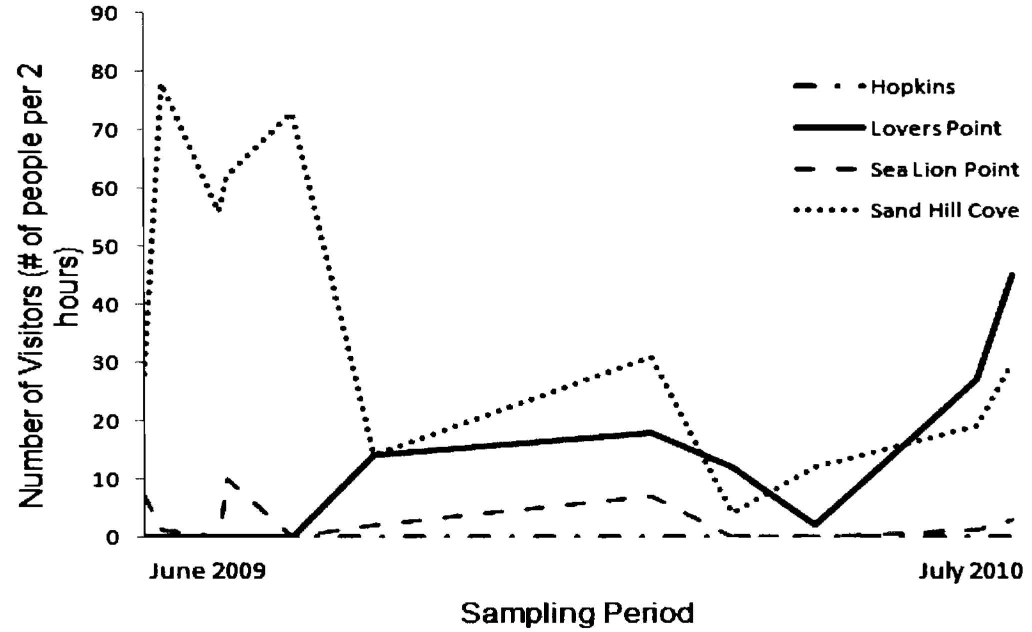


Figure 18: Number of visitors per site over each 2-hour sampling period during the entire study period (June 2009 to July 2010). Lovers Point observations did not start until November 2009.

There was no statistically significant association between site access and visitor behavior (Table 19). Overall, more visitors were passive than active (Figure 19). The expected values predicted 35% of visitor's time was active and 65% was passive. The observed values were the same for the high access sites, but slightly different at 20% active and 80% passive for low access sites, but not enough to show statistical significance.

Table 19: Results of Pearson's Chi-squared test.

	Value	DF	*P*
χ^2	1.6	1	0.2071

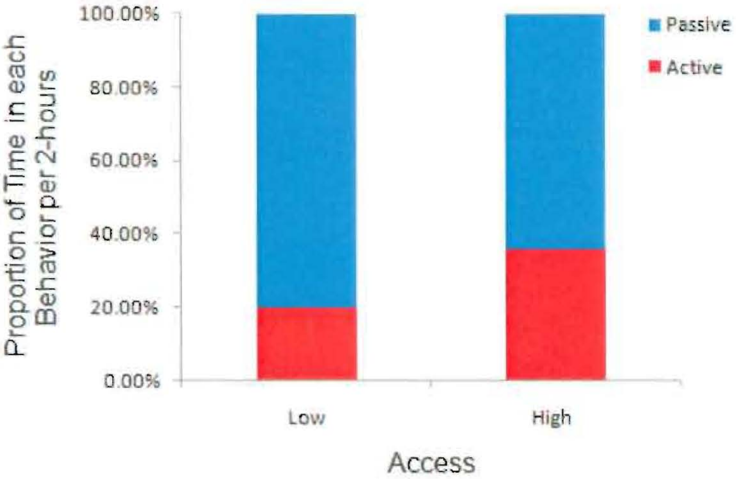


Figure 19: The observed proportion of time visitors spent exhibiting active or passive behavior over 2 hour time periods from June 2009 to July 2010. Low Access sites include Sea Lion Point and Hopkins, High Access sites include Sand Hill Cove and Lovers Point. Note, there were no visitors at Hopkins during the study period (http://www.stanford.edu/group/dbr/visitor_schedule.htm).

CHAPTER 4

DISCUSSION

The objective of this study was to investigate variation in owl limpet size, owl limpet density and community species diversity as a function of human access at study sites within Point Lobos, California and southern Monterey Bay, California. The results from this study indicate there were more large limpets at sites with high human access than at sites with low human access, which is contrary to previous findings that owl limpets have smaller shell sizes with increased human access (Kido and Murray 2003; Roy et al. 2003; Sagarin et al. 2007) (Table 20).

Table 20: Size comparison between this study and southern California studies.

Study	High Access Mean Size	Low Access Mean Size
This Study	**51 mm**	**41.8 mm**
Kido and Murray (2003)	27.8 mm	31 mm
Roy et al. (2003)	32 mm	45 mm
Sagarin et al. (2007)	36.2 mm	47.7 mm

Owl limpets were less dense at high access sites than low access sites. These results are consistent with previous studies of owl limpets and other invertebrates that found denser populations in low access sites vs. high access sites (Lindberg et al. 1998; Kido and Murray 2003; Smith and Murray 2005; Sagarin et al. 2007; Smith et al. 2008; Ramirez et al. 2009). A high degree of harvesting pressure was the common link believed to account for the results of these studies and may explain the differences observed in this current study. Since there is no-take of owl limpets allowed at the study sites, which are all in State Marine Reserves (SMRs), the absence of legal harvesting pressure is likely a reason for the difference in results since limpets were not smaller in high access sites, which has been observed as a results of size selective harvesting (Lindberg et al. 1998; Sagarin et al. 2007; Ramirez et al. 2009). However, while there is no legal harvesting pressure, visitation can impact limpet size and density.

Human trampling can have detrimental effects on rocky intertidal communities (Addessi 1994; Murray et al. 1999; Smith and Murray 2005; Smith et al.; 2008). Human impacts may indirectly impact owl limpets by altering community-level dynamics linked to limpet size and density, such as species diversity and grazing patch area. Human trampling increases bare rock and mussel bed percent cover, which decreases the number of species (Brosnan 1994; Fletcher and Flid 1996; Van De Werfhorst and Pearse 2007). This study found that in low access sites, where there were fewer visitors, species diversity was higher, grazing patch area was smaller and limpets were smaller and more abundant. One reason for these results is that where limpets are more abundant, there may be an increase in intraspecific competition leading to density dependent population growth, a pattern that has been observed in other invertebrate species (Creese and Underwood 1982; Dungan 1986; Wright 1989; Boaventura et al. 2003; Huchette et al. 2003; Robles et al. 2009). As limpets are competing with each other for space, they may have less energy to spend feeding and are therefore smaller in size. In areas where owl limpets are in high density there may be more younger females than in low density areas where limpets can grow larger (Wright 1989). The size of limpets and grazing patch size may be associated. Owl limpets clear grazing patches by bulldozing out other species (Stimson 1970; Wright 1989). Smaller limpets were associated with smaller grazing patches, likely due to intraspecific competition as limpets would have to spend more energy competing rather than eating more and grazing larger patches. Species diversity was greater potentially due to intraspecific competition between owl limpets because the grazing patch size was smaller and there is likely more room for other species at the scale of a 1m^2 plot.

In high access sites, where there were more visitors, species diversity was lower, grazing patch size was greater and limpets were larger and less abundant. Where limpets are less abundant, there should be a decrease in intraspecific competition. Owl limpets are protandrous and there is a direct connection between density and sex change (Lindberg and Wright 1985; Wright 1989). As the limpets do not need to compete against each other for space, they have more energy to feed. Owl limpets in low densities have been shown to change sex more frequently (Wright and Lindberg 1982; Lindberg and Wright 1985; Wright 1989), potentially because they are able to grow larger. Larger limpets would likely experience lower rates of intraspecific competition as they are free to spend more energy grazing, creating a larger grazing patch to support their size. Species diversity was lower at the 1m^2 scale, potentially due to the higher disturbance. As larger limpets are maintaining larger grazing patches, there would be less room for other species.

Another objective of this study was to investigate differences in visitor behavior. Visitor behavior was not different between high and low access sites and most people (80%) were categorized as exhibiting passive (less destructive) behavior and only 20% of visitors were considered active (more destructive). These results are consistent with previous studies that also found 18-20% of visitors to be engaged in active behaviors (Addessi 1994; Tenera Environmental 2003). While visitor behavior was consistent over all sites, because there were more total visitors to high access sites than low access sties, the impact of visitation on high access sites is presumably greater. While all sites were within MPAs, high access sites in Monterey Bay may have lower access than high access sites previously studied in southern California due to the higher amount of regulations.

POLICY IMPLICATIONS

The results of this study directly relate to the MLPA's goals of protecting natural diversity and abundance of marine life. As owl limpets clear patches and therefore limit macroalgae from dominating, they can help sustain the natural diversity of rocky intertidal communities by creating a patchwork of intermediate disturbances (Connell 1978). Marine Protected Areas (MPAs) are one of the tools used to address the MLPA's goals. The effects of MPAs have been used in the management of subtidal fisheries and have been promoted as the cause of subsequent increases in biomass and density of targeted species inside MPAs (Halpern 2003; CDFG et al. 2008; Calliet and Andrews 2008). However, MPAs may not take into account effects on community-level dynamics for species with sessile/sedentary adults. For instance, low mobility invertebrates may not disperse like other species, which fit the model of greater size, greater density and higher biomass that are some main goals of MPAs for targeted fish species (Halpern 2003; CDFG et al. 2008). Since owl limpets do not disperse great distances, they cannot move as limpet density increases, therefore resulting in a density dependent feedback. Other studies have shown unintended results of MPAs in marine invertebrate species (Pinnegar et al. 2000; Benedettie-Cecchi et al. 2003; Behrens and Lafferty 2004). Behrens and Lafferty (2004) found that inside MPAs, purple urchins were less abundant than outside reserves due to the protection of two urchin predators, causing a trophic cascade. In another study, humans were excluded from a rocky intertidal area in Chile causing an increase in keyhole limpets resulting in a decline in macroalgae (Moreno et al. 1984; Pinnegar et al. 2000). In a similar study, where limpets were completely removed, macroalgae dominated (Moreno and Jaramillo 2003; Pinnegar et a. 2000). Benedettie-Cecchi et al. (2003) observed that rocky intertidal assemblages in the northwest Mediterranean post MPA establishment differed from the expected outcomes of the MPA relating to mean density of several taxa, in which MPAs had no effect on population density. This study found variation in owl limpet populations within SMRs as a result of variation in human access.

This study relates to the NMSA's goals of promoting scientific research and long-term monitoring of marine resources. This study has provided a set of site-specific data on owl limpet size and density in the context of human use. It is important to have site-specific data in order to know what to expect under certain circumstances such as MPA establishment and variation in human access. If decisions in central California were made based on southern California data, policy makers could be misinformed with information from a different system. The best available science needs to be site-specific for low-mobility invertebrates where variation can occur on a small scale and at a local level. There are different oceanographic conditions and human activities that can influence rocky intertidal systems at a local scale, which can impact how these systems are managed. This study also provided photo records of species diversity that can be used as a historical record by Monterey Bay National Marine Sanctuary (MBNMS) staff for long-term monitoring and serve as a foundation for future climate changes and potential environmental disasters such as oil spills.

Owl limpets provide ecological and ecosystem services to rocky intertidal ecosystems that may be important to MBNMS in terms of monitoring. Owl limpets are also ecosystem engineers in rocky intertidal ecosystems, modifying the habitat by clearing macroalgae and invertebrates and creating homescars (Stimson 1970). Their shells also provide physical structure for other smaller limpets to attach (Gutierrez et al. 2003). MBNMS is concerned with monitoring and protecting the diversity of the habitat. Removal of owl limpets has been shown to allow for an increase in macroalgae cover (Wooton 1992; Lindberg et al. 1998). .

Owl limpets provide the provisioning service of food as they were historically harvested and are currently harvested in southern California (Vedder and Norris 1963; Lindberg et al. 1998). Owl limpet harvesting is not believed to account for changes in owl limpet size and density in this study, however it does occur in southern California and could become an issue in Monterey Bay. Illegal harvesting of owl limpets remains a possibility; however, it is not a likely explanation for the larger size of owl limpets in areas with high human access. Harvesting in southern California is more prevalent and thought to account for body size reduction in owl limpet populations (Kido and Murray 2005; Sagarin et al. 2007). Removing large individuals from a population can lead to decreased reproduction rates, which could change owl limpet size and density patterns over time and therefore change the community structure in rocky intertidal habitats. Since owl limpets are long-lived and slow growing, and the central California MPAs were established in 2007, it is possible that there has been insufficient time for the MPAs with high human access to respond to the relatively new protections.

Owl limpets contribute to the cultural services provided by rocky intertidal ecosystems such as aesthetic and recreational values. Though the particular value of owl limpets to humans is unknown, the value of owl limpets to rocky intertidal ecosystems is important (Stimson 1970; Wright and Lindberg 1982; Lindberg et al. 1987). Changes in owl limpet density and size via human activities such as trampling can potentially alter the mosaic of intertidal diversity and therefore decrease the cultural services provided. According to Chan and Ruckelshaus (2010), ecosystem service modeling as a tool for marine policy and management is growing and the largest gap is that of cultural ecosystem services because they are primarily non-market values and do not fit into quantitative models. Qualitative approaches such as determining multiple drivers of change such as human activities and oceanographic changes on ecosystem services may be beneficial to marine ecosystem policy and management (Chan and Ruckelshaus 2010). This study looked at human activity as a driver of change in owl limpet size and density. Owl limpets are important in rocky intertidal ecosystems and therefore changes in owl limpet populations may affect services provided by rocky intertidal ecosystems. There is a need for mapping the intensity and distribution of human activity in relation to marine ecosystem services (Lester et al. 2010). In this study, there were a greater number of people in easy to access areas and therefore likely to have a greater impact on the system. Determining the tradeoff between cultural values (human visitation and activity) and community health in rocky intertidal ecosystems may be a way to guide future policy and conservation efforts regarding rocky intertidal ecosystems as has been done in fisheries management (Chan and Ruckelshaus 2010; Lester et al. 2010).

While this study did not measure abiotic effects on owl limpet size and density it would be useful to understand how these factors can impact owl limpet populations. There were also only four study sites. More study sites would be useful in allowing for more replication and a more extensive set of data. The study sites were chosen based on the presence of owl limpets and similarity of oceanographic conditions as paired sites were in close proximity to each other, however some variation in both owl limpet size and density may be attributed to effects not tested in this study such as recruitment rates, desiccation stress, and wave velocity. These abiotic effects as well as future changes in oceanographic conditions including rises in sea level and temperature may also be drivers of changes in owl limpet populations and rocky intertidal ecosystems. Determining interactions between human activities and abiotic factors and their impacts on owl limpets will improve our understanding of how changes in owl limpet size and density could impact rocky intertidal ecosystems in the future.

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APPENDIX A

COASTAL MARINE ECOSYSTEM SERVICES

BACKGROUND

Understanding the overlap between human activities and ecosystem services can provide insight on the importance of valuation in ecosystems for future monitoring or conservation programs (Chan and Ruckelshaus 2010). Marine ecosystem service modeling is a growing approach being incorporated into marine planning and policy making. Marine ecosystem services especially in rocky intertidal ecosystems are harder to model than traditional terrestrial services because they are limited to mostly non-market values (Chan and Ruckelshaus 2010). Qualitative approaches, such as determining multiple drivers of change like human activities and oceanographic changes on ecosystem services, may be beneficial to marine ecosystem policy and management (Chan and Ruckelshaus 2010). This study looked at human activities as a driver of changes in owl limpet size and density.

Owl limpets are ecosystem engineers in rocky intertidal habitats and therefore changes in owl limpet populations may affect services provided by rocky intertidal ecosystems. Determining interactions between human activities and abiotic factors and their impacts on owl limpets may allow for a greater understanding of how to model marine ecosystem services. There is a need for mapping the intensity and distribution of human activity in relation to marine ecosystem services (Lester et al. 2010). This study looked at intensity of human activity via visitation and distribution via site access. There was higher visitation in easy to access areas and thus a higher intensity of human activity in concentrated areas. Determining the tradeoff between ecosystem services such as cultural values (human visitation and activity) and community viability in rocky intertidal ecosystems may be a way to guide future policy and conservation efforts regarding rocky intertidal ecosystems as has been done in fisheries management (Chan and Ruckelshaus 2010; Lester et al. 2010). The concept of ecosystem services is reviewed in the following section and includes a discussion of how ecosystem services can be applied to marine ecosystem services including rocky intertidal ecosystems.

ECOSYSTEM SERVICES

Ecosystem services are not a new idea, they have been around since humans have used the land and its natural resources. Ecosystem services by definition are: the conditions and processes created by natural ecosystems and species that help sustain human life (Daily 1997). These services include provisioning services (food, water and fiber), regulating services (climate regulation, nutrient cycling), cultural services (recreation, spiritual, aesthetic) and supporting services (primary production and soil formation) (Ehrlich and Ehrlich 1992; Millennium Ecosystem Assessment 2005). These services are rarely directly paid for, which is why they are taken for granted and overexploited (Daily 1997; Millennium Ecosystem Assessment 2005). According to Alcamo et al. (2005), the demand for ecosystem services is estimated to substantially increase over the next 40 years. The provisioning services of fish consumption and freshwater withdrawal are expected to have the highest demand (Alcamo et al. 2005). The Millennium Ecosystem Assessment (2005) and Tallis and Kareiva (2005) have found that over half of the ecosystem services worldwide are degraded or overexploited. As the demand for ecosystem services increases, less of them will be available unless more conservation measures are taken (Alcamo et al. 2005; Tallis and Kareiva 2005).

ECOSYSTEM SERVICES: VALUATION AND STATUS

Economic valuation of ecosystem services has been one way to increase awareness of conservation of ecosystem services (Costanza et al.1997; Millennium Ecosystem Assessment 2005). Economic values can be classified as either use or non-use (Edwards and Abivardi 1997). Use values are identified in three categories: direct use (e.g., fish, timber, tourism etc.), ecological function (e.g., photosynthesis, nutrient cycles etc.), and option values (e.g., substitutes, complements of new technologies etc.) (Edwards and Abivardi 1997). Non-use values are identified in two categories: existence (satisfaction of a resource, also intrinsic value) and bequest (future generation use) (Edwards and Abivardi 1997). Costanza et al. (1997) addressed the economic value of ecosystem services in terms of how much it would cost to reproduce them in an artificial biosphere. They reviewed market values (directly paid for by consumers, i.e. lumber) and non-market values (not directly paid for, i.e. carbon sequestration) to produce a total economic value of ecosystem services of 16 to 54 trillion dollars per year (Costanza et al. 1997). The Costanza et al. (1997) study has gained attention from around the world; however, there have also been many debates on the issue of ecosystem service valuation. Some believe it is impossible to put a value on services that are non-marketable or that economic value should not be the only means of ecosystem service conservation (Costanza et al. 1998). One of the main questions from this study is if ecosystem services do not have an associated economic value, are they worth conserving? The application of Costanza et al. (1997) is more for noting that ecosystem services are important and may have economic value.

The Millennium Ecosystem Assessment (2005) was also a large-scale study, which addressed global ecosystem services' status, trends and possible future responses. The result of this study was a type of scorecard, which showed different ecosystem types including forests, dry lands, coastal, marine, mountains, and polar and associated status in habitat change, climate change, invasive species, over-exploitation and pollution (Millennium Ecosystem Assessment 2005). Climate change and pollution showed an increasing impact in all ecosystem types. The Millennium Ecosystem Assessment (2005) also gained global attention because it is a good resource for general information regarding broad ecosystem service status. However, it is a synthesis and does not represent local ecosystems within the broad categories. In conservation and management strategies, knowing how local ecosystems function is important because not all ecosystems function the same, it is dependent on many factors.

ECOSYSTEM SERVICES AND BIODIVERSITY

Biodiversity is measured as the number of species or organisms present in specific ecological systems and is declining about 1000 times faster than rates found in the fossil record (Millennium Ecosystem Assessment 2005; Balvanera et al. 2006). Some of the anthropogenic factors affecting biodiversity are changes in land use, pollution, invasive species introduction, harvest and resource consumption, and external inputs like fertilizers (Edwards and Abivardi 1997; Millennium Ecosystem Assessment 2005). There are contradicting views of whether or not biodiversity supports ecosystem services. Naidoo et al. (2008) suggest biodiversity and ecosystem services are separate ecological functions, but may overlap in certain areas in which conservation would be highly favorable. Ehrlich and

Ehrlich (1992), Edwards and Abivardi (1997), and Balvanera et al. (2006) believe increased biodiversity promotes ecosystem service function and production. They suggest conservation strategies geared more toward protection of high biodiversity, which will then lead to high ecosystem service production.

MARINE ECOSYSTEM SERVICES

There have been many ecosystem service studies done on marine ecosystems including the ocean, coral reefs, mangroves, seagrass beds, and estuaries (Costanza et al. 1997; Moberg and Folke 1999; Miller and Auyong 1999; Zedler 2000; Bhat 2003; Ledaux 2003). Marine ecosystems vary in services provided. The ocean provides food web support and provisioning (food) services through fisheries (Pinnegar et al. 2000; Millennium Ecosystem Assessment 2005). Coral reefs provide protection of coastlines from erosion and storm events, habitat for many species, aesthetic value to humans and fish for consumption (Bhat 2003). Mangroves and seagrass beds provide natural water purification of inorganic nutrients and pollutants, stabilization of shorelines and provisioning services such as fish (Moberg and Ronnback 2003). Wetlands and estuaries provide water, raw material, recreation and aesthetic values and natural water purification (Costanza et al. 1997; Zedler 2000). In most studies related to ecosystem services, human impacts have been the common link in the decrease in biodiversity and degradation of marine ecosystems (Moberg and Folke 1999; Miller and Auyong 1999; Ledaux 2003). Some of the anthropogenic impacts on marine ecosystems include overfishing, habitat degradation through use of fishing gear, pollution and exploitive recreation including collection and disturbance of species (Bhat 2003). Halpern et al. (2008) did a study of spatial distribution of human activities and the overlap of those activities on marine ecosystems and found that no area is unaffected by human impacts.

ROCKY INTERTIDAL ECOSYSTEM SERVICES

Human impacts are suggested to be the highest in nearshore and coastal zones due to the proximity of most of the world's population are near coastlines (Morrison and Hunt 2007). The rocky intertidal is considered a nearshore ecosystem defined as the area between low-tide and high-tide marks composed of rocky substrate such as boulders or shale

(Peterson 1991). The main services provided by the rocky intertidal include provisioning (food) and cultural (recreation and aesthetic) services. The main species harvested from the rocky intertidal in California are black abalone, mussels, and owl limpets (Becker 2005, Smith and Murray 2005, Smith et al. 2006). The owl limpet is increasing in harvest because it is now considered "the poor man's abalone," in that it tastes similar to the more pricy abalone (Sagarin et al. 2007). Black abalone was listed as an endangered species in 2009 and harvesting is illegal. Some problems associated with these communities in the rocky intertidal are size-harvesting and trampling (Smith and Murray 2005; Sagarin et al. 2007; Fenberg and Roy 2008). Size-based harvesting of larger individuals has been linked to loss of reproductive success and evolutionary change in body size (Roy et al. 2003; Fenberg and Roy 2008). Cultural services of the rocky intertidal such as aesthetic value and recreation have drawn many visitors to this ecosystem (Miller and Auyong 1991, Hall et al. 2002, Davenport and Davenport 2006). Visitation can both drive economic gain and decrease biodiversity (Thompson et al. 2002). Millions of tourists are attracted to beaches and coasts every year and these areas drive coastal economies (Miller and Auyong 1991). However, tourism is also indirectly detrimental to the marine environment because infrastructure and other amenities are built to accommodate tourists (Miller and Auyong 1991; Bhat 2002). Some of the direct impacts of visitation on rocky intertidal ecosystems are pollution, collection of species, and trampling (Fox 1994; Thompson et al. 2002; Smith et al. 2008). Most of these impacts are caused by a lack of education and no sense of stewardship by visitors to the rocky intertidal (Hall et al. 2002).

Some important methods that have been used in determining visitation effects are visitor surveys, observation of visitor behaviors and surveys of species diversity. Tenera Environmental (2003) studied visitor behavior and species diversity at Point Pinos, California and found that first time visitors were unaware of regulations and 14 out or 18 returning visitors knew of the regulations, in observation of visitor behavior found 18 percent of all visitors engaged in active behaviors including handling, turning rocks or collecting species that may be detrimental to the ecosystem and found that invertebrate density was higher in areas not exposed to visitation. Smith et al. (2008) looked at mussel bed communities inside and outside MPAs and found the percent cover of mussels was lower in sites with high visitor use than in areas with lower visitor use. Sagarin et al. (2007) observed illegal poaching of owl limpets and found that the take of larger limpets had an effect on the size structures resulting in smaller limpets in unprotected areas. Murray et al. (1999) found similar results by witnessing visitors prying mussels off rocks for fishing bait as well as collecting limpets, urchins and octopus. All four studies question the effectiveness of enforcement within marine reserves that were established to protect coastal resources and suggest more long-term research and management of rocky intertidal areas.

Many other studies have mentioned the need for more research on rocky intertidal ecosystem services and conservation. Hall et al (2002) observed visitors trampling and illegally collecting species from the rocky intertidal in southern California. Fox (1994) also observed illegal collecting and trampling in Oregon rocky intertidal areas. Rocky intertidal studies are pertinent, especially in California because the effects of humans are continually increasing and could be irreversible if nothing is done (Fox 1994; Ledaux 2003). Other studies mention that Marine Protected Areas (MPAs) should protect rocky intertidal areas because they often include coastlines; however MPAs are not effectively protecting these areas (Murray et al. 1999; Hall et al. 2002; Smith et al. 2008). One of the main reasons MPAs are not effective in protecting rocky intertidal areas is lack of enforcement (Hall et al. 2002). There are usually no boundaries or limits of where people can go in the intertidal, whereas in the ocean there are specific areas where no activities of fishing or recreation can take place (Hall et al. 2002; Smith et al. 2008). Open access to rocky intertidal areas may be another reason why it is difficult to protect and enforce regulations. There is also a gap in knowledge of trampling and collecting in the rocky intertidal (Murray et al. 1999). Many visitors of these areas are unaware of the harm their actions could cause because there is often no signage or public information regarding regulations (Murray et al. 1999).

CONCLUSION

There has been recognition of ecosystem services since people began utilizing natural resources. The importance of ecosystem services as a value to humans, biodiversity, and conservation has been well defined in the literature. Numerous studies have looked at marine ecosystem services; however there is a gap in the literature regarding rocky intertidal ecosystem services and in the management and conservation of rocky intertidal ecosystem services. Specifically, there have not been many studies that connect the ecosystem service of visitation to the specific aspects such as accessibility or species diversity of the rocky intertidal that provide that service. In this study, the relationship between human activity and owl limpet populations was examined. Limpet size, limpet density and species diversity were measured. Larger limpets in lower density were found at high access sites and smaller limpets in higher density were found at low access sites. This study found that species diversity was higher in low access sites while grazing patch (essentially bare rock) area was higher in high access sites. Where species diversity was higher, grazing patch area was smaller and limpets were smaller and more abundant. Where species diversity was lower, grazing patch area was greater and limpets were larger and less abundant. These findings suggest humans do impact rocky intertidal areas to some extent. Inevitably, where there is more human activity there will likely be a greater impact on the ecosystem. More research is needed in order to determine tradeoffs between value of human visitation and value of ecosystem viability and biodiversity.

APPENDIX B

R STATISTICAL COMPUTING CODE

MIXED EFFECT MODEL: OWL LIMPET DENSITY ANALYSIS

```
library(nlme)
rm(list=ls())
freds_qqnorm <- function( vec, lims=NULL ) {
+   std <- ( vec - mean( vec ) ) / sd( vec )
+   qqnorm( std, pch="+", col="red", cex=0.8, xlim=lims, ylim=lims )
+   lines( -2:2, -2:2, col="black")
+   std <- sort( std )
+   lines( qnorm( pmin( 0.999, pmax( 0.001,
+     pnorm( std ) - 0.886 / sqrt( length( std ))))), std, lty=2 )
+   lines( qnorm( pmin( 0.999, pmax( 0.001,
+     pnorm( std ) + 0.886 / sqrt( length( std ))))), std, lty=2 )
+ }
d<-read.csv(file.choose())    #Limpet_Size_Data
d[1:10,]
summary( lme_NS )$coef
$fixed
summary( lme_NS )$tTable
lme_NS = lme( Size ~ Access, random = ~ 1|SitePlot, data=dNS )
summary( lme_NS )
hist(lme1$residuals[,3])
freds_qqnorm(lme1$residuals[,3],lims=c(-3,3))
freds_qqnorm(lme1$residuals[,3],lims=c(-0.5,0.5))
```

NEGATIVE BINOMIAL GLM: OWL LIMPET SIZE ANALYSIS

```
 # Read the data:
d<-read.csv(file.choose())   #North or South_Date_Density
# Take a look at the data
d
attach(d)
# The raw data have the following attributes:
# - 'Location' is the fixed effect of interest (whether human use is low vs high)
# - 'Site' is like "Point Pinos". 6 sites were surveyed, three for each 'Location'.
#   Sites are grouped in pairs, with one having 'High' Location and the other 'Low' Location.
#   So 'pairs' is really a random effect.
# - 'Plot' is a random effect, meaning something like a 'quadrat' within which individual
#   limpets were counted.
#   The Plot random effect
```

```
# Take a quick graphical look at the raw data:
windows(9,11)
par(mfrow=c(1,1))
summary(d$Density)
hist(d$Density, main=" ", xlab= "Density (# of limpets per plot m^2)", ylab="Frequency (# of plots with the given Density)")
abline(v=6.5, col="dark blue", lty="dashed")
# Define a compound variable called SitePlot that crosses Site with Plot.
# This is to make every single plot considered to be unique,
# rather than having any plot named 'Plot 1' to be considered part of the
# same Plot regardless of which Site it came from.
# (You can see the effect of doing it one way vs the other by examining which
#  coefficients lme() gives you. If it gives you only one coefficient for all
#  Plots named '1', then that's a problem. The effect of being in Plot 1 at Site C
#  is not the same as the effect of being in Plot 1 at Site P.)
SitePlot=paste(d$Site,".",d$Plot,sep="")
SitePlot = as.factor(SitePlot)
d$SitePlot = SitePlot

library (MASS)
m<-glm.nb(Density~Location, link=identity, data=d)
summary(m)

par(mfcol=c(2,2))

freds_qq.glm.nb = function( m, type="q" ) {
# A generic function for the QQ plot of any glm.nb fit.
# Specify:
#  - type "h" for fitted histogram plot.
#  - type "p" for P-P plot.
#  - type "q" for Q-Q plot.
#  - type "a" for Q-Q plot, add to existing plot.

# By Fred Watson, 2 Apr 2011.

 y = m$model[[1]]
 maxobs = max(y)
 headroom=1.5
 domain = 0:round(maxobs*headroom); domain.left = 0:(max(domain)-1)
 nd = length(domain)
 preds = m$fitted.values
 n = length(preds)
 td = rep(0,nd-1) # td = theoretical_density
 for( i in 1:n ) {
  td = td + dnbinom( x=domain.left, mu=preds[i], size=m$theta )
 }
```

```
 td = td / n
 d=hist(x=y,breaks=domain,plot=F,right=F)$density
 if(any(type=="h")) { # Histogram Plot
  plot(domain.left,d,typ="h")
  points(domain.left,td,pch=20,col="red")
 }
 cum_td=td
 for(i in 2:(nd-1) ) cum_td[i] = cum_td[i-1] + td[i]
 cum_d=d
 for(i in 2:(nd-1) ) cum_d[i] = cum_d[i-1] + d[i]
 if(any(type=="p")) { # PP Plot
  plot(cum_td,cum_d,pch=20,
  xlab="Theoretical cumulative probability",
  ylab="Observed cumulative probability")
  lines(c(0,1),c(0,1))
 }
 if(any(type=="q") | any(type=="a")) { # QQ Plot
  sy = sort(y)
  r = rank(sy)
  # Plotting position. Found 0.3 by trial and error.
  # (0.5 seemed to lead to under-estimated theoretical upper quantiles)
  p = (r-0.3)/n
  tq = approx( x=cum_td, y=domain.left, yleft=0, xout=p )$y
  lim=c(0,max(tq,sy))
  if(any(type=="a")) { # QQ Plot
   points(tq,sy,pch='.' )
  } else {
   plot(tq,sy,xlim=lim,ylim=lim,pch=20,
    xlab="Theoretical NegBinom quantile",
    ylab="Observed NegBinom quantile" )
   lines(lim,lim)
  }
 }
}

# Code to test freds_qq.glm.nb() function:
if( 0 ) {
 library("MASS"); set.seed(1)
 par(mfcol=c(3,4));par(mfcol=c(1,1))
 for( j in 1:12 ) {
  n=1000; theta=20; mu=20
  test=2
  if(test==1) { # Generate a sample with no predictor, and fit.
   y = rnbinom( n=n, mu=mu, size=theta )
   m = glm.nb( y~1, link="identity" )
  }
```

```
   else if(test==2) { # Generate a sample with a predictor, and fit
    x=c(rep(0,n/2),rep(1,n/2))
    mu=10+x*30
    y=rnbinom(n=n,mu=mu,size=theta)
    m = glm.nb( y~x, link="identity" )
   }
   freds_qq.glm.nb( m, type=ifelse(j==1,"q","a"))
  }
}

freds_qq.glm.nb( m, type=c("h","p","q"))
```

NEGATIVE BINOMIAL GLM: NUMBER OF VISITORS

```
d<-read.csv(file.choose())  #reads data
attach(d)
 summary(Visitors)
 library(MASS)
 m<-glm.nb(Visitors~Site, link=identity, data=d)
 summary(m)
```

CHI-SQUARE: VISITOR BEHAVIOR

```
> C<-matrix(c(389,139,26,5),nrow=2) # set-up contingency table
> C
    [,1] [,2]
[1,]  389   26
[2,]  139    5
> x2<-chisq.test(C, correct=F)
> x2

        Pearson's Chi-squared test

data:  C
X-squared = 1.5919, df = 1, p-value = 0.2071

> x2E<-stack(data.frame(t(x2$expected))) #expected values
> x2E
```

T-TEST: SPECIES DIVERSITY

```
d[1:10,]   #look at the data
attach(d)
hist(Diversity)
shapiro.test(Diversity)   # normal, proceed with t-test
div<-t.test(Diversity~Access)
div
```

Wilcoxon Rank Sum: Grazing Patch

```
 d[1:10,]    #look at the data
attach(d)
 hist(Patch)
 shapiro.test(Patch)  # not normal, run wilcox test
```

LINEAR REGRESSIONS

```
#Read Data
 d<-read.csv(file.choose())   #  Diversity_R
 d[1:10,]       #check data
fit <- lm(Density ~ Diversity, data=d) #fit linear regression> summary (fit)
```