Human Impacts on Rocky Intertidal Gastropods: Are Marine Protected Areas Effective?

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HUMAN IMPACTS ON ROCKY INTERTIDAL GASTROPODS: ARE MARINE PROTECTED AREAS EFFECTIVE?

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ABSTRACT

As the human population has exponentially increased, so have anthropogenic effects on the ocean including pollution, eutrophication, acidification, changes in sea level, and overfishing. The California coast is visited by millions of people every year and is subject to a range of impacts. In the near-shore marine environment, people collect intertidal gastropods for food, bait or recreation. Collecting these animals has caused a decline in body size because humans preferentially take the largest individuals. Marine protected areas (MPAs), established to protect marine resources, may serve to reduce impacts to species, including gastropods. I collected 2510 individual samples to determine the body size and frequency of five gastropod species along the central California coast to assess whether MPAs may protect intertidal species from over-exploitation. I hypothesized that gastropods in MPAs, compared to non-MPAs zones, would have larger body sizes and be more frequent and be similar in size to museum specimens. I found that, for two of the five species studied, gastropods were larger inside MPA field locations; for most species the average size of specimens from MPA sites was significantly larger than museum specimens and collected gastropods had higher frequencies of presence inside MPAs. For coastal managers, these results indicate that MPAs are effective for some gastropod species studied, but in order for all species to benefit fully from MPA protection continued research is necessary to determine species-specific requirements.
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Introduction

Background

Although many people view the ocean as an inexhaustible resource that can supply the global demand for fish, shellfish and other marine resources (Nicolson, 1979), the collapse of fisheries and decline of many marine species have shown this view to be incorrect. Overfishing and highly destructive harvesting practices are endangering ocean systems (Jackson et al., 2001). Fishing regulations and pollution prevention are two common methods to protect and restore ocean resources. These two strategies have been coupled with the use of marine protected areas (MPAs) (California Department of Fish and Wildlife Code, 2013), which are designed to protect natural resources in an approach similar to terrestrial parks. The use of MPAs began in the 1930s to protect and restore natural and cultural resources, but MPAs are still far behind terrestrial parks in terms of coverage. As of 2005, 12% of the earth’s land surface was protected in terrestrial parks (Chape, Harrison, Spalding & Lysenko, 2005). As of 2010 only 1.2% of the ocean’s surface protected by MPAs (Spalding, Wood, Fitzgerald & Gjerde, 2010), however the numbers of MPAs have been increased dramatically over the last 30 years (Fox et al., 2012) and they have become an integral part of ocean conservation. As the number of MPAs increases and as MPAs become more heavily relied on for ocean management, continued study of their effectiveness is essential.

Research indicates that MPAs have had a positive effect on fish populations (Castilla, 1998; Halpern, 2003), coral (Selig & Bruno, 2010), algae (Castilla, Campo & Bustamonte, 2007) and gastropods (Roy, Collins, Becker, Begovic & Engle, 2003;
Fenberg & Rivadeneira, 2011) and indicate that, in many ways, MPAs have been effective. But protected areas still face challenges. Pollution and oil spills can infiltrate these areas, and in many regions poachers are able to continue extracting resources illegally because enforcement of MPA policy is lacking. Even in areas with sufficient enforcement, tourism, which is cited as a goal of many MPAs, can have the undesired effect of causing negative impacts such as habitat and wildlife disturbance and degradation (Garcia-Charton et al., 2008). Continuing to assess the impact that humans and human activity have on these protected areas is essential for management. People may be having substantial impacts in sensitive MPAs which, in part, carry the goal of restoring overall ocean health in addition to the area within MPA boundaries.

The marine intertidal, or littoral community, is especially vulnerable to visitor impacts because of its accessibility and diversity. The intertidal zone along the Pacific coast of North America is a biological hotspot, primarily because of the nutrient-rich waters produced from seasonal upwelling (Ricketts, Calvin, Hedgepeth & Phillips, 1985). The abundant nutrients support diversity along the coast in open water, the near-shore kelp forests and the rocky intertidal. The rocky intertidal is a unique environment in part because it is affected by physical and biological forces from marine and terrestrial environments. The transition from ocean to land along the intertidal is usually broken down in zones, characterized by tide levels. The “uppermost horizon” is where the highest spray from storm waves reaches and where only the most desiccation tolerant organisms, such as periwinkle snails, can survive. Below the uppermost horizon is the “high intertidal,” which is measured from the mean tide line to the high tide line. This
area is dominated by organisms like barnacles, which can survive in open air for up to 12 hours. The “middle intertidal” is measured from the mean high tide line to the mean low tide line and is exposed to the air twice daily, for at most 6 hours. The “low intertidal” is below the low-tide line and is only exposed during semimonthly minus tides (tides that are lower than the average low tide). These zones are not fixed lines in the intertidal; rather they vary based on season, location and regional oceanographic conditions (Ricketts et al., 1985). The small area on the border between land and sea provides a wealth of habitat for a diversity of organisms that must survive a wide range of conditions.

Organisms living in the rocky intertidal zone must meet the challenges of limited space, exposure to wave action, altered salinity levels, different substrates, radiation, variable oxygen availability and the threat of desiccation (Light et al., 1975). One of the greatest limiting factors in this zone is predation. The pressures of predation come from marine and terrestrial sources. The diversity and complexities of this dynamic system have been studied in several classic papers. *Food Web Complexity and Species Diversity*, has become a classic example of trophic cascades (Paine, 1966). Predation by the starfish *Pisaster* was a driving force in controlling the abundance of other organisms such as barnacles, *Balanus glandula* and mussels, *Mytilus californianus*, and preventing them from dominating the available space on the rocky substrate habitat. The importance of predation was also highlighted by Dayton (1971), who also examined how physical factors, such as wave exposure, damage from drift logs, and desiccation, impacted the intertidal community. In an example of the intermediate disturbance hypothesis, Dayton
(1971) also examined the biological impacts of competition between sessile organisms and predation by gastropods. He found the combination of these factors worked to increase the diversity in this system by removing organisms that would otherwise dominate in the absence of predators and disturbances. These two classic studies highlight the complexity and interwoven nature of the intertidal systems.

Although natural disturbances in the intertidal zone can impact diversity, human disturbances can upset the balance and work to decrease the system’s diversity and natural functions. Many human disturbances that affect the open ocean, such as pollution, eutrophication, over-fishing and changing sea levels and temperatures, following anthropogenic global warming, also affect the intertidal. In addition the intertidal is subject to unique landside disturbances such as trampling and collecting of the gastropod species *Lottia gigantea* and *Tegulla* (also known as *Clorostoma*) *funebralis* which are an important part of the intertidal community.

The impacts of humans on the intertidal have been documented worldwide in South Africa (Hockey & Bosman, 1986; Bally & Griffiths, 1988), Australia (Keough, Quinn & King, 1993; Sharpe & Keough, 1998), Chile (Moreno, Jara & Sutherland, 1984; Castilla & Duran, 1985), the Pacific Northwest (Brosnan & Crumrine, 1994), and along the CA coast (Beauchamp & Gowing, 1982; Goldstein, 1992; Addessi, 1994; Pombo & Escofet, 1996; Lindberg, 1998; Murray, Denis, Kido & Smith, 1999; Kido & Murray, 2003; Smith & Murray, 2005; Van de Werfhorst & Pearse, 2007; Sagarin, 2007; Fenberg & Roy, 2012). Changes to gastropod communities can affect the whole intertidal community by altering species abundance and diversity. These impacts can have a
cascade effect, altering predation habits by changing prey availability (Lindberg, 1998), and they can shift intertidal communities to be more similar over a large geographical region (Hockey & Bosman, 1986). Protecting the species in these biodiversity hotspots can help these systems be more resilient to the effects of climate change (Hughes et al., 2009). Protecting intertidal areas largely has been found to be an effective management strategy to increase the diversity and abundance of species within their borders (Halpern, 2003). However, even protected areas are influenced by human activities. For this reason, continued research into anthropogenic impacts on the intertidal before and after implementation of MPAs is essential to mitigate negative effects and to help the recovery of these ecosystems.

The purpose of this research is to determine if MPAs along the central California coast are effective at protecting intertidal gastropods, as assessed by their body size and frequency. Although the effects of human activity on the intertidal have been extensively studied in this region, the effects of MPAs on impacts is not known. I designed this study based on similar research conducted by Roy et al. (2003) in Southern California, which found significant positive effects from MPAs with respect to gastropod body size. My study extends this research to Northern CA by comparing shell sizes of a number of gastropod species within MPAs to those outside MPAs and also to museum specimens. This study is designed to provide MPA managers and implementers with the information they need to make informed decisions about how MPAs should be enforced and created with respect to the sensitive and unique intertidal habitat.
Literature Review

Theoretical Basis

**Biodiversity.** As the human population has increased, so have the anthropogenic effects on the ocean. Human effects on the ocean include pollution, eutrophication, acidification, changes in sea level and temperature, and overfishing. These effects can result in habitat degradation and decreases in biodiversity (Jackson et al., 2001). MPAs may be created to protect a particular economically valuable or popular species, but the larger goal of these areas is to maintain and restore the biodiversity that is natural to a particular area. The benefits of biodiversity include both economic potential and the environmental value of ecosystems and organisms. The economic potential of biodiversity is difficult to quantify because of the number of variables and unknowns that exist in the natural world, but ecosystem services are one way that value is placed on the environment (Turner, Brandon, Brooks & Costanza, 2007). Turner et al. (2007) found in terrestrial systems that areas of high biodiversity yielded the highest economic value. In the marine environment, ecosystem services such as fisheries, aquaculture, and recreation have been recognized for their profitability for hundreds of years. Marine ecosystem services that are not as recognized for their economic value include carbon sequestration, flood protection, photosynthesis, and nutrient recycling (Fujita, Moxley, DeBey, Van Leuven & Leumer, 2013). Although a monetary value has not been assigned to all of these services, as disturbances to terrestrial and marine environments continue, methods to manage and restore biodiversity hotspots become increasingly important.
**Impacts of Human Predation on Biodiversity and Body Size.** Human impacts on the environment are working to decrease the abundance and diversity of species and ecosystems worldwide (Hooper, Chapin III, Ewe, Hector & Inchausti, 2005). This decrease can be partially attributed to indirect effects such as pollution and climate change but also to the direct impacts of predation by humans. Although this direct pressure has been placed on terrestrial environments since the beginning of human history, the exponential increase in the human population has increased the impact of predation. The most direct effect of human predation or harvesting, is the reduction in population of a particular species, but impacts can extend beyond reductions in numbers. Because humans are preferentially selecting those species with ecologically beneficially traits, those left behind usually exhibit less desirable ecological traits such as smaller body size and early maturity. This can ultimately impact species fecundity (Allendorf & Hard, 2009). Harvesting can also lead to genetic changes and the loss of genetic variation because of reduced population sizes (Allendorf, England, Luikart, Ritchie & Ryman, 2008).

In terrestrial ecosystems, the impacts of human predation on body size have often been analyzed for animals hunted for trophies. Coltman et al. (2003) and Garel et al. (2007) focused on two populations of commonly hunted sheep in Canada and France, respectively. Both studies found that ram body weight and size decreased in less than 30 years for both populations as a result of human harvesting. This trend has also been seen in deer populations in Hungary (Rivrud, Sonkoly, Lehoczki, Csanyi & Storvik, 2013) and kangaroo populations in Australia (Tenhumberg, Tyre, Pople, & Possingham, 2004). The
largest animals were removed before they could pass on their genetic traits resulting in an overall reduction in body size for their population. This phenomenon has also been witnessed in the marine environment in the fisheries that humans are dependent on for food.

The impacts of human harvesting in the marine environment have reduced many fishery populations to the point of collapse (Jackson et al., 2001). Heino (1998) conducted a meta-analysis of literature on global fish stocks and found that the most heavily exploited fisheries now mature at a younger age and a smaller size. This shift in maturation has been hypothesized as the reason many fisheries have not been able to recover to historic sizes and populations, even when fishing pressure has stopped. Swain Sinclair & Hanson (2007) examined cod populations in the southern Gulf on the coast of the United States. They found that cod stocks accessed in the 1980s matured more quickly and at a smaller size than those measured in the 1970s. This genetic shift in the cod population meant that stocks were not reaching the size considered adequate for fishing. Although factors including temperature changes and other environmental factors could have contributed to the inability of the fishery to rebound, Swain et al. (2007) argued that fishing pressure was likely the greatest pressure driving this shift.

This reduction in body size has also been documented in commonly collected intertidal gastropods. Roy et al. (2003), Erlandson, Rick, Braje, Steinberg & Vellanoweth (2008), McCoy (2008), Braje et al. (2008), and Erlandson et al. (2010) all studied historical specimens of intertidal gastropods and found that increases in human coastal populations corresponded with decreases in shell size of exploited species. The
consequences of body size changes can be detrimental to both the ecological communities and the human communities that are depending on these organisms for sustenance. Changes that have been seen in intertidal communities are transitions to inedible organisms (Hockey & Bosman, 1985), sex ratios shifts (Kido & Murray, 1998) and lower fecundity (Fenberg & Roy, 2012). These consequences of these changes, in addition to the consequences of pollution, habitat degradation and climate change, have led to regulations and protective policies designed to help overfished and overexploited communities rebound.

**Effectiveness of Marine Protected Areas.** Marine protected areas are one strategy used to maintain biodiversity and mitigate human impacts. Global controversy surrounds the implementation of MPAs because of fears of lost fishing revenue, both by local fishermen and corporate fisheries. In addition to these fears, others argue that MPAs are not actually protecting species and ecosystems effectively (McClanahan, 1999). McClanahan (1999) found that only 71% of MPAs were effective. This was, in part due to of lack of management and because of the exploitive practices that were allowed within the MPAs. Many MPAs allow fishing and collecting of fish and invertebrate species. Dayton, Sala, Tegner & Thrush, (2000) used the Monterey Bay National Marine Sanctuary (MBNMS) to explain some of the specific shortcomings of protected areas. Although there are smaller, more extensively protected, areas and reserves within the Sanctuary, the larger Sanctuary only prohibits oil drilling and scientific research without a permit. Other practices, known to be destructive including gill-netting, are allowed at depths of 30 fathoms, despite the negative consequences such
as incidental mortalities of marine mammals and diving seabirds. McClanahan (1999) supported the creation of more “no-take” reserves that prohibit exploitation of all organisms, along with increased enforcement, increased replication of larger protected areas, and increased scientific research to evaluate MPA effectiveness.

Although the effectiveness of different types of MPAs is variable, as McClanahan (1999) states, marine reserves have largely been found to have positive, ecological impacts. Halpern and Warner (2002) and Halpern (2003) examined studies conducted in over 80 marine reserves to determine if reserves were more effective when larger and how quickly they work to restore degraded populations of fish, invertebrates, seabirds, algae and mammals. Halpern and Warner (2002) found that reserves were able to reach mean levels of biodiversity, biomass and organism size and density after 1-3 years of protection and that they maintained these levels. In one case the levels were sustained even 40 years after the establishment of the reserve. The only exception was the recovery of invertebrates within reserves, which was inconclusive. Halpern (2003) also found that reserves were effective at increasing diversity, biomass and size of organisms and density. He also found that reserve size was not a predictor for the level of effectiveness of the reserve. The results of these reviews are encouraging for areas with small reserves, but Halpern (2003) cautioned that larger reserves still result in a larger overall area of protection and should be implemented where possible.

One case study that focused on the effectiveness of a particular marine reserve and its impact on a single algal species, bull kelp (*Durvillaea Antarctica*), was conducted in the marine reserve of Las Cruces along the coast of Chile. In this area, bull kelp was
commonly harvested by indigenous people before European settlement and continued until the reserve was created in 1982. The area was fenced off in an attempt to completely exclude human visitors with the exception of researchers and scientists. Castilla et al. (2007) recorded data before and after the implementation of the marine reserve as well as a nearby area outside the reserve that continued to allow kelp harvesting after 1982. Recovery of the kelp occurred within 5-7 years in the reserve, and areas outside the reserve experienced spillover recovery, although at a delayed rate. Marine reserves do not only increase diversity, biomass, and density within their boundary, but they are exhibiting the desired “spillover” effect.

Positive impacts of MPAs include increases in the biodiversity, species abundance and species richness as well as physiological impacts such as increase in size and gonadal production. Villamor and Becerro (2012) conducted a study over 200 km on the east coast of Spain, which examined five different MPAs and corresponding areas outside of the MPAs. Instead of looking at specific individual species located in each area, Villamor and Becerro (2012) looked at the levels of functional diversity (the number of biological roles, rather than number of species, present in a community) within each area to account for geographic variance that existed between the different locations. They found that although the number of individuals and the species diversity were not always higher, the functional diversity was higher inside MPAs and top predators were significantly more abundant within MPAs. Large scale studies such as that conducted by Villamor and Becerro (2012) can be difficult because of the geographic variance between different locations. However using functional diversity as an indicator allowed the
researchers to make generalizations about the health of these areas despite their other differences.

Castilla et al. (2007) was able to study the effects of a marine reserve that had effectively restricted all human visitation but for many marine reserves human exclusion is not possible because tourism and visitor education are goals of many MPAs. Increased visitation can make MPAs more vulnerable to human disturbance and exploitation. This can inhibit protection and restoration, especially if enforcement of MPA policies is not adequate. For the intertidal community, this can be true as shown by Smith, Fong, Peggy & Ambrose (2008) who studied the effectiveness of marine reserves in protecting mussel beds along the coast of California. Because mussel beds are often exposed, they are vulnerable to trampling or overturning rocks at low tides. Reserve protection was not enough to prevent destruction of mussel beds and biomass and coverage were not higher within reserves. Although contradictory to most of the results from study of marine reserves, this research exposes that even marine reserves are susceptible to anthropogenic impacts, especially in exposed intertidal zones that experience heavy human visitation.

Most studies attempting to quantify the effectiveness of MPAs choose to focus on one or a few species in smaller areas, but knowing the appropriate scale for a study is imperative. Lasiak (2006) used a combination of spatial scales to evaluate the effectiveness of marine protected areas and also to determine at which scale effectiveness was best measured. She found that, at these particular sites along the coast of South Africa, variability at the site (largest scale) level was small, but that variability between shores (medium scale) and plots (smallest scale) was much higher. Because variability
can be high on small scales, Lasiak (2006) recommended using several species as indicators, rather than focusing on only one, and that many replicates were needed at the plot and shore level in order to account for high variability.

Branch and Odendaal (2003) conducted a study along the same shoreline in South Africa and examined whether MPAs were specifically impacting the intertidal limpet *Cymbula oculus*. They found that within the MPAs limpets were 30-50% larger, consisted of older individuals, and had increased survivorship and higher reproductive output, than those outside of the MPA. Species diversity was higher outside of the MPAs, which Branch and Odendaal (2003) attributed to the intermediate disturbance hypothesis (Connell, 1978), because harvesting could have produced more open space allowing for recruitment of more species. Branch and Odendaal (2003) also found significant recovery of *C. oculus*, suggesting that this MPA has been effective, despite the variability of the area, later recognized by Lasiak (2006). These two studies show that even in this dynamic system, patterns can be revealed as long as the spatial scale and species are chosen correctly. The variability in the success of MPAs highlights potential gaps in MPA protection and why there is a need for continued monitoring and research. In addition understanding the human activities that continue within MPAs and the impact of those activities can help managers rectify some of the gaps in protection, which may be a result of tourism and other public access.

**Vulnerability of Intertidal Zones**

**Effects of Trampling on the Intertidal.** Anthropogenic impacts have extended to every ecosystem in the ocean but the intertidal is the most accessible and therefore the
most vulnerable portion of this environment. This region is susceptible to pollution and overfishing that extends out to sea, and it is also victim to trampling and collecting. This area has received more focus from the scientific community as the impact of these seemingly benign activities have become more apparent. Some researchers have chosen to examine the effects of trampling and collecting separately, but others have combined these often linked impacts. Studies that have focused on impacts of direct trampling include Beauchamp and Gowing (1982), Bally and Griffiths (1988), Povey and Keough (1991), Goldsten (1992), Schiel and Taylor (1999) and Van der Werfhorst and Pearse (2007).

Beauchamp and Gowing (1982) quantified how the intertidal was impacted by human traffic. Their research, along the coast of central California next to Natural Bridges State Park (part of Natural Bridges State Marine Reserve), compared three sites with varying levels of human attendance. These sites were close enough to each other to be considered comparable habitat but one plot was easily accessible and regularly visited, the second plot less accessible and only moderately visited and the third plot, was difficult to access and characterized as “untrampled”. The number of visitors was counted at each plot, in order to determine how much trampling occurred at each, and the level of diversity of each plot was measured using the Shannon-Wiener diversity index. Beauchamp and Gowing (1982) found that less trampled sites had larger biomass of CA mussels (Mytilus californianus) as well as more bivalves and more algal cover, but overall diversity was similar between the three sites. This study was reexamined by Van de Werfhorst and Pearse (2007), who added a stratified sampling technique that took tidal
height into account. This method allowed Van de Werfhorst and Pearse (2007) to account for variability at different tidal heights. They found that diversity decreased significantly with the number of human visitors to the specific plot.

In a South African marine reserve, Bally and Griffiths (1988) studied how different types of footwear and different levels of trampling affected the intertidal communities. Most visitors were found to wear no footwear or neoprene thongs and had relatively low impact on intertidal organisms, even at high levels of trampling. They hypothesized that the strong wave action experienced by this area was more impactful than the effects of human trampling. Povey and Keogh (1991) also examined trampling at different levels of intensity, specifically focusing on intertidal gastropods and algae. Because they had observed individuals kicking limpets to dislodge them, they included this activity in their trampling study. Gastropods were not impacted substantially by trampling, even when it occurred at high intensities. Conversely, algal species were found to lose as much as 20% of their biomass with a single step and had only recovered by 50% five months after trampling events (Povey & Keogh, 1991).

Similar to Bally and Griffiths (1988) and Povey and Keogh (1991), Schiel and Taylor (1999) examined how different levels of trampling impacted the algal species, _Hormosira banksii_, in New Zealand. They experimentally conducted trampling at different levels of intensity and found that up to 90% of the algae was removed from intense levels of trampling. The timing of the trampling events was also important because recruitment for this species only occurred in the summer. These three studies show how difficult quantifying intertidal community impacts are because of the large
number of forces at work. The organisms that live in this dynamic system are resilient to physical and biological stresses because they have evolved with exposure to wave action, radiation and predation from terrestrial and marine environments. Although significant impacts were detected by Van de Werfhorst and Pearse (2007) and Povey and Keogh (1991), in most trampling research conducted in the intertidal, once organisms were no longer exposed to the disturbance they were able to recruit juveniles and recover biomass. With the exception of Beauchamp and Gowing (1982) these studies were conducted for one season and not repeated in the same area. They did not address the effect of long term trampling over time nor if persistent disturbances could drive shifts in community structure or a decrease in biodiversity.

**Effects of Collecting on the Intertidal.** Collection of intertidal organisms is common for human consumption, bait, souvenirs and aquaria (Murray et al., 1999). The effects of collection on the intertidal has been more widely documented than the effects of trampling. Moreno et al. (1984) studied the impacts of Chilean fishermen on intertidal communities in a newly established marine reserve near Mehuin, Chile. They found that after the exclusion of humans from this area the levels of macroalgae declined significantly and the commonly collected intertidal limpet, *Fissurella* spp., increased in abundance and size. Comparatively, the size of another intertidal gastropod common in the area but not collected, *Siphonaria lessoni*, decreased in size after the creation of the marine reserve. Moreno et al. (1984) concluded that *Fissurella* spp. were keystone herbivores and once protected from collection they dominated the macroalgae food source. In the absence of *Fissurella* spp., *S. lessoni* were able to thrive.
Also along the Chilean coast, Castilla and Duran (1985) studied the impacts of a newly created preserve and how protection impacted the intertidal community structure. Like *Fissurella* spp., studied in Moreno et al. (1984) the intertidal gastropod, *Concholepas concholepas*, was another economically important and frequently collected organism in the region. After protection Castilla and Duran (1985) observed significantly higher numbers of *C. concholepas* and a decrease in the local mussel species, *Perumytilus purpuratus*. To further investigate the impacts of collection, they experimentally collected *P. purpuratus* within the protected region. They found that, in regions where *P. purpuratus* was collected, mussel bed cover remained high and overall diversity was reduced because there was less bare rock for other algae and sessile organisms to settle on.

Although Castilla and Duran (1985) found a decrease in diversity as a result of collecting, Hockey and Bosman (1986) found opposite results along the east coast of South Africa. The region of study was commonly used as a collection site for the indigenous people so they were able to make comparisons between several exploited and protected sites. In addition they were also able to determine the most common and the size of species being collected from the “middens” or shell piles, left by the indigenous people. They found that although there was a reduction of size and abundance of the species that were most exploited, species diversity remained high because of the influx of inedible species that began to dominate the intertidal. They also found that exploited areas had shifted to more similar community assemblages, regardless of what had been there before. Although diversity remained high, the shift toward inedible species led
Hockey and Bosman (1986) to suggest a “crop-rotation” strategy for the people
dependent on the intertidal gastropods, to allow the intertidal to recover and maintain
edible species abundance.

Several studies which have examined the impacts of intertidal collection have also
taken place along the coast of Australia. Sharpe and Keough (1998) and Keough et al.
(1993) looked at the frequency and kinds of collection as well as what physiological
impacts and community structure impacts collection had on the intertidal community.
Like the Chilean and South African studies, Sharpe and Keough (1998) and Keough et al.
(1993) found that collection resulted in larger amount of macroalgae cover and that
species of gastropods that were preferentially collected exhibited smaller sizes. There
was no change in the size or abundance of species that subject to collection. Across the
globe, these studies have found that human collecting can have large impacts on
community structure, diversity and species abundance but because the intertidal is a
resilient system, impacts can be mitigated through enforced protection.

In the United States the majority of intertidal collection studies have been
conducted along the southern California coast. Addessi (1994) focused on the
intermediate disturbance hypothesis (Connell, 1978) and if human disturbances, such as
over-turning boulders and walking, acted to increase diversity and abundance or if the
level of disturbance was pushing the community over the level from which it could
recover. Like previous studies, Addessi (1994) documented the level of human visitation
but unlike regions in the southern hemisphere, the highest visitation occurred during
high-tides so the intertidal was largely protected. She also determined the frequency of
overturned rocks as well as the abundance of commonly collected invertebrates using band transects. She found that the act of overturning rocks had large community impacts because it interrupted the successional processes of algal growth and subsequent recruitment of other organisms.

Lindberg (1998) further explored how community structures are impacted by human collection and included an intertidal predator, the black oystercatcher (*Haematopus bachmani*). Because oystercatchers largely avoid areas of high human visitation they conducted this study on San Nicolas Island, off the coast of San Diego as well as a few sites in central, mainland California. They found that in areas with a high frequency of black oystercatchers, owl limpets (*Lottia gigantea*) were found only on vertical substrates. They also experimentally removed large owl limpets which resulted in higher numbers of small limpet species. After removing the smaller limpet species, erect algal species were free to dominate the open space. The experimental removal of the integral owl limpet exposed how impactful human collection can be and how many trophic levels can be affected by changes to a single species.

Although MPAs have been established along the southern coast of California in an attempt to prevent areas from being overexploited, Murray et al. (1999) found that even in California Marine Life Refuges (similar to MPAs before the passage of the Marine Life Protection Act in 1999) and State Ecological Reserves, visitors were collecting illegally and enforcement was rare. Murray et al. (1999) studied the frequency of human attendance to the intertidal as well as the species and the amount of each species most collected. They found that most of the species collected (i.e. mussels,
trochid snails, limpets, urchins, and octopi) were broadcast spawners (reproduction strategy in which females release eggs into the water column and males release spermatozoa to fertilize the eggs), which needed higher numbers to maintain reproductive success. They also found that the species that were collected most frequently had the lowest abundances in the field. This study highlighted that although protection is an important aspect of protecting the marine enforcement, even within areas of protection, exploitation can have substantial consequences.

Kido and Murray (1998) focused on the community structure forming owl limpet in four sites within MPAs along the coast of southern California, but unlike Lindberg et al. (1998), in the absence of the already extirpated, black oystercatcher. They measured limpet size, growth rate, age, sex ratios, gonadal production and abundance as a function of human visitation. They found that the largest limpets were within MPAs and that the level of human visitation had a negative correlation with limpet size. At some sites, they found that the abundance of small owl limpets was higher than expected but they conjectured that this may have been because there was less territory being dominated by larger individuals. This is similar to the results seen in Castilla and Duran (1985) and Murray (1999). However because larger female owl limpets have exponentially larger gonadal production as they increase in size, Kido and Murray (1998) emphasized that removing larger individuals could have large impacts on the fecundity of the species. In addition because owl limpets are protodandrous hermaphrodites, and become female only as they get larger and older, removing the largest individuals skewed sex ratios and caused males to become females at a smaller size than seen in unexploited populations.
As males become females earlier and at smaller sizes, they may reproduce less effectively in the future and population size could suffer (Fenberg & Roy, 2012). Like Lindberg et al. (1998), Kido and Murray’s (1998) study showed the cascade of reactions that can result from collection. Although the impacts on exploited species can be detrimental, human impacts can reach even further to impact whole community structures.

In many cases, in order to collect organisms, fishers and collectors must trample a site. Smith and Murray (2005) looked at the combined impacts of collecting and trampling on mussel beds (Mytilus californianus) in Monarch Bay, south of Los Angeles. They experimentally trampled sites at different intensity levels and at certain plots (0.5 m x 0.7 m) removed two mussels per month. Smith and Murray (2005) found that at sites that had received trampling and mussel removal, mussel mass was reduced by up to 80%. They also compared the amount of mussel mass at the time of their study with the mussel mass from measurements taken in the 1970’s. The previous research had reported 10 times the amount of mussel mass as the 2005 study and that mussel beds in the past had been composed of several layers, as opposed to the single layer beds seen today (Straughan & Kanter, 1977).

Because the processes in the intertidal are so interconnected, distinguishing what is causing the highest impact can be difficult. Sagarin et al. (2007) wanted to differentiate the impacts of human visitation, human foraging, animal predation, geographic gradients and sampling biases. They examined habitats north of Santa Barbara, CA, on either side of Point Conception and at several sites off the coast of CA on the Channel Islands. Using sites on either side of Point Conception as a test of
geographic gradients, because of the regions large shift in temperature, nutrient availability and wave action, they found that limpets showed similar size on each side. By comparing the mainland sites, where black oystercatchers had been extirpated, with island sites, where oystercatchers were common, they were able to examine the effects of predation. They found that oystercatcher predation did not have a great impact on the size of owl limpets because they did not preferentially take the largest specimens. Human foraging however was impactful, as seen in previous studies, and drove owl limpet size down. Levels of human visitation did not influence the size of limpets; however, Sagarin (2007) acknowledged that with increased human visitation, the likelihood of poaching probably increased as well.

Although many of these studies show how different reactions can be to anthropogenic impacts they also show that these impacts can have detrimental consequences. In some ecosystems human disturbance is not powerful enough to decrease diversity and it can work to increase diversity. It can also lead to dramatic community structure shifts and changes in trophic interactions. For some species impacts are felt more strongly because of their life histories and biology. Because coastal populations are continuing to grow, understanding the impacts of trampling and collecting are going to continue to be critical components of ocean management and conservation. This understanding can be enhanced by looking into the past to build a picture of what human impacts on the intertidal have been throughout human history.

**Establishing Baseline Data for Intertidal Gastropods.** In order to better understand the impact that humans have had through time, collecting baseline data is vital
to give managers and conservationists have a more complete picture of what “baseline conditions” once were. Archeological studies have attempted to fill in the gap in baseline data through examination of middens or shell mounds left behind by indigenous peoples. Many of these studies have been conducted on the Channel Islands off the coast of California because of the availability of preserved middens and the relatively well known history of human occupation (Braje, Kennett, Erlandson, & Culleton, 2007; Erlandson et al., 2008; Erlandson et al., 2010).

Erlandson et al. (2008) and Erlandson et al. (2010) both conducted studies on the Channel Islands off the coast of Santa Barbara, California. Using over 10,000 years of data from the shell middens on the islands they were able to determine what species were commonly eaten by the prehistoric inhabitants as well as the shifts in animal shell size, and how what people were eating changed through time. They found that mollusk shells decreased significantly from the middle to late Holocene period (7500 BP – 3360 BP). They compared their results to sea temperature to ensure that their findings were due to human exploitation and found no significant correlation between shell size and sea temperatures. In fact, the greatest decrease in shell sizes were seen during periods of large human population growth on the islands. Erlandson et al. (2010) hypothesized that even with these decreases in size, the island people maintained the mollusk populations in a somewhat sustainable way by rotating through sites, leaving some areas unexploited for long periods of time.

In a similar study conducted on the Channel Islands, Braje et al. (2007) examined Santa Rosa Island specifically and the prehistoric human impacts on the intertidal. By
looking at shells and bones from middens they found that as human populations on the islands were increasing, the size of mussels decreased. They also found a decline in the number of red and black abalone found in the middens, as populations of those species declined. As mussels decreased in size and abalone abundance decreased, the Chumash Native Americans, switched from depending mostly on the intertidal, to depending mainly on pelagic fish as their primary food source. One benefit of having a long data set is Braje et al. (2007) were able to see how fluctuations like warm and cold cycles in sea surface temperature effected intertidal organisms, and like Erlandson et al. (2008, 2010), separate those effects from human effects.

McCoy (2008) conducted a unique study on the Hawaiian island of Moloka‘i which combined data from archeological specimen, present day specimens, wave action and the effects of rapid human population decline on the intertidal (McCoy, 2008). The Kalaupapa peninsular, the focal study site for this research, showed signs of human activity from around 1100 AD but only had a permanent population of indigenous people from around 1650. In 1866, after European settlement of the islands, individuals with Hansen’s disease (leprosy) were moved to this relatively isolated area. This resulted in a dramatic decline in the population from over 3000 to less than 300 people. They found that the focal species, the limpet Cellana spp., had been decreasing in size until 1866 when the human population declined. From the time that Hansen’s patients were relocated, the size of this species steadily increased. This event acted as protection for this area and allowed McCoy to observe the switch from an exploited environment to an unexploited environment in a single area within a short period of time.
These four studies allowed modern day researchers to better understand how humanity has altered the marine environment through time, rather than only focusing on the present day. They also provide more baseline data so that current research is able to accurately measure the impacts seen today. The areas chosen for these studies were unique because they were preserved in such a way that allowed for thousands of years of data to be studied and analyzed. In most locations researchers are confined to their own lifetimes or the data sets of previous research. However a few studies have overcome this limitation by studying the specimens housed in museums. Although these collections do not always reach as far back as archeological middens they can provide further insight into what “baselines” conditions are for many locations.

One such study, conducted in along the coast of southern California, compared the size of present organisms with historical specimens, dating back to 1869, to determine if species size had change through time (Roy et al., 2003). Using four species, two collected by humans and two uncollected by humans, they made comparisons between species before and after the largest human populations increases southern California. They found decreases in the body size of exploited populations and in one of the unexploited species. Roy et al. (2003) triangulated their results by also examining the effects of protection on their focal species. Measurements of museum and modern specimens from the protected area showed that after protection, shells began to significantly increase in size. Because managers and researchers are basing the effectiveness of MPAs off of baseline data studies like Roy et al. (2003) this research is essential for understanding of what populations and communities were like in the ocean
before human exploitation became as extreme as it is today. Although the history of the impacts humans have had on the ocean may never be fully complete, continuing to examine what conditions were like in the past can help guide our actions for managing and protecting the ocean in the future.

**Research Objectives**

The human impact on the ocean is widespread and is substantially altering the marine environment. In the intertidal, trampling and collecting gastropods and other intertidal species decreases body size in affected populations. Changes in animal sizes can have significant impacts on the community structure and ecology of these organisms and the ecosystems they inhabit. MPAs are one way of protecting species and habitats from exploitation, but varying protection and enforcement can limit the effectiveness of many of these areas. Understanding which protected areas are working effectively is essential for creators and managers of MPAs so that they can continue to evolve how MPAs are established and maintained.

This study documented the sizes and frequencies of five gastropod species at specific locations along the central California marine intertidal zone inside and outside MPAs, to assess the efficacy of MPAs in protecting gastropod populations from decreases in average body size and frequency. I assessed this question by addressing the following research questions and hypotheses:

**Q1:** How do focal species differ in body size within MPA and within non-MPA field locations?
Q2: What factors may contribute to the gastropod sizes and frequencies observed? For example, do species’ life histories, whether organisms are collected or not, typical exposure (under or on top of rocks) or other obvious factors seem to play a role in the size, abundance or prevalence of each species?

H₀₁: The average body size of gastropod species sampled inside MPAs – both those species collected and those not collected by humans--will not differ from:
   a) non-MPA field locations or
   b) museum specimens.

H₀₂: For both collected and uncollected species the frequency of gastropod species present inside MPAs will not differ from non-MPA field locations.

H₀₃: Museum specimens before 1950 will not differ in average body size from those collected after 1950.

Methods

Study Site

The Monterey Bay National Marine Sanctuary (MBNMS or the Sanctuary) is located along the central coast of California, stretching from the San Francisco Bay to Cambria, CA (Figure 1). The Sanctuary is administered by the National Oceanic and Atmospheric Administration, National Ocean Services of the U.S. Department of Commerce. The Monterey Bay (the Bay) area is characterized by moderate dry summers with high cloud cover from May to October and a wet season from November to April. The Bay and the surrounding area are considered biodiversity hotspots, largely due to the
oceanographic pattern of seasonal upwelling (February to July) that brings cold, nutrient rich waters from the deep ocean to support a wide variety of species (Ricketts et al., 1985).

Twenty-four marine protected areas (MPAs) have been established within the MBNMS along the coast of California as part of the Marine Life Protection Act of 1999. These MPAs include state marine reserves (SMR) and state marine conservation areas (SMCA). SMRs are no-take areas that do not allow the removal of any species from within their boundaries. SMCAs allow commercial and recreational take of certain species (Table 1). The central coast MPAs were officially established in 2007 and the north central coast MPAs were established in 2010. One MPA from the north central coast and five from the central coast are the focal locations for this study. From north to south, these MPAs include: Montera SMR, Año Nuevo SMCA, Natural Bridges SMR, Pacific Grove Marine Gardens SMCA (Point Pinos) and Asilomar SMR. (Figure 2).
Figure 1 Monterey Bay National Marine Sanctuary along the coast California, including State Conservation Areas and State Reserves (Google Earth, 2014).
Table 1. Central Coast MPA Take Allowances. X indicates the allowed take from each of the central California coast SMRs and SMCAs sampled for this study (California Department of Fish and Wildlife Code, 2013). (G) indicates giant kelp (Macrocystis pyrifera) and (B) indicates bull kelp (Nereocystis luetkeana).

<table>
<thead>
<tr>
<th>MPA</th>
<th>Year Official MPA Began</th>
<th>Location</th>
<th>Commercial Take</th>
<th>Recreational Take</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monterey SMR</td>
<td>2010</td>
<td>37°31'17.15&quot;N 122°30'55.36&quot;W</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Año Nuevo SMCA</td>
<td>2007</td>
<td>37°5'15.87&quot;N 122°16'29.18&quot;W</td>
<td>X</td>
<td>X X X X</td>
</tr>
<tr>
<td>Natural Bridges SMR</td>
<td>2007</td>
<td>36°56'57.87&quot;N 122°3'42.52&quot;W</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Asilomar SMR</td>
<td>2007</td>
<td>36°38'4.19&quot;N 121°56'21.26&quot;W</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific Grove Marine Gardens SMCA</td>
<td>2007</td>
<td>36°38'14.31&quot;N 121°56'9.81&quot;W</td>
<td>X X</td>
<td>X</td>
</tr>
</tbody>
</table>
Figure 2. Study Region. Map of the central California coast study sites (Google Earth, 2014) with protected sites (MPA sites) outlined by circles and unprotected sites (non-MPA sites) outlined by rectangles. Black circles represent protected sites that were only compared to museum data.
Natural Bridges was partially protected before the official creation of the MPAs by state park rangers who had been present in the area since the creation of the adjoining state park in 1954 (CA Department of Fish and Wildlife, 2014). Point Pinos was also protected as the Pacific Grove Gardens Marine Refuge beginning in 1952 (Kimura, 2003).

The SMCAs in this area prohibit the take of all living marine resources, with the exceptions of some commercial and recreational take, including giant kelp (Macrocystis pyrifera), bull kelp (Nereocystis luetkeana), squid, salmon and other finfish (Table 1). The SMRs prohibit take of all living marine resources (California Department of Fish and Wildlife, 2013). Within the MBNMS and each of the SMCAs and SMRs are a variety of habitats that make up the coast, such as sandy beaches and estuaries, but this research will focus only on the rocky intertidal.

The rocky intertidal is often divided into descriptive zones characterized by tide levels for ease of study. The uppermost horizon is mainly composed of bare rock, where only the splashes of large waves reach. Species that reside in this area can survive for long periods of time without exposure to the marine environment. The high intertidal, between the high tide line and the mean tide line, is more diverse than the uppermost region. This area experiences two high tides daily and can also maintain permanent tide pools. The more diverse middle intertidal is uncovered daily by most low tides. This area is home to beds of anemones (Actiniaria), limpets (Acmaeidea and Patellidae), seastars (Asteroidea), crabs (Brachyura), sponges (Porifera), chitons (Polyplocophora), brittle stars (Ophioroidea), isopods (Isopoda), as well as other low intertidal organisms.
that remain protected under lush algal growth. The low intertidal is only exposed at minus tides that only occur a few times per month. This is the most diverse of the intertidal zones but often the most difficult to study because it is the least accessible (Ricketts et al., 1985). This research will focus on species living in the three highest zones, the uppermost horizon, high intertidal and middle intertidal.

The focal organisms for this study were gastropod species including one limpet species, *Lottia gigantea*, one snail species, *Tegula funebralis*, and three whelk species, *Nucella emarginata/ostrina, Ocenebra circumtexta, and Acanthinucella spirata/punctulata*. These species are all common in the rocky intertidal along the central California coast. Two of the species (*Lottia gigantea* and *Acanthinucella spirata/punctulata*) chosen for this study were the same as studied by Roy et al. (2003) in southern California. *Ocenbrina circumtexta* was chosen because it is easily identified, common in the intertidal and not known to be a collected species (Light, 1975). *Tegula funebralis* was selected because it is extremely common in the intertidal, known to be collected, and is easily identified. Specimens of the focal species for this study were examined at the Pacific Grove Natural History Museum, California Academy of Science (San Francisco), University of California Museum of Paleontology (Berkeley) and Santa Barbara Museum of Natural History.

**Study Design**

Nine field locations, six north of Monterey Bay and three south of Monterey Bay, were chosen based the presence of rocky intertidal habitat and presence of focal species.
For the northern field locations three pairs of MPA and non-MPA field locations were selected. From north to south these paired field locations were Fitzgerald (MPA) and Pigeon Pt. (non-MPA), Ano Nuevo (MPA) and Davenport Landing (non-MPA), Natural Bridges (MPA) and Almar St. (non-MPA) (Figure 2). An additional field location was added at Natural Bridges because this second area was less accessible to the general public (J. Pearse, pers. comm.). The three southern locations were all MPA field locations: Pt. Pinos, Asilomar and Asilomar 2. At each field location at least 20 points were sampled with the intention of measuring at least 20 specimens of each species.

Museums and universities were contacted to determine if specimens from the central California coast region were available from their collections. The Pacific Grove Natural History Museum, California Academy of Science (San Francisco), University of California Museum of Paleontology (Berkeley) and Santa Barbara Museum of Natural History had collections with specimens from the desired region. All specimens in the collections that had been collected in the study region were measured, including areas nearby to the selected field locations, with the intention of obtaining museum measurements from at least 20 individuals of each species from each field location.

**Data Collection.** I determined MPA and non-MPA field site locations by visiting each area and identifying suitable habitat of low, high and middle intertidal at each field location. GPS coordinates were taken at each location so that suitable field sites could be found using Google Earth. Using Google Earth and the Earth Point grid (http://www.earthpoint.us/) a 1 m² resolution grid was laid over each intertidal field location selected for this study. Using Earth Point and a random number generator
(http://www.random.org/), 30 points were selected at each intertidal location. Twenty of these were randomly selected for initial sampling and 10 extra were reserved if additional sampling points were needed in the event 20 individual specimen of each species were not be found at the first 20 points. A GPS unit was used in the field to locate each preselected point using UMI coordinates. Sampling was conducted from June 2014 to September 2014, an hour and a half before and after low tide.

I measured adult specimens, whether in the field or in the museum, that were above the minimum size at which the species could be visually identified and distinguished from other species (Table 2). Specimens were measured at the longest point on the shell using calipers (Figure 3) to the nearest 0.5mm. A California State Park System permit was obtained to conduct research within Natural Bridges, Año Nuevo and Asilomar State Parks. A Fish and Wildlife Scientific Collections Permit and County of San Mateo Scientific Research and Collections Permit were obtain to conduct research with Montera SMR. It was determined that, using these methods, IACUC approval or an exemption was not necessary (L. Young, pers. comm, 04/22/14).

Table 2. Focal Species. Thresholds and collection status shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Threshold</th>
<th>Collected for food or bait?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lottia gigantea</td>
<td>Owl Limpet</td>
<td>3.0cm</td>
<td>Yes</td>
</tr>
<tr>
<td>Ocenebra circumtexta</td>
<td>Circle Dwarf Triton</td>
<td>1.5cm</td>
<td>No</td>
</tr>
<tr>
<td>Acanthinucella spriata/punctulata</td>
<td>Angular Unicorn</td>
<td>1.5cm</td>
<td>No</td>
</tr>
<tr>
<td>Tegula funebralis</td>
<td>Black Turban Snail</td>
<td>1.5cm</td>
<td>Yes</td>
</tr>
<tr>
<td>Nucella emarginata/ostrina</td>
<td>Emarginate Dog Winkle</td>
<td>1.5cm</td>
<td>No</td>
</tr>
</tbody>
</table>
Figure 3. Measuring a specimen, using calipers to measure the length of a L. gigantea specimen at the longest point on the shell (C. Bednar, personal photograph, July, 2014).

Specimen size was measured in the field and at museums. Only specimens over a predetermined threshold were measured (Table 2). These threshold sizes represent the minimum adult size for each species and the minimum size at which these species can be distinguished easily from each other.

Individuals of Lottia gigantea, Acanthinucella spriata/punctulata, Ocenbra circumtexta and Nucella emarginata/ostrina were measured at the pre-selected 20 sampling points. I searched for any individuals over the threshold size in a circular pattern moving slowly outward. Searching continued for seven minutes including measurements, at each grid point. If no specimens were found of one of the species, an
extra grid point was selected from the 10 extras and that species was searched for in that new area until at least one individual of each target species has been located at each GPS point or all 30 grid points have been exhausted. The slippery, rocky terrain at the Pigeon Pt. field location required additional search time at each sampling point so approximately seven minutes of effort was put in at each sampling point. Because of the relative rarity of *Lottia gigantea*, *Ocenebra circumtexta* and *Acanthinucella spirata/punctulataa* all individuals found within the seven minute period were measured.

*Tegula funebralis* was much more common than other species therefore quadrats were used for sampling of this species. I collected data in a 0.25 m$^2$ plot at each one of the 20 preselected points. Ten individuals of *Tegula funebralis* within the 0.25 m$^2$ plot and over the threshold size (Table 2) were measured using calipers at the longest point on the shell. Measurements of individuals closest to the perimeter of the square were measured first. If 10 individuals were not available within the 0.25 m$^2$, as many as could be found within the square were measured. If no individuals could be found within the square, the first individual found outside of the square (during the search for the other focal species) was measured. Any *Tegula funebralis* shells that were inhabited by *Pagurus* spp. (hermit crabs) were not measured, in order to avoid disturbing the crabs.

For museum specimens, I recorded the date of collection, or latest possible date of collection, collector, collection site, and size of each individual (Figure 4). If there was no collection date recorded for a specimen, the latest possible date was extrapolated based on the life span of the collector. The earliest specimen measured was dated 1883 and the latest was dated 1989. For analysis, organisms were divided into two time
periods, before 1950 and after 1950. The reason for this division was to test if the increase in human population along the central coast after 1950 had an impact on the body size of focal intertidal gastropods.

Figure 4. Museum Specimen. Drawer of *T. funebrallis* at University of California Berkeley (C. Bednar, personal photograph, November, 2014).

**Data Analysis.** For analysis, all measurements collected at a single GPS point were averaged and represented a plot. Museum specimen that were collected from the same region within the same year were averaged to represent a plot.

The independent variables analyzed for this study included field site locations (categorical), whether the site was an MPA or non-MPA (categorical) and the time period of museum specimen (before 1950 and 1950 or later) (categorical). The dependent
variables analyzed for this study were gastropod shell size (continuous) and presence/absence (categorical). ANOVA, or Kruskal Wallis for data that did not meet assumptions for normality and homogeneity of variance were used to determine differences between MPA field locations and non-MPAs field locations and differences between pre-1950 and post-1950 museum samples and each of these parameters compared to each other. Chi-square test was used to determine if there were a difference in the presence of species between the actual and expected values.

**Results**

Individuals of all five focal species were measured at ten field locations, three non-MPA and seven MPA, as well as at three museums. A total of 2510 individual specimens were measured, 1228 individuals at 520 sampling points from field locations and 1282 individuals from museums. For museum specimens, the mean of individuals with the same year and site collected was determined for a total of 138 samples. There was variability within non-MPA field locations and within MPA field locations for all species sampled. Thus compiling non-MPA field locations and MPA field locations together captured a range of variability on the central California coast (Tables 3, 4 and 5).
Table 3. Summary of non-MPA Field Location Data. The number of plots in which organisms were found at each field location, sampled between June – August, shown with mean body size ($\bar{X}$) ± standard error (SE).

<table>
<thead>
<tr>
<th>Species</th>
<th>Davenport</th>
<th>Almar St.</th>
<th>Pigeon Pt.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td># of Plots</td>
<td>$\bar{X}$ ± SE</td>
<td># of Plots</td>
</tr>
<tr>
<td>A. spirata/punctulata</td>
<td>11</td>
<td>1.83 ± 0.06</td>
<td>2</td>
</tr>
<tr>
<td>N. emarginata/ostrina</td>
<td>20</td>
<td>1.70 ± 0.04</td>
<td>19</td>
</tr>
<tr>
<td>L. gigantea</td>
<td>1</td>
<td>3.33</td>
<td>10</td>
</tr>
<tr>
<td>C. funebrallis</td>
<td>20</td>
<td>1.83 ± 0.05</td>
<td>19</td>
</tr>
<tr>
<td>O. circumtexta</td>
<td>1</td>
<td>1.54</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 4. Summary of Museum Data. The number of plots (individuals collected within the same year at the same location) shown with mean body size ($\bar{X}$) ± standard error (SE).

<table>
<thead>
<tr>
<th>Species</th>
<th>Pre-1950</th>
<th>Post-1950</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td># of Plots</td>
<td>$\bar{X}$ ± SE</td>
</tr>
<tr>
<td>A. spirata/punctulata</td>
<td>22</td>
<td>2.27 ± 0.08</td>
</tr>
<tr>
<td>N. emarginata/ostrina</td>
<td>12</td>
<td>2.33 ± 0.13</td>
</tr>
<tr>
<td>L. gigantea</td>
<td>11</td>
<td>5.07 ± 0.46</td>
</tr>
<tr>
<td>C. funebrallis</td>
<td>8</td>
<td>2.24 ± 0.14</td>
</tr>
<tr>
<td>O. circumtexta</td>
<td>9</td>
<td>1.80 ± 0.06</td>
</tr>
</tbody>
</table>
Table 5. Summary of MPA Field Location Data. The number of plots in which organisms were found at each field location, sampled between June – August, shown with mean body size ($\bar{X}$) ± standard error (SE).

<table>
<thead>
<tr>
<th>Species</th>
<th>Ano Nuevo</th>
<th>Point Pinos</th>
<th>Asilomar</th>
<th>Asilomar 2</th>
<th>Natural Bridges</th>
<th>Fitzgerald</th>
<th>Natural Bridges</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td># of Plots</td>
<td># of Plots</td>
<td># of Plots</td>
<td># of Plots</td>
<td># of Plots</td>
<td># of Plots</td>
<td># of Plots</td>
</tr>
<tr>
<td>A. spirata/punctulata</td>
<td>17</td>
<td>18</td>
<td>20</td>
<td>1</td>
<td>1</td>
<td>20</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2.08 ± 0.04</td>
<td>2.02 ± 0.06</td>
<td>1.92 ± 0.05</td>
<td>1.96</td>
<td>1.53</td>
<td>2.14 ± 0.04</td>
<td>0</td>
</tr>
<tr>
<td>N. emarginata/ostrina</td>
<td>10</td>
<td>8</td>
<td>0</td>
<td>12</td>
<td>20</td>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>1.62 ± 0.04</td>
<td>2.20 ± 0.17</td>
<td>-</td>
<td>2.13 ± 0.04</td>
<td>1.74 ± 0.05</td>
<td>1.58 ± 0.03</td>
<td>1.66 ± 0.03</td>
</tr>
<tr>
<td>L. gigantea</td>
<td>0</td>
<td>-</td>
<td>11</td>
<td>0</td>
<td>14</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>4.96 ± 0.19</td>
<td>5.04 ± 0.20</td>
<td>4.32 ± 0.33</td>
<td>5.32 ± 0.31</td>
<td>6.33 ± 0.23</td>
</tr>
<tr>
<td>C. funebrallis</td>
<td>25</td>
<td>20</td>
<td>20</td>
<td>17</td>
<td>14</td>
<td>10</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>2.08 ± 0.05</td>
<td>1.76 ± 0.05</td>
<td>1.76 ± 0.04</td>
<td>1.81 ± 0.06</td>
<td>1.73 ± 0.03</td>
<td>1.91 ± 0.03</td>
<td>1.66 ± 0.04</td>
</tr>
<tr>
<td>O. circumtexta</td>
<td>0</td>
<td>1</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>1.55</td>
<td>1.69 ± 0.09</td>
<td>-</td>
<td>-</td>
<td>0</td>
<td>1.87 ± 0.04</td>
</tr>
</tbody>
</table>
**Acanthinucella spirata/punctulata**

*A. spirata/punctulata* average body size differed comparing pre-1950, post-1950, non-MPA field locations and MPA locations (H=22.83, p<0.001). There was no difference in the average body size between museum specimens collected before 1950 and those collected after 1950 (U=182.00, p=0.859). However, the average body size of *A. spirata/punctulata* from MPA field locations (2.03±0.055 SE) was larger than the average body size inside non-MPA locations (1.87±0.055 SE) (U=688.00, p=0.031). The average body size of *A. spirata/punctulata* from museum specimens, both those collected before (2.27±0.0.08 SE) and after 1950 (2.29±0.10 SE), was significantly larger than MPA specimens (U=844.50, p<0.001) and non-MPA specimens (U=423.00, p<0.001) (Figure 5).

![Figure 5](image-url)

**Figure 5. Museum and Field Data for A. spirata/punctulata.** Mean body size of *A. spirata/punctulata* from pre- and post-1950 museum specimens and non-MPA and MPA samples. The median line is shown surrounded by 2nd and 3rd quartiles. Whiskers show maximum and minimum values. Number of plots shown below boxes.
The frequency of *A. spirata/punctulata* was significantly greater than predicted at MPA field locations and significantly less at non-MPA field locations ($\chi^2=14.8$, df=1, p<0.001) (Table 6).

**Table 6. Frequency of Species.** Chi square analysis of frequency of presence for of *A. spirata/punctulata, N. emarginata/ostrina, L. gigantea, C. funebralis and O. circumtexta* in MPA and non-MPA field locations.

<table>
<thead>
<tr>
<th>Species</th>
<th>% Actual</th>
<th>Actual</th>
<th>Expected</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. spirata/punctulata</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPA Present</td>
<td>55.00%</td>
<td>77</td>
<td>63</td>
<td>140</td>
</tr>
<tr>
<td>Non-MPA Present</td>
<td>32.50%</td>
<td>13</td>
<td>27</td>
<td>40</td>
</tr>
<tr>
<td><strong>N. emarginata/ostrina</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPA Present</td>
<td>43.04%</td>
<td>73</td>
<td>96.6</td>
<td>169.6</td>
</tr>
<tr>
<td>Non-MPA Present</td>
<td>61.09%</td>
<td>65</td>
<td>41.4</td>
<td>106.4</td>
</tr>
<tr>
<td><strong>L. gigantea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPA Present</td>
<td>54.42%</td>
<td>56</td>
<td>46.9</td>
<td>102.9</td>
</tr>
<tr>
<td>Non-MPA Present</td>
<td>35.37%</td>
<td>11</td>
<td>20.1</td>
<td>31.1</td>
</tr>
<tr>
<td><strong>C. funebralis</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPA Present</td>
<td>57.04%</td>
<td>166</td>
<td>125</td>
<td>291</td>
</tr>
<tr>
<td>Non-MPA Present</td>
<td>53.98%</td>
<td>63</td>
<td>53.7</td>
<td>116.7</td>
</tr>
<tr>
<td><strong>O. circumtexta</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPA Present</td>
<td>57.83%</td>
<td>24</td>
<td>17.5</td>
<td>41.5</td>
</tr>
<tr>
<td>Non-MPA Present</td>
<td>11.76%</td>
<td>1</td>
<td>7.5</td>
<td>8.5</td>
</tr>
</tbody>
</table>

**Nucella emarginata/ostrina**

The average shell sizes *N. emarginata/ostrina* differed comparing pre-1950, post-1950, present non-MPA field locations and present MPA locations (H=34.96, p<0.001). The average body size did not differ between MPA field locations (1.76±0.03 SE) and non-MPA field locations (1.76±0.04 SE) (U=2445.00, p=0.76). Nor was there a difference in *N. emarginata/ostrina* average body size between museum specimens collected before 1950 (2.33 ± 0.13 SE) and those after 1950 (2.29 ± 0.12 SE) (U=110.00, p=0.70). The average body size of *N. emarginata/ostrina* from museum specimens, both
pre- and post-1950, were significantly larger than present day specimens, from both non-MPA (U=1770.00, p<0.001) and MPA field locations (U=425.00, p<0.001) (Figure 6).

![Figure 6. Museum and Field Data for *N. emarginata/ostrina*. Mean body size of *N. emarginata/ostrina* from museum specimens and field samples. Median line shown surrounded by 2nd and 3rd quartiles. Whiskers show maximum and minimum values. Number of plots shown below boxes.](image)

The frequency of *N. emarginata/ostrina* present was significantly less than the predicted at MPA field locations and more at non-MPA field locations ($\chi^2=35.6$, df=1, p<0.001) (Table 6).

**Lottia gigantea**

On average, *L. gigantea* body size differed comparing pre-1950 (4.73±0.33 SE), post-1950 (5.065±0.35 SE), non-MPA field locations (4.73 ± 0.40 SE) and MPA locations (5.29±0.16 SE) (H=8.03, p=0.045). The average body size of specimens from MPA field locations was larger than those from non-MPA field locations (U=445.50,
p=0.02), while there was no difference in the body size of *L. gigantea* comparing museum specimens collected before and after 1950 (U=58.00, p=0.43). There was also no difference between museum specimens collected either before or after 1950 and MPA field locations (U=855.00, p=0.06) or non-MPA field locations (U=148.00, p=0.57) (Figure 7).

<table>
<thead>
<tr>
<th></th>
<th>Pre 1950</th>
<th>Post 1950</th>
<th>Non-MPA</th>
<th>MPA</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>n</em></td>
<td>11</td>
<td>13</td>
<td>11</td>
<td>56</td>
</tr>
<tr>
<td><strong>Body Size (cm)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6.00</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>7.00</td>
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<td></td>
<td></td>
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<tr>
<td>8.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Figure 7. Museum and Field Data for *L. gigantea*. Mean body size of *L. gigantea* from museum specimens and field samples. Median line shown surrounded by 2\textsuperscript{nd} and 3\textsuperscript{rd} quartiles. Whiskers show maximum and minimum values. Number of plots shown below boxes.*

The frequency of *L. gigantea* in plots was significantly greater than predicted at MPA field locations and less at non-MPA field locations ($\chi^2=7.58$, df=1, p=0.006) (Table 6).
**Tegula funebralis**

On average *T. funebralis* differed comparing museum specimens from pre-1950, post-1950, non-MPA field locations and MPA locations (H=43.21, p<0.001). The average body size of *T. funebralis* at non-MPA field locations (1.84±0.03 SE) was not different from MPA field locations (1.84±0.02 SE) (U=4398.00, p=0.76). The average body size *T. funebralis* from museum specimens did not differ between those collected pre 1950 (2.24 ± 0.14 SE) versus those collected post 1950 (2.31±0.08 SE) (U=108.00, p=0.47). The body size of *T. funebralis* from museum specimens, both those collected pre and post 1950, was significantly larger than present day specimens, both from non-MPA (U=1705.00, p<0.001) and MPA field locations (U=579.50, p<0.001) (Figure 8).

![Figure 8](image_url)

*Figure 8. Museum and Field Data for T. funebralis. Mean body size of T. funebralis from museum and field specimen. Median line shown surrounded by 2nd and 3rd quartiles. Whiskers show maximum and minimum values. Number of plots shown below boxes*
The observed frequencies of presence and absence of *T. funebralis* was significantly more than the predicted values in MPA field locations and less in non-MPA field locations ($\chi^2=5.70$, df=1, p=0.017) (Table 6).

*Ocenebra circumtexta*

An insufficient number of samples were found of *O. circumtexta* to compare the average body size from non-MPA and MPA field locations. The average body size of *O. circumtexta* was not found to be different in museum specimen collected pre1950 (1.80 ± 0.06 SE) versus those collected post 1950 (1.84 ± 0.06 SE) ($t=-0.539$, df=16, p=0.60). The observed frequency of *O. circumtexta* was significantly more than the predicted values in MPA field locations and less in non-MPA field locations ($\chi^2=8.87$, df=1, p=0.003) (Table 6).

**Discussion**

The purpose of this study was to assess how effectively MPAs protect intertidal gastropods along the central coast of California. I used three metrics to test MPA efficacy: average gastropod body size within and outside MPAs, average body size of field specimens versus museum specimens, and the frequency of species inside MPAs and non-MPA field locations. Two of the species studied, *A. spirata/punctulata* and *L. gigantea*, were found to have larger average body size inside MPAs when compared with non-MPA field locations. I also found these two species also had higher frequencies inside MPAs. These results indicate that MPA protection is benefiting these two species. Roy et al. (2003) also found that in southern California, these species had larger body
size inside a MPA when compared to non-MPA locations. Roy et al. (2003) also found the body size of *L. gigantea* inside MPAs matched or even slightly exceeded museum specimens. This result, combined with the results of the other two metrics, suggests that MPA protection may be especially effective for *L. gigantea*.

Roy et al. (2003) found that *L. gigantea* collected in MPAs were not merely equaling the average size of museum specimens, but significantly exceeding them. This result may be attributed to the method Roy et al. (2003) used, which specifically targeted the largest specimen for their field measurements. This method was used in Roy et al. (2003) in part because it was assumed that museum collections would consist of mostly large individuals. *L. gigantea* along the central California coast may be benefiting from MPA protection as much as *L. gigantea* in southern California, but because my study randomly selected individuals, these results are conservative in comparison to Roy et al. (2003).

Alternatively, *L. gigantea* along the central California coast may need more time to grow to larger body sizes. The central coast and north central coast MPA networks were only established in 2007 and 2010 respectively. Since *L. gigantea* can live up to 30-40 years (Fenberg & Roy, 2012) this species may continue to benefit from MPA protection and grow to larger body sizes in the future. Future studies of *L. gigantea* should continue to include comparisons to baseline date to determine if this species continues to grow to larger sizes in this region.
Unlike *L. gigantea*, the average body size for *A. spirata/punctulata* inside MPAs was smaller than the average body size of museum specimens. Roy et al. (2003) found that the average body size of museum specimens was larger than MPA specimens. As with *L. gigantea*, this difference in results could be due to the different sampling methods. However there could also be additional factors, such as life history traits or environmental factors, which are preventing *A. spirata/punctulata* from growing to historic body sizes at the same rate as *L. gigantea*. Future research of these species in southern California should include random sampling of specimens, to determine whether the difference in methods between my study and Roy et al. (2003) contributed to the difference in results.

The second collected species, *T. funebralis* did not differ in body size between MPAs and non-MPA field locations; however, *T. funebralis* did occur in greater frequency inside MPAs. This result indicates that, although MPA protection does not appear to be impacting *T. funebralis* body size, it may be having a positive impact on its frequency. Roy et al. (2003) found that a similar turban snail species, *Tegula aureotincta* (brown turban snail) had larger average body size in a MPA versus non-MPA locations. This difference suggests that collection may have less of an impact along the central California coast than it does in southern California.

The difference between Roy et al. (2003) and my study could also be due to differences in food availability for *T. funebralis* between Northern and Southern CA. The body size of this herbivorous species is impacted by the abundance and diversity of algal species that are available in the intertidal (Best, 2014). The availability of certain
algal species could be a more important predictor of body size than MPA protection for this species. Since collection of certain types of algal species are allowed within some MPAs (Table 1), and because different algal species are more common at different field locations, further research on *T. funebralis* should include sampling of algal abundance and diversity within MPAs.

Another factor that could be affecting *T. funebralis* body size is the catastrophic die-off of a keystone predator of the intertidal, *P. ochraceus*, along with most other sea star species, reported in the summer of 2014. *P. ochraceus* is a main predator of *T. funebralis* and it affects the distribution of different size classes of *T. funebralis* within the different intertidal zones (Markowitz, 1980). Because the die-off of *P. ochraceus* was happening concurrently with sampling for this study, the full impacts are unknown. Future research should address how the absence of *P. ochraceus* is impacting *T. funebralis* as well the whole intertidal community.

*O. circumtexta* occurred in greater frequency inside MPA than in non-MPA locations indicating that, for this uncollected species, MPA may be providing beneficial protection. Because so few individuals of this species were found the other two metrics for this study could not be applied to *O. circumtexta*. The low number of individuals of *O. circumtexta* that were found is not believed to be a reflection that this species is struggling, rather that it is a less common species than the others sampled for this study. Future research on *O. circumtexta* should focus on finding and sampling in locations where this species is more common.
The other species not collected for human use, *N. emarginata/ostrina*, did not appear to benefit from MPA protection with respect to any of the metrics used for this study. In fact I found this species more frequently in non-MPAs than in MPA field locations. This result greatly differs from the results seen for the similar uncollected species, *A. spirata/punctulata*, which was larger and more frequent in MPA locations. This result and the results seen from the collected species *L. gigantea* and *T. funebralis* reveal that MPAs are not benefiting all collected and all uncollected species in the same way.

The positive results for *L. gigantea*, *A. spirata/punctulata* and *T. funebralis* indicate that some species are benefiting from MPA protection. Managers of MPA must continue to enforce the MPA no-take policy for intertidal gastropods in order to continue improvement in body sizes and abundances. Managers should also consider increasing the amount of enforcement in the intertidal to discourage poaching. Educating the public about certain life history traits, such as the largest individuals of *L. gigantea* having the greatest reproductive success, could also lead to changes in the choices people make when collecting in the intertidal. Further research for *L. gigantea* and *A. spirata/punctulata* should include long term monitoring to determine if MPAs continue to have beneficial impacts and if *A. spirata/punctulata* is able to reach historic body sizes.

For *T. funebralis*, managers should consider more stringent protection that completely prevents human visitation to see how animals respond. Future research on this species should include analysis between SMCAs, which allow some harvesting of species such as kelp, which could be impacting *T. funebralis*, and SMRs, which do not
allow any take. This comparison could reveal if more complete protection is a solution for increasing the body size of this species. The recent die-off of sea stars should be examined in future research of *T. funbralisis* to see how this species responds to the absence of one of its main predators.

For the uncollected species, *A. spirata/punctulata, O. circumtexta* and *N. emarginata/ostrina*, managers of MPAs should consider increasing education for the public about species that do not have direct consumptive value. Increased education about these and other uncollected intertidal gastropods may help visitors to the intertidal understand the importance of maintaining species abundance and diversity even outside the boundaries of MPAs. Since too few samples of *O. circumtexta* were found to perform complete analysis for this study, further research could expand the study region to include more MPA and non-MPA field locations in order to increase sample size and better determine how MPA protection is impacting this species.

Future research should also focus on the non-consumptive impacts of human visitation. Comparing sites that completely exclude human visitation to MPA and non-MPA locations could reveal how impacts like trampling, or over-turning rocks are effecting species. In addition including the levels of human visitation to these sites as a metric could allow managers to make more informed decisions about when and where to use enforcement resources.

As human populations along the coast continue to expand, implementing effective protection for the coastal environmental becomes more essential. The results from this
study suggest that MPAs can be very effective for certain species. Future research is necessary to determine if species continue to respond positively to MPAs and whether human and environmental impacts may be negatively impacting other species. Because MPAs are a main component for maintaining marine ecosystems and resources, continued research is imperative to determine how MPAs can be made effective for even more intertidal species.


