DO MARINE PROTECTED AREAS FACILITATE CORAL REEF ECOSYSTEM HEALTH?

AN INVESTIGATION OF CORAL DISEASE AND ITS ASSOCIATED FACTORS IN OAHU'S MARINE LIFE CONSERVATION DISTRICTS

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ABSTRACT

Management actions, such as the use of Marine Protected Areas (MPAs), which enhance fish abundance and diversity, could have important downstream impacts on coral reef ecosystem health and coral reef resilience. Past studies have suggested that protection status not only influences the abundance of fish, macroalgal levels, and coral cover but also the number of diseased coral colonies. Despite the awareness of disease as a coral reef stressor, there has been limited research on the prevalence of disease within Oahu's Marine Life Conservation Districts (MLCDs) which function as no take reserves. Coral reef health in Oahu's three MLCDs compared to three comparable unprotected reefs was investigated. Field surveys were used to quantify coral disease prevalence, coral cover, macroalgal cover, fish abundance and diversity, and coral community size structure at each of the sites. Environmental variables including inorganic-organic carbon fractions of sediments and sediment grain size categories were also measured. Disease assemblages were significantly different between locations and across protection boundaries. Biological and environmental parameters as well as protection status were used in statistical models to determine which variables were the best performing explanatory variables for the prevalence and abundance of five common lesion types in Oahu. Four out of five common lesion types for at least one of the three locations, showed significantly higher levels of prevalence within MLCDs compared to adjacent unprotected areas. Percent cover of the host coral species was the strongest predictor for four out of five models of utilizing disease abundance. Additionally, growth anomalies on *Porites lobata* were more commonly observed on larger colonies than on smaller colonies. Fish density was significantly higher at the Pupukea MLCD compared to the adjacent unprotected area and coral cover was significantly higher in the Hanauma Bay MLCD and Pupukea MLCD compared to adjacent control sites. Finally while fish density and coral cover were higher in some protected areas compared to control areas, there was no detectable difference in macroalgal cover across protection boundaries for all locations. MLCDs may act as a refuge for fish, but their high coral host abundance may make them vulnerable to more frequent and severe disease outbreaks compared to other locations. Finally while current regulations in MLCDs protect some aspects of coral reef ecosystem health, incorporating strategies aimed at watershed management may further improve MLCD effectiveness and provide more comprehensive protection for coral reefs.

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HISTORY AND PURPOSE OF MARINE LIFE CONSERVATION DISTRICTS

The state of Hawaii has invested in the establishment of several Marine Protected Areas (MPAs) as a strategy to conserve marine life. There are different kinds of MPAs in Hawaii ranging in scale from large to small, in depth from shallow near shore habitats to deeper offshore habitats, and in protection from complete “no take” to rotational closures. The largest MPA in the state of Hawaii is the Papahanaumokuakea Marine National Monument (PMNM), which protects 362,073 square kilometers and is the largest conservation area in the United States. Other examples of MPAs in Hawaii include the Kahekili Herbivore Fisheries Management Area, which has regulations in place to protect fish of the families Kyphosidae, Scaridae, and Acanthuridae, and Bottomfish Restricted Fishing Areas (BRFAs), which prevent fishing of seven bottomfish species. MPAs in the state of Hawaii also include Marine Life Conservation Districts (MLCDs), which aim to replenish and conserve marine life (Hawaii Division of Aquatic Resources 1992). There are eleven MLCDs in the state of Hawaii. Hawaii island has five MLCDs: Kealakekua Bay, Lapakahi, Old Kona Airport, Waialea Bay, and Waiopae Tidepools. Maui County has three MLCDs: Honolua-Mouleia Bay, Manele-Hulopoe, and Molokini Shoal. The island of Oahu, the most populated island in the state of Hawaii, has three MLCDs: Hanauma Bay, Pupukea, and Waikiki (Figure 1).

Historically MLCDs in Hawaii were created to fulfill a three-fold purpose. First, they were seen as a management strategy that could be used to combat declines in marine life from fishing, collecting, and other extractive practices. Second, they were envisioned as places where educational activities for the public and scientific research could be carried out. Third, managers felt that it was important that MLCDs provide a safe place for ocean recreation.

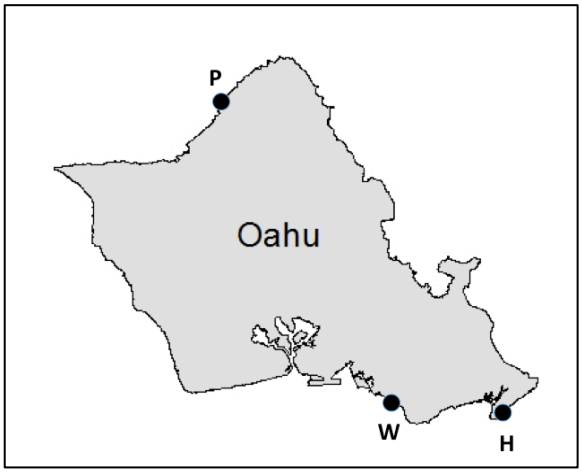

Figure 1. The three Marine Life Conservation Districts (Pupukea (P), Hanauma Bay (H), and Waikiki (W)) on Oahu, Hawaii are shown as black dots.

MLCDs in Oahu differ in their oceanographic conditions, proximity to dense human populations, as well as their level of human use. The Waikiki MLCD and Hanauma Bay MLCD are located on the south shore of Oahu and experience much lower amounts of wave energy than the Pupukea MLCD on Oahu's north shore. North swells are frequent in the winter months on the north shore of Oahu and higher levels of wave energy can influence coral community size structure as well as the flushing of sediment and land based pollutants (Rodgers et al. 2012; Franklin et al. 2013). The number of ocean users at each of the MLCDs in Oahu could have potential impacts on coral reef ecosystem health. While all of the MLCDs on Oahu are popular with both residents and tourists, the two MLCDs on the south shore of the island (Hanauma Bay and Waikiki MLCDs) are closer to the more densely populated south shore of Oahu and therefore experience higher levels of human use. In fact, around 70% of the population in the state of Hawaii resides in Honolulu County, which is located on the south shore of Oahu. Stakeholders participate in a wide range of activities at each of the sites ranging from recreational activities such as diving and swimming to activities centered around community level engagement such as informal monitoring of MLCD regulations.

Hanauma Bay MLCD

MLCDs were first established in the state of Hawaii in 1967 with the opening of the Hanauma Bay MLCD. Historically Hanauma Bay was a popular fishing and recreational area. Prior to the establishment of Hanauma Bay as a MLCD, there was concern that extractive uses of the Bay were unsustainable. A 1964 study estimated 1092 fish and 468 coral heads were removed annually from the area, although extractive users made up only 12% of the overall visitors (Reese 1965). The results of this study led to a proposal for the Bay to be set-aside as a protected area, and this proposal eventually developed into state regulation overseen by Hawaii's Department of Land and Natural Resources (DLNR). The Hanauma Bay MLCD is a no-take reserve and the taking of any type of living material (fishes, eggs, shells, corals, and algae) is prohibited.

The Hanauma Bay MLCD remains one of the most heavily visited coastal areas in the state of Hawaii. Peak usage of the Bay occurred in the late 1980s with 3.7 million visitors a year and approximately 13,000 visitors per day (Maurin 2008). The most current (2002) human use data shows a decline in usage with reports showing the MLCD receiving 1 million visitors each year and approximately 3000 visitors a day through controlled access to the area (Maurin 2008) (Figure 2). Hanauma Bay employees help to regulate the flow of visitors to the area and no more than 2000 people are allowed to access the beach portion of the Bay at any one time. Hanauma Bay greatly benefited from the establishment of an education center in 2002 which provides visitors information on safe ways to snorkel and view marine wildlife without harming the reef. Other improvements included a ban on fish feeding in the park in 1999 and a switchover from

cesspools to connection with the nearest sewage treatment plant in the early 1990s (Dr. Kaipo Perez, Hanauma Bay, pers. comm.)

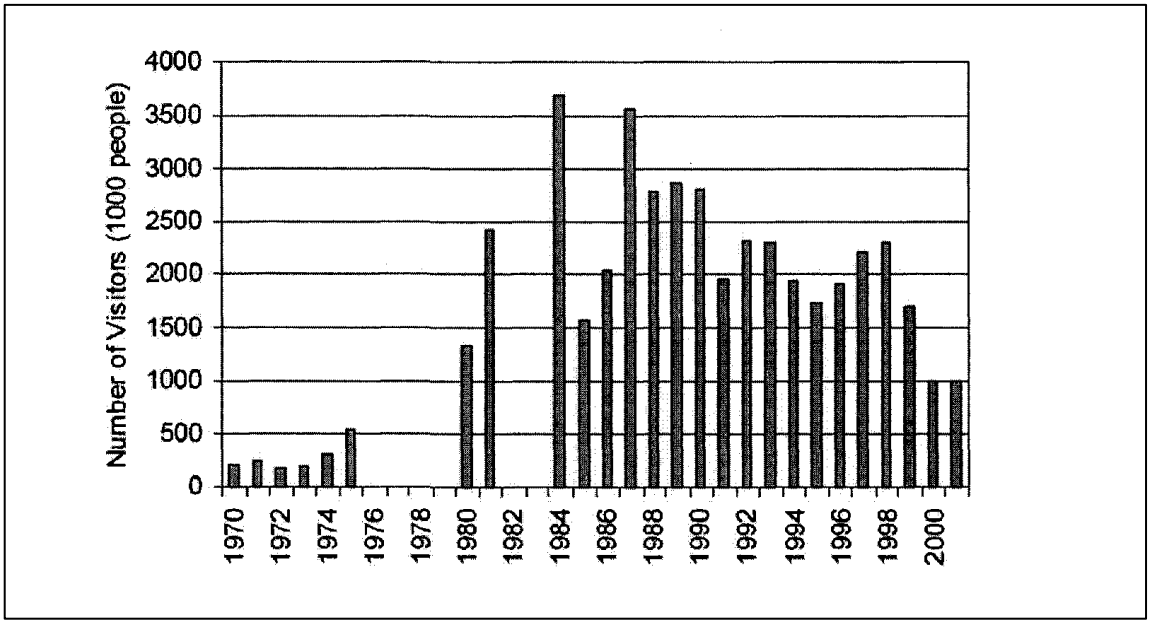

Figure 2. Human use (number of visitors per year) at the Hanauma Bay MLCD from 1970-2002. (Source: Maurin 2008)

Pupukea MLCD

The Pupukea MLCD was opened in 1983. The establishment of the Pupukea MLCD was almost 15 years in the making and included meetings with the North Shore neighborhood board in 1970, a study conducted by Sea Grant in 1975 to find potential sites for new MLCDs, and public meetings facilitated by DLNR beginning in 1978. The Pupukea MLCD was expanded in 2003 to include Waimea Bay and the boundary was also extended further offshore in the Sharks Cove and Three Tables area. With the expansion there was a greater depth and range in benthic habitat in the MLCD. There is strong community involvement in this area through the non-profit Malama Pupukea Waimea, which has been in existence since 2005, and the Makai Watch Program. Members of Malama Pupukea Waimea participate in biological and human use monitoring, awareness raising and outreach, and documentation and reporting of poaching in the MLCD.

There are restrictions regulating the taking of living material with some exceptions in the Pupukea MLCD. Limu (algae) may be harvested as long as the holdfasts are left in place, finfish may be caught within Waimea Bay (the southern part of the Pupukea MLCD) with a hook and line from shore. Opelu (*Decapterus sanctae-helenae)* may be fished from August to September, and akule (*Trachurops crumenophtalmus)* may be fished from November to December.

The Pupukea MLCD supports many different stakeholder groups including snorkelers, divers, swimmers, sunbathers, surfers, fishermen, and boaters. However, compared to Hanauma Bay, the Pupukea MLCD receives far fewer visitors. A report quantifying carrying capacity showed visitors at Three Tables in the southern part of Pupukea MLCD “encountering” 61 other users on average and visitors of Sharks Cove in the northern part of the MLCD “encountering” an average of 92 other users per visit (Needham et al. 2008). “Encounters” were measured through a closed ended format survey asking respondents to estimate how many people they saw that day using 15 different levels (0, 5, 10, 20, 35, 50, 75, 100, 200, 350, 500, 750, 1000, 1500, 2000+ people) (Needham et al. 2008). There has also been extensive research concerning fishing pressure in the adjacent unprotected areas. While there are low levels of poaching in the MLCD, the fishing effort outside of the protected area is seven times higher (Stamoulis and Friedlander 2013)(**Figure 3**). The majority of fishing takes place during the week with use of a pole as the main gear type (Stamoulis and Friedlander 2013) (Figure 4). Spatial analyses of fishing effort showed fishermen mostly concentrated near the protection boundary (Stamoulis and Friedlander 2013) (Figure 5).

A study from 2008 showed ocean-users of the Pupukea sites to have strong protectionist values towards coral reefs, and survey participants reporting that reef-damaging activities would most likely not be supported at the site (Needham et al. 2008). When survey respondents in the same study were presented with a list of management strategies that could potentially be put in place in the Pupukea MLCD, they were most supportive of more interpretive and educational information and less supportive of upkeep, increasing the number of facilities, and restricting the number of visitors (Needham et al. 2008).

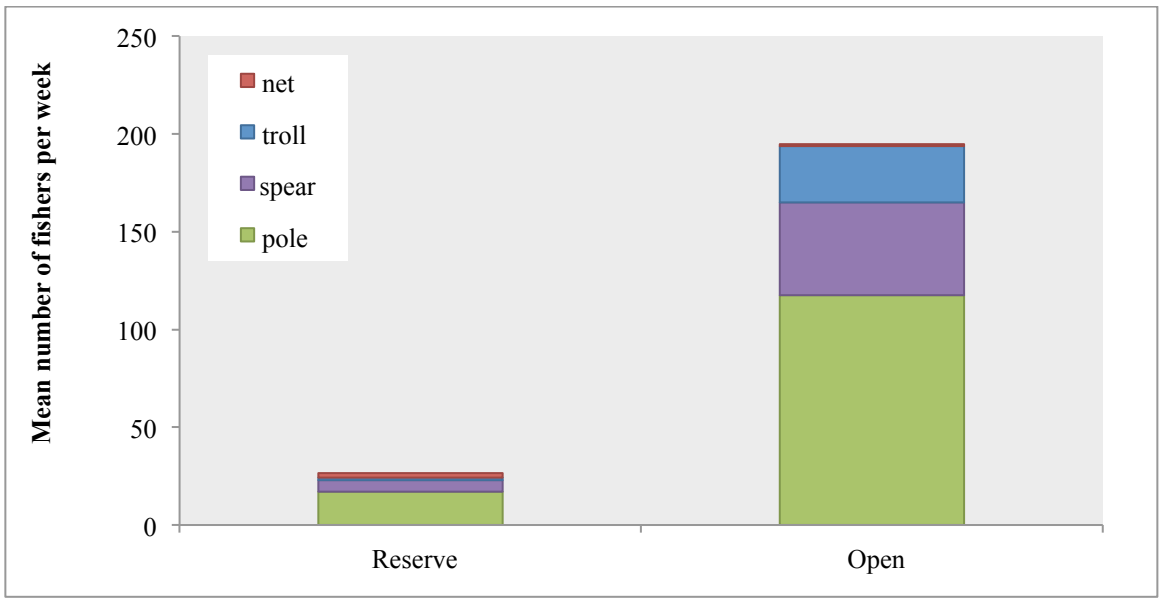

Figure 3. Fishing gear type and mean number of fishers per week. (Source: Stamoulis and Friedlander 2013).

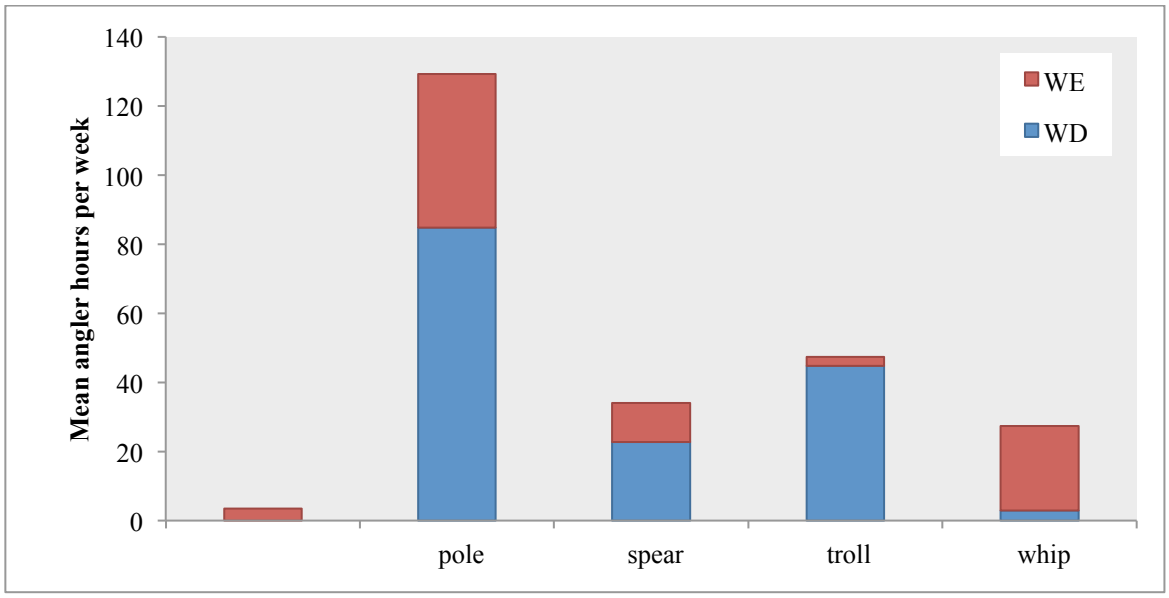

Figure 4. Fishing effort on the weekend (WE) and weekdays (WD). (Source: Stamoulis and Friedlander 2013).

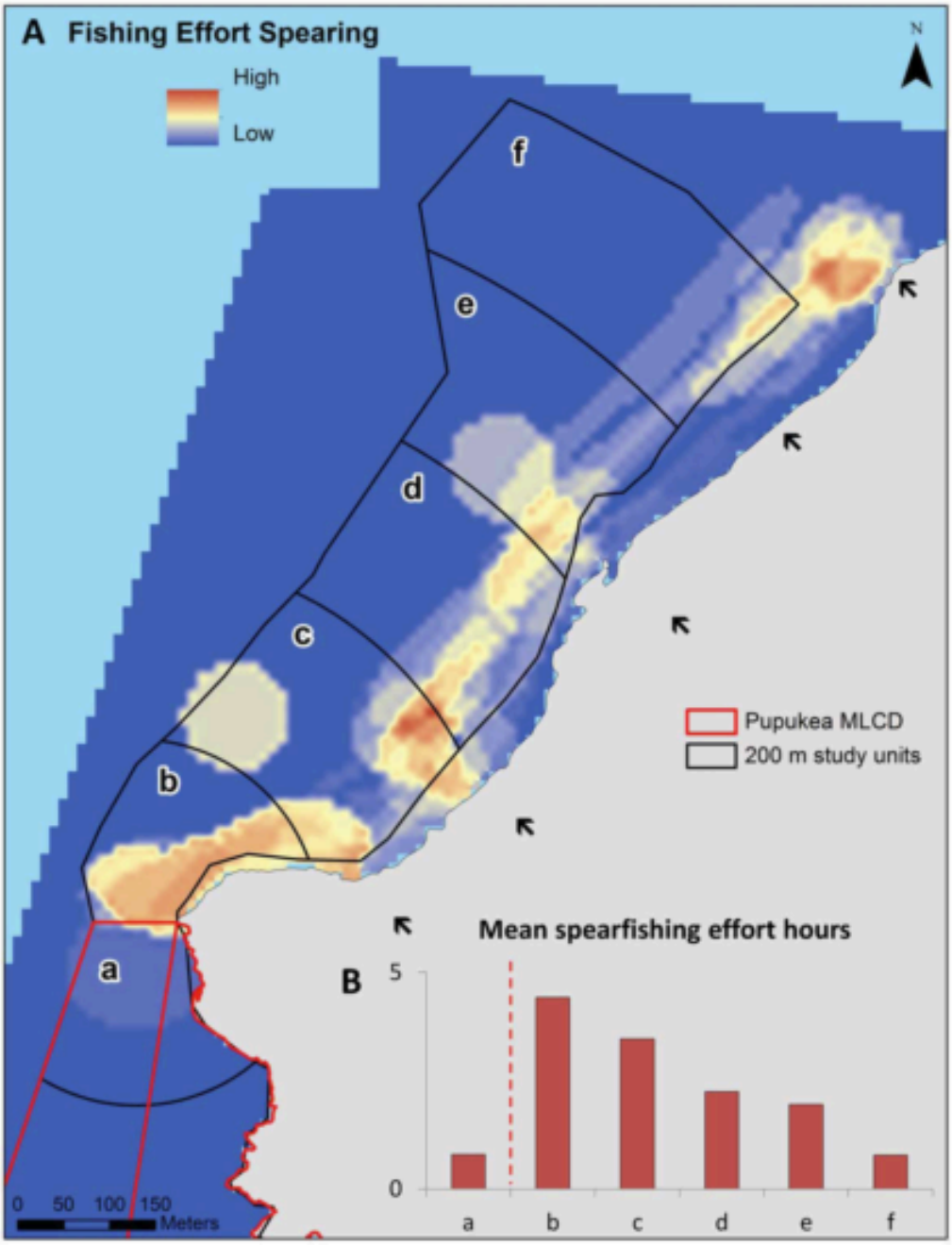

Figure 5. Spearfishing effort in the Pupukea-Unprotected site. (Source: Stamoulis and Friedlander 2013).

Waikiki MLCD

The Waikiki MLCD was formed in 1988 as a no-take reserve with regulations preventing the taking of any type of living material (fishes, eggs, shells, corals, and algae). This MLCD is unique because it is directly adjacent to the Waikiki-Diamond Head Fisheries Managed Area (FMA), which is under rotational closure. This particular FMA is open to fishing on even numbered years and closed to fishing on odd numbered years.

Compared to the Pupukea and Hanauma Bay MLCDs, the Waikiki MLCD has faced many alterations and disturbances to its marine habitats. Waikiki has undergone significant land use and land cover change over the last 100 years, changing from a wetland to a highly altered coastline with sea walls, dredging, and landfills (Miller and Fletcher 2003). Long term ecological research conducted in the MLCD have shown the reef to be dominated by macroalgae and have minimal coral cover since 1975 (Kinzie 2008) **(**Figure 6**).** A report from Edmondson in 1928, however, paints a different picture of the reef flat in the area currently occupied by the Waikiki MLCD (Edmondson 1928) (Figure 7). Edmondson's map shows 18 different species of coral and a heavily populated reef flat (Figure 7). Another report from Pollock in 1928 reports the Waikiki area being dominated by *Porites compressa* and "finger coral structures containing 18-30% coral" (Pollock 1928). The surveys conducted for this research showed at most 6 different species per transect in the Waikiki MLCD and mean coral cover of 2.245%. The historical data show a potential connection between extensive alteration of the coastline and adjacent wetland, and the shift in coral reef commuity structure over the last century.

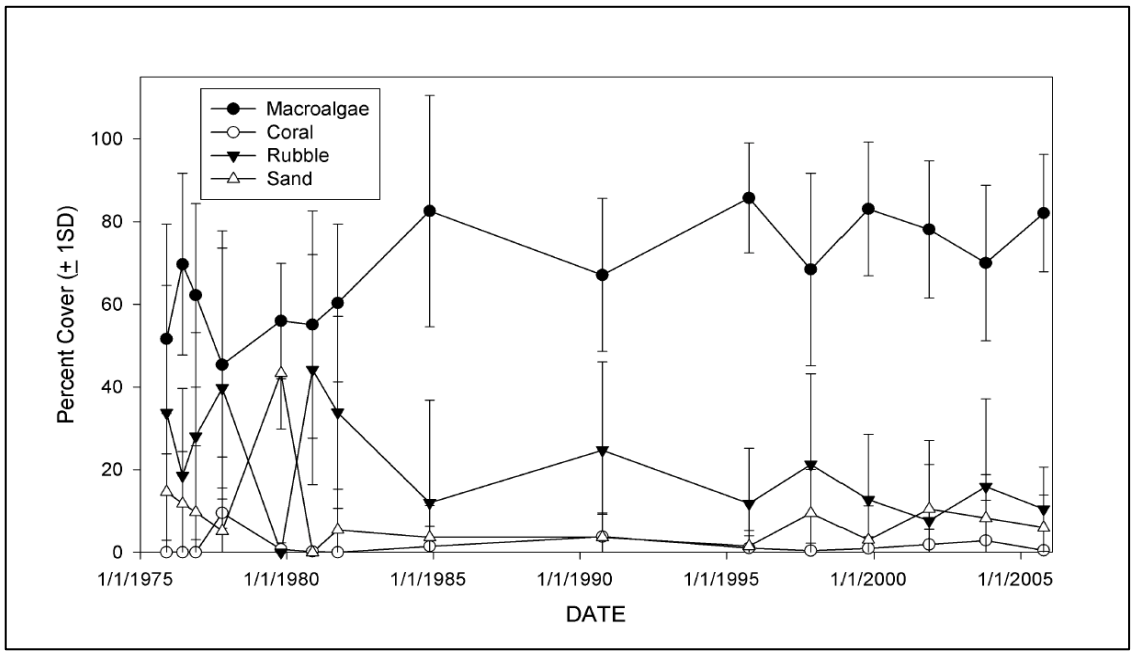

Figure 6. Mean percent coral and macroalgal cover in the Waikiki MLCD from 1975 to 2005 (Source: Kinzie 2008).

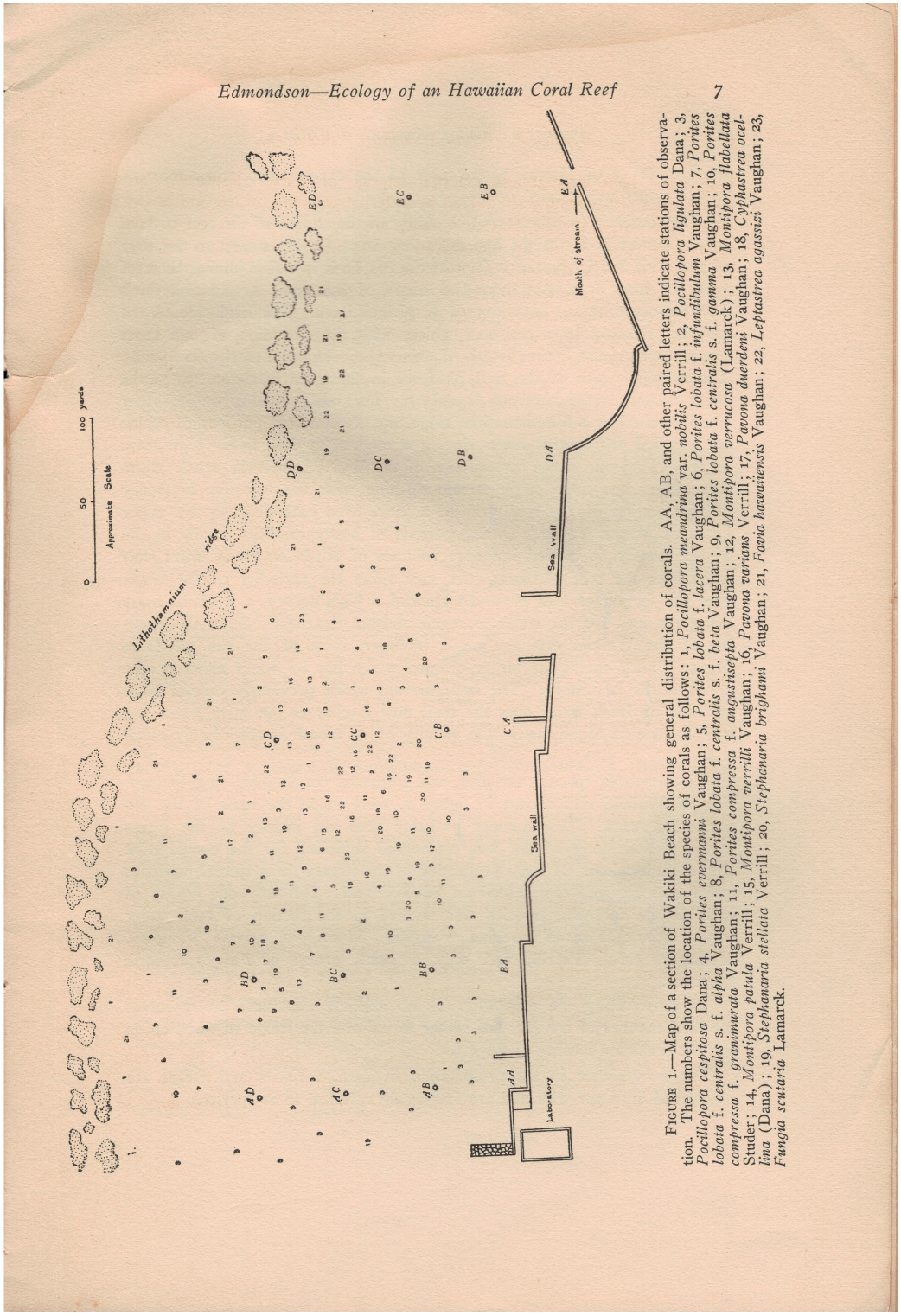

FIGURE 1.—Map of a section of Wakiki Beach showing general distribution of corals. AA, AB, and other paired letters indicate stations of observation. The numbers show the location of the species of corals as follows: 1, *Pocillopora meandrina* var. *nobilis* Verrill; 2, *Pocillopora ligulata* Dana; 3, *Pocillopora cespitosa* Dana; 4, *Porites evermanni* Vaughan; 5, *Porites lobata* f. *lacera* Vaughan; 6, *Porites lobata* f. *infundibulum* Vaughan; 7, *Porites lobata* f. *centralis* s. f. *alpha* Vaughan; 8, *Porites lobata* f. *centralis* s. f. *beta* Vaughan; 9, *Porites lobata* f. *centralis* s. f. *gamma* Vaughan; 10, *Porites compressa* f. *granimurata* Vaughan; 11, *Porites compressa* f. *angustisepta* Vaughan; 12, *Montipora verrucosa* (Lamarck); 13, *Montipora flabellata* Studer; 14, *Montipora patula* Verrill; 15, *Montipora verrilli* Vaughan; 16, *Pavona varians* Verrill; 17, *Pavona duerdeni* Vaughan; 18, *Cyphastrea ocellina* (Dana); 19, *Stephanaria stellata* Verrill; 20, *Stephanaria brighami* Vaughan; 21, *Favia hawaiensis* Vaughan; 22, *Leptastrea agassizi* Vaughan; 23, *Fungia scutaria* Lamarck.

Figure 7. Map of coral colonies in what is now the Waikiki MLCD from 1928 (Source: Edmondson 1928). The “mouth of stream” marked on the map coincides with what is now Kapahulu Street and the “laboratory” is approximately at the site of the snack bar at Sans Souci State Recreational Park.

The Waikiki location in this study had the highest level of human use compared to the Pupukea and Hanauma Bay MLCDs. Waikiki Beach has been estimated to receive over 8 million visitors (Friedlander et al. 2005) (**Table 1**). Additionally the Waikiki district, to the West of the MLCD, receives an average of 72,490 people daily and has a density of 119,380 people per square mile, making Waikiki the densest region in the state of Hawaii (Lim 2012). Surveys administered to Waikiki residents in 2011 showed a varied group of stakeholders with the majority of responders ranking “going to the beach” as a top activity and “fishing” as the lowest ranked activity (Barrett 2011) (

Table 2). Data collected from surveys also showed that 57% of Waikiki residents think that the conditions at Waikiki have deteriorated over time (Barrett 2011). When respondents were asked what activities were most detrimental to reef health they chose littering (78%), storm water runoff (72%), and non native species (67%) (Barrett 2011) (**Figure** 8).

Table 1. Summaries of human use in the three locations used in this study (Waikiki, Hanauma Bay, and Pupukea). Data for Waikiki and Hanauma Bay is from the Department of Business Economic Development and Tourism (DBEDT). (Source: Friedlander et al. 2005)**.**

LOCATION	NO. OF VISITORS
Waikiki Beach, Oahu	8,355,448[1]
Hanauma Bay, Oahu	1,751,318[1]
Pupukea, Oahu	177,600[2, 3]
Manele/Hulapoe Bays, Lanai	277,400[2]
Molokini Shoal, Maui	400,000[4]
Honolua/Mokuleia Bays, Maui	160,000[2]
Kealakekua Bay, Hawaii	189,800[2]

[1] DBEDT State Data Book, 2002.
[2] Adapted from Holland and Meyer, 2003 (based on mean hourly usage).
[3] Reflects only summer use for five months, as there is minimal use in the winter.
[4] Estimation by S. Hau, pers. comm.
* MLCDs are marine protected areas established to conserve and protect marine resources.

Table 2. Recreational priorities (2a) and importance of continued access in the future (2b) taken from (Barrett 2011).

2a.	Ranking of recreational activities by total participation
1	Go to the beach (92.04%)
2	Picnic (58.41%)
3	Snorkel (32.74%)
4	Sail/boating (28.32%)
5	Surf (27.43%)
6	Paddle (19.47%)
7	Dive (18.58%)
8	Fishing (17.70%)

2b.	Relative importance* of continued access to activity
1	Go to the beach (71.68%)
2	Surf (46.90%)
3	Picnic (39.82%)
4	Snorkel (32.74%)
5	Paddle (27.43%)
6	Sail/boating (23.89%)
7	Dive (23.01%)
8	Fishing (19.47%)
9	Smoking on the beach (16.81%)

**comprised of responses of "very important" and "extremely important"*

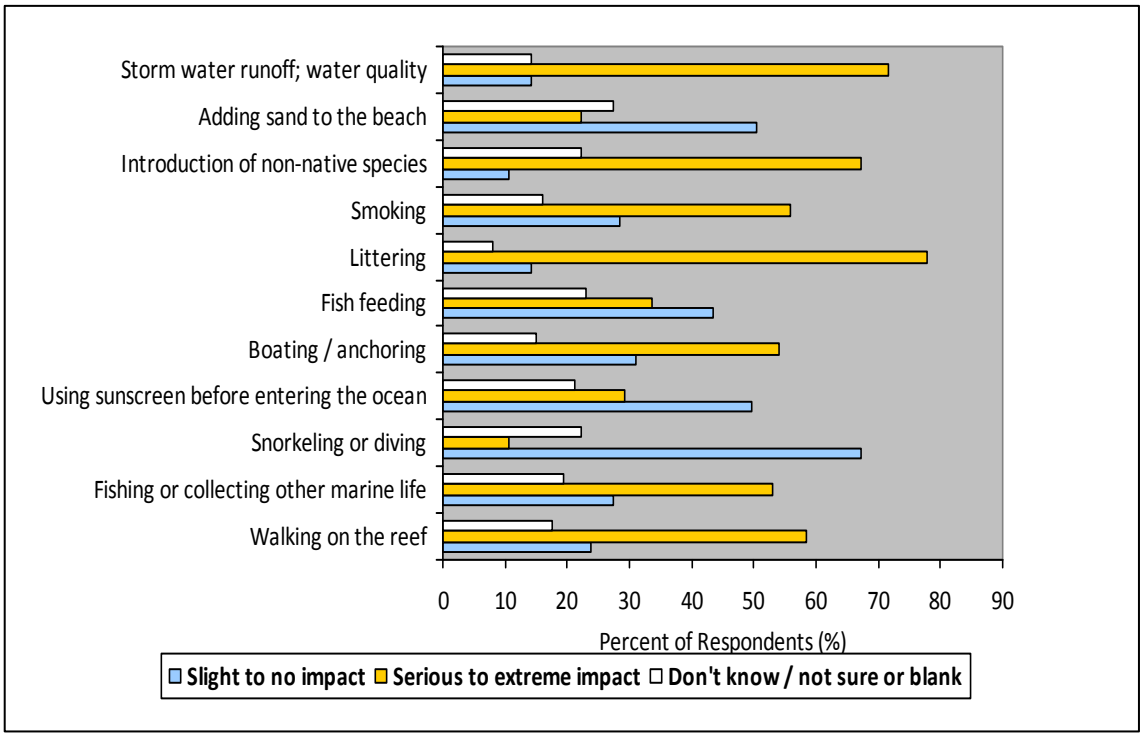

Figure 8. Perceived Impacts of human activities taken from (Barrett 2011).

CHAPTER 2: Do Marine Protected Areas facilitate coral reef ecosystem health?

INTRODUCTION

In response to recognition of the global degradation of coral reefs, there has been increased interest in marine resource management as a conservation tool (Halpern 2003). The creation of Marine Protected Areas (MPAs) in particular has received a great deal of support from both the scientific community and resource managers. The regulations that are enforced in MPAs can vary from no-take reserves, to areas with seasonal closures, species restrictions, and/or catch limits (Lester and Halpern 2008).

The benefits of MPAs are well established in the literature. Marine reserves in coral reef areas have been shown to have increased fish and invertebrate biomass (Acosta 2002; Friedlander et al. 2003), reduced macroalgal cover (Mumby et al. 2006), and increased coral recruitment (Mumby et al. 2007). The relationship, however, between MPAs and one of the major causes of coral mortality on reefs, coral disease (Aronson et al. 1998; Richardson 1998), still remains unclear. While some studies report no difference in coral disease prevalence between protected and unprotected areas (Page et al. 2009) others report lower disease prevalence inside MPAs (Raymundo et al. 2009). Despite awareness of the threat that disease poses to corals, there has been limited research on the prevalence of disease within Oahu's Marine Life Conservation Districts (Hunter 1999).

Coral disease is one of the top contributors to coral mortality and can have profound impacts on coral reef community structure (Harvell et al. 2002; Bellwood et al. 2004). Disease outbreaks of white plague that followed coral bleaching in the US Virgin Islands caused an average loss of 51.5% of the existing coral cover (Miller et al. 2009). *Montipora* white syndrome outbreaks in Kaneohe Bay, Hawaii had a reported case fatality rate of 28% over a 2-year period (Aeby et al. 2010). Also, reports of coral disease globally have risen over the last three decades (Harvell et al. 2004) and reports of coral disease in both the Main Hawaiian Islands and the Northwestern Hawaiian Islands are on the rise as well (Aeby 2009; Aeby et al. 2010, 2011b). The rise in disease reports and evidence of coral disease as a major player in coral mortality worldwide are concerning as disease can also impact the growth and fecundity of corals (Aeby 1991; Hunter and Field 1997; Stimson 2010a; Sudek et al. 2011). Increased knowledge of coral disease levels within MLCDs and other types of MPAs is especially important if disease can impact the reproductive capabilities of corals and in turn the ability of these areas to serve as source habitats that reseed surrounding unprotected areas (Figure 9).

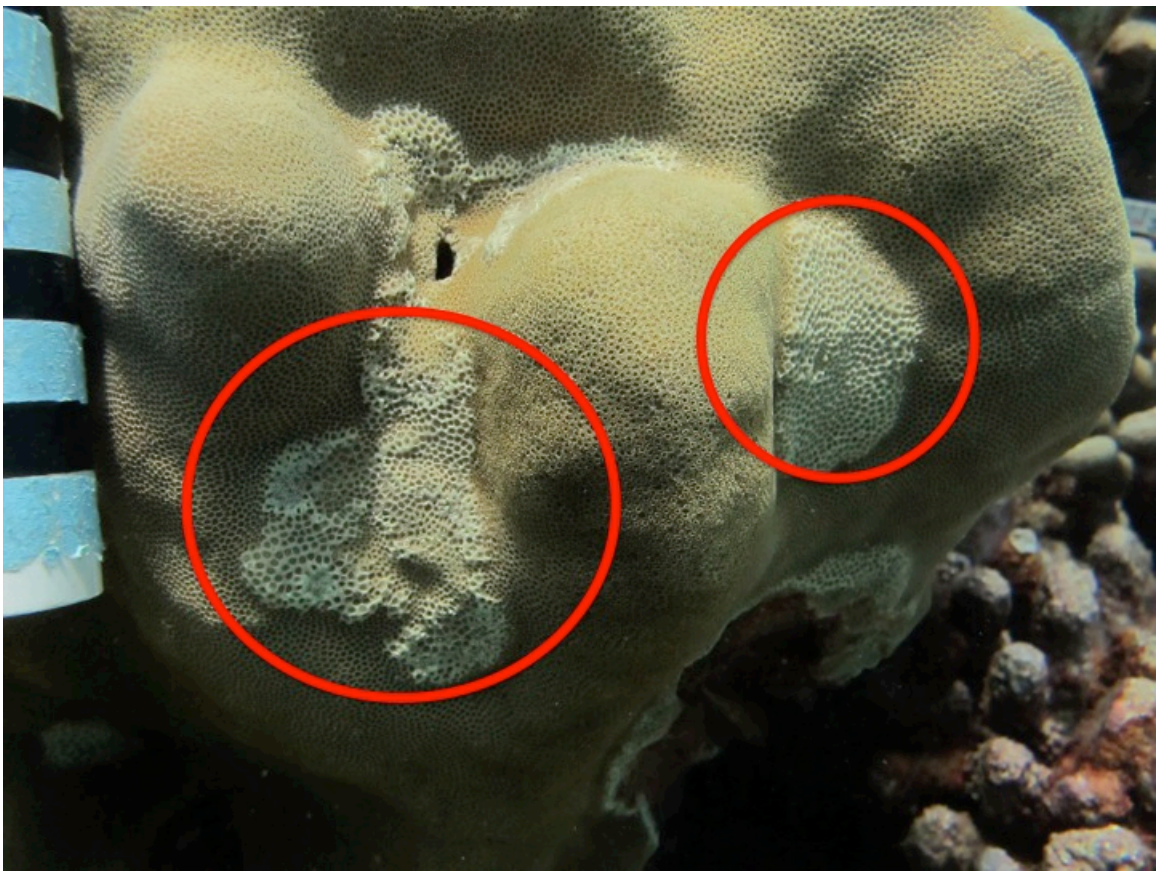

Figure 9. Growth anomalies (circled in red) on a *Porites lobata colony* from Hanauma Bay.

There are a total of three MLCDs on the island of Oahu, all of which have been in existence for 25 years or longer: Hanauma Bay, Pupukea, and Waikiki MLCDs. There has been substantial research in Oahu's MLCDs investigating reserve effects on fish communities (Friedlander et al. 2007; Stamoulis and Friedlander 2013). Friedlander and colleague's study of all eleven MLCDs in the state of Hawaii found MLCDs to have 2.6 times greater biomass of fish compared to unprotected areas, more abundant populations of apex predators, and higher levels of species richness and diversity (Friedlander et al. 2007). A study in the Pupukea MLCD showed evidence of fish spillover from the reserve into the neighboring unprotected area at a local scale of less than 1 km (Stamoulis and Friedlander 2013). While fish communities are more abundant in Oahu's MLCDs, corals have shown less promising responses. The Coral Reef Assessment and Monitoring Program (CRAMP) has conducted long term monitoring of coral reef communities in the Main Hawaiian Islands since 1999, and the Hanauma Bay MLCD and Pupukea MLCD are included in their sixty permanent reef sites. Analysis of the first three years of monitoring (1999-2002) showed significant decrease in coral cover for shallow sites (< 5m) at the Pupukea MLCD and significant decrease in coral cover for deep sites at the Hanauma MLCD (> 5m) (Jokiel et al. 2004).

MLCDs may be revealing places to study coral disease as their regulations may control many aspects of disease processes. First, protected areas may have higher host abundance and density than adjacent unprotected areas. Second, fishing regulations that increase fish abundance may potentially affect coral reef ecosystem health. Lastly, the fishing regulations currently in place in MLCDs leave coral reefs vulnerable to impacts from climate change, increased temperature, increased sedimentation and decreased water quality (Selig and Bruno 2010). Depending on aspects of disease etiology such as transmission (e.g. vector or direct contact), population thresholds, and influence of anthropogenic stressors on coral immunity, protective status could have varying impacts coral disease prevalence and coral reef ecosystem health.

MPAs and host density

Many coral diseases have a strong relationship with host abundance (Bruno et al. 2007; Myers and Raymundo 2009; Williams et al. 2010). With denser populations of coral, there is decreased distance between individuals, which may potentially lead to higher levels of transmission (Begon et al. 2002). A global analysis of MPAs in areas with coral reefs showed more constant coral cover through time in protected areas compared to unprotected areas which tended to have declines in coral cover over time (Selig and Bruno 2010). Historically, MLCDs in Oahu were chosen for their biological attributes including their higher levels of coral cover (Kimmerer and Durbim 1975). This higher abundance of host coral species could potentially make Oahu's MLCDs more vulnerable to disease outbreaks than other areas with lower densities of coral.

MPAs, fish, and pathogens

MPAs may also enhance fish abundance and diversity, and thereby have important downstream impacts on coral health. It has been suggested that increases in the abundance of herbivorous fishes may help coral reefs recover from long-term climatic impacts and enhance coral cover (Mumby and Harborne 2010). Recent studies have also indicated the importance of reef fish communities in maintaining the integrity of coral reef systems. A study conducted in aquaria observing black band disease on *Montastraea faveolata*, showed that the butterflyfish *Chaetodon capistratus* was involved in transmission of the disease between coral colonies (Aeby and Santavy 2006). Transmission of black band disease through *Chaetodon capistratus* could occur through direct oral transmission or through indirect fecal transmission (Aeby and Santavy 2006). Fish can also impact the progression of a disease. A study from Lizard Island, Great Barrier Reef showed several species of corallivorous fish to selectively target disease lesions while feeding, thereby potentially reducing disease progression of black band disease and brown band disease on *Acropora sp.* (Cole et al. 2009; Chong-Seng et al. 2010). Another study using statistical modeling showed that some coral diseases (*Porites* tissue loss and *Montipora* white

syndrome) observed in Kaneohe Bay were most strongly predicted by lower abundance of butterflyfish and juvenile parrotfish (Williams et al. 2010).

The dynamics between herbivorous fish populations and macroalgal levels may also influence disease rates. Contact with the macroalga *Halimeda opuntia* spurred an infection of white plague type II on coral colonies of *Montastrea faveolata* (Nugues et al. 2004). The alga is believed to act as a reservoir for disease pathogens. Herbivorous fish also serve a critical functional role on coral reefs and their abundance can shape benthic community structure. A cage experiment conducted in Hawaii showed algal biomass to be greatest in surfaces exposed to both nutrient enrichment and exclusion of herbivorous fish (Smith et al. 2001). Functional groups of herbivores have also been proposed as useful indicators of coral reef resilience (Green and Bellwood 2009) and parrotfish who are functionally classified as excavators and bio-eroders are reported to be positively associated with levels of live coral cover (Heenan and Williams 2013).

MPAs and environment

While there are some management strategies that can be used to address stressors such as elevated temperature, decreased water quality (Bradley et al. 2010) and increased sedimentation, regulation of environmental stressors through protected areas can be difficult. The majority of coral reef management resources and efforts have been directed towards the establishment of marine reserves and less so to strategies that improve water quality (Mumby and Steneck 2008). There is, however, a growing body of literature calling for increased focus on watershed management in tandem with coral reef management (Richmond et al. 2007) and increased recognition of environmental changes (i.e. decreased water quality and increased sediment loads) and their influences on disease dynamics (Harvell et al. 2007).

Mass coral bleaching events are thought to be primarily triggered by sustained sea surface temperatures of 1-2ºC above mean summer maxima (Glynn 1993; Hoegh-Guldberg 1999). Increases in temperature may also contribute to the frequency of coral diseases (Bruno et al. 2007), pathogen virulence (Banin et al. 2003), and host susceptibility (Harvell et al. 1999)

Water quality has also proven to be important to maintaining healthy coral populations. Nutrient enrichment (increased phosphorous, nitrate, and ammonium) has been shown to increase the severity of yellow band disease on *Montastrea species* in the Caribbean (Bruno et al. 2003) and sewage exposure has been associated with higher prevalence of black band disease and white plague type II (Kaczmarsky et al. 2005). Terrestrial runoff and sedimentation have negative effects on the growth, survival, reproduction, and recruitment of hard corals (Fabricius 2005). Sedimentation may also cause tissue necrosis in some species of corals (Riegl 1995).

Despite awareness of the threat that diseases pose to corals, there has been limited research on the prevalence of disease within Oahu's Marine Life Conservation Districts (Hunter 1999). This project aims to gain an understanding of Oahu's MLCDs compared to unprotected areas and also draws connections between environmental variables, fish diversity, coral community structure, and disease prevalence. The results of this study will clarify the impact that fishing restrictions have on Oahu's MLCDs and the importance of these restrictions in promoting coral health. This studies objectives were to 1) examine whether disease assemblages differ between locations (Hanauma, Pupukea, and Waikiki) 2) examine whether disease assemblages differ across protection boundaries 3) explore associations between biological and environmental predictors and the prevalence of five common diseases through statistical modeling 4) determine whether there are any size-class level differences in disease susceptibility and finally 5) understand which aspects of coral reef ecosystem health (fish abundance, coral cover, and macroalgal cover) are preserved under protective status.

METHODS

Study area and sampling design

This project investigated coral reef ecosystem health at Oahu's three Marine Life Conservation Districts (Hanauma Bay, Pupukea, and Waikiki MLCDs). These three MLCDs and the chosen "control" sites (either directly adjacent to or as nearby and comparable to them as possible) are referred to in this study as the six "sites" (Hanauma Protected, Hanauma Unprotected, Pupukea Protected, Pupukea Unprotected, Waikiki Protected, and Waikiki Unprotected) (Figure 10). Each of the paired protected and unprotected sites fall under what will be referred to as the three "locations" (Hanauma, Pupukea, and Waikiki locations).

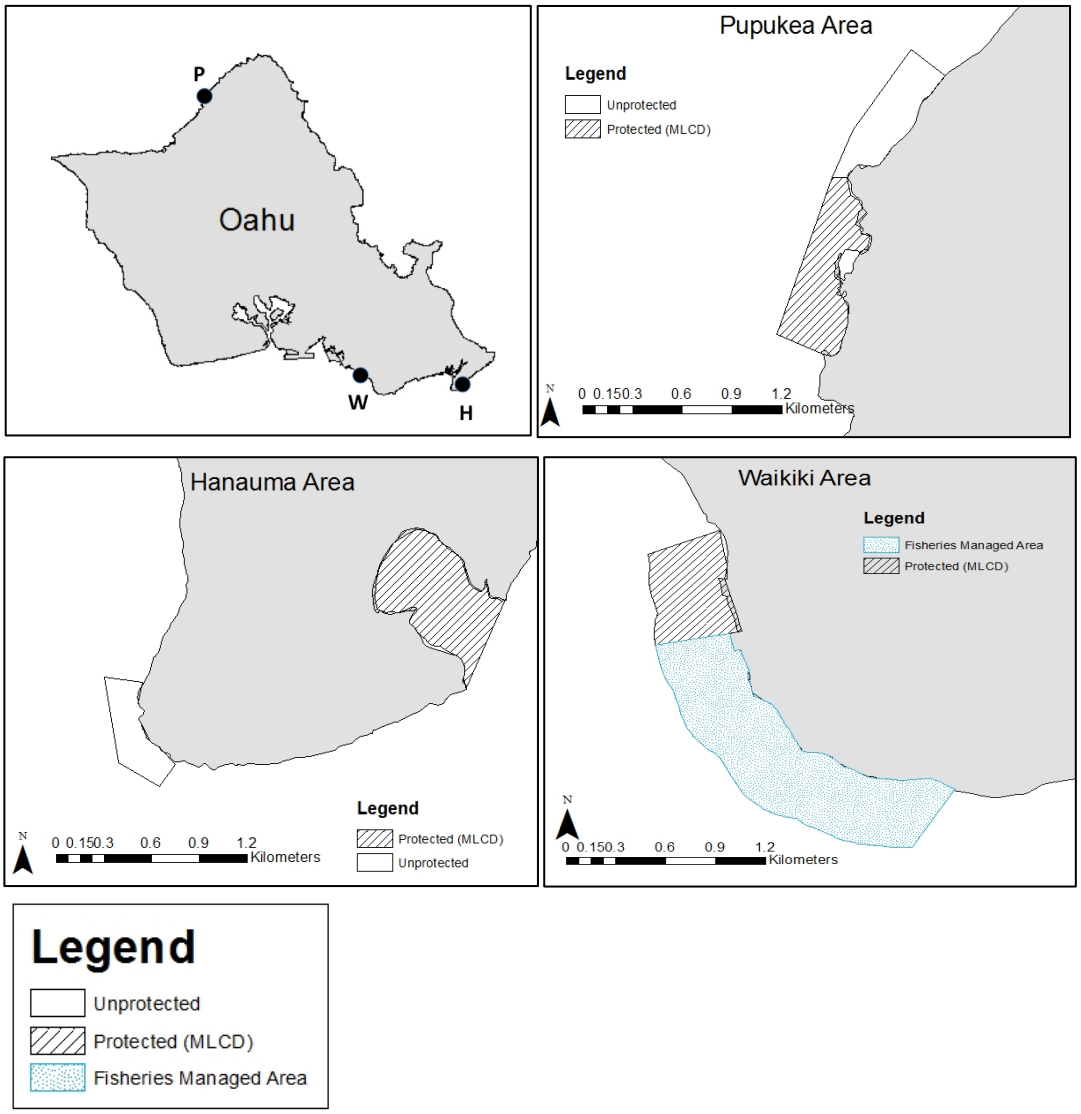

Figure 10. The three Marine Life Conservation Districts (Pupukea (P), Hanauma Bay (H), and Waikiki (W)) on Oahu, Hawaii are shown as black dots, with closer views of the protected (shaded) and unprotected (clear) control areas at each location. Note that the control site at Waikiki is a Fisheries Managed Area (blue shaded) that is under an alternating one-year rotational closure.

Survey points were chosen using a stratified random sampling approach using ArcMap10 (Figure 11). A shallow water benthic habitat map was used to identify areas within the six sites that had coral cover of 10% or more and 20 random points for each site were assigned to this habitat stratum (Battista et al. 2007). This particular benthic habitat map was useful in that it had 14 detailed geomorphological structure classes (including sand, coral, rock, etc.) and 8 major biological cover types (coral, macroalgae, etc.). Additionally each biological cover type had three abundance levels (10-50%, 50-90%, 90-100%). Areas with less than 10% of a biological cover type were not included as they would be more aptly characterized using one of the other geomorphological structures or a more dominant biological cover type. At the two Waikiki sites, there were no existing patches of greater than 10% coral cover. For these two sites, habitat classified as sand was clipped from the site maps and random points were assigned to the remaining habitat strata (macroalgae 10-50%, macroalgae 50-90%, and turf 50-90%).

Points selected through this process were converted from Universal Transverse Mercator (UTM) to latitude and longitude coordinates and entered into a GPS for use in the field. Garmin GPS76 units were used to navigate to starting points of surveys in the field.

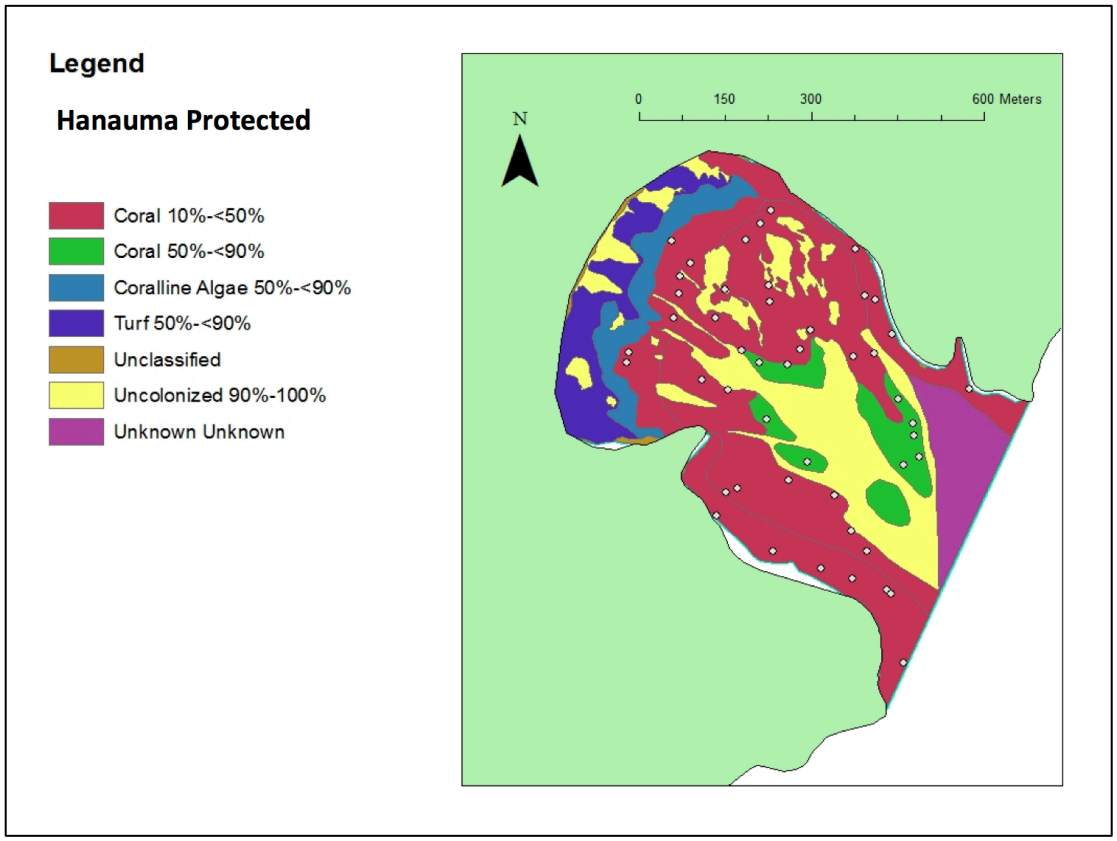

Figure 11. Map of Hanauma-Protected site showing an example of survey points chosen using the stratified random sampling approach. Areas with greater than 10% coral cover (marked in red and green) were selected using ArcMap 10 and starting points for surveys were randomly projected into these areas of interest.

Field surveys documenting coral reef ecosystem factors

Surveys were conducted at 119 transects at the three Marine Life Conservation Districts on Oahu (Hanauma Bay, Pupukea, Waikiki locations) and three unprotected sites from 2012-2013. Surveys conducted on the north shore of Oahu were constrained in timing due to winter swells, which sometimes made sites inaccessible. At each transect, a 10 m line was deployed along depth contours. Coral colony density was documented along the 10 m line by counting and recording all of the coral colonies whose centers fell within 1 meter on either side of the transect line. Due to the size and shape of colonies it was possible to have colonies whose centers fell within the transect field but whose boundaries extended beyond the survey area; these colonies were included in the surveys. Colonies were identified to the species level and placed into one of seven size classes: <5 cm, 5-10 cm, 10-20 cm, 20-40 cm, 40-80 cm, 80-160 cm, >160 cm.

Disease assessments were conducted within the same transect field and all colonies with signs of disease were counted and photographed. Coral colonies with disease lesions were classified by lesion type: tissue loss, discoloration, or growth anomalies (Work and Aeby 2006). For each survey, coral disease prevalence was calculated as the total number of colonies of a specific coral species with a specific lesion type divided by the total number of colonies of that species (both healthy and diseased). Coral disease abundance was calculated as the total number or “raw count” of colonies of a specific coral species with a specific lesion type.

Coral cover was calculated from high-resolution digital images taken along a 10 m transect. A Canon-G12 camera with underwater housing was mounted on a monopod frame, 1 m from the substrate to provide a 35 cm x 45 cm image. Photographs were taken every 0.5 m along the 10 m line to provide 20 non-overlapping images. Photographs were imported into the program Coral Point Count (CPCe; Kohler and Gill 2006) where 25 randomly selected points were projected onto each image for a total of 500 points per transect. Total coral cover, coral cover of individual species, and macroalgal cover were calculated through CPCe (Kohler and Gill 2006).

Reef fish abundance and diversity were recorded using a visual belt transect survey method (Brock 1982). Divers swam along a 25 m x 5 m transect belt (the first 10 m of the same belt was used for coral surveys) and all fish encountered were identified to the lowest possible taxon, tallied, and assigned an estimated total length to the nearest centimeter. Fish were grouped into six trophic guilds (herbivores, mobile invertebrate feeders, sessile invertebrate feeders, piscivores, zooplanktivores, and detritivores).

Sediment samples were collected at each of the 119 transects. Sediment composition and grain size is reflective of wave action regimes and therefore useful in beginning to characterize oceanographic differences between sites. Additionally silt sediment fractions are an indicator of terrigenous runoff and a proxy for sedimentation. Sediment samples were mixed and wet sieved through standard brass sieves. Sieves had mesh sizes of 2.8 mm, 500 µm, 250 µm, 63 µm, plus a catch pan and were used to determine grain size fractions (rubble, gravel, coarse

sand, fine sand, and silt, respectively). Sediment remaining in each sieve was emptied onto preweighed filter paper (Wattman Brand grade 114 wet-strength, 25 µm). The filters were air dried in the laboratory for one week and weighed. Grain size fractions were calculated by dividing the weight of each size fraction by the total sample weight.

Sediment samples were also used to calculate inorganic-organic carbon fractions. The percent of organic material in sediment samples is made up of both ocean based and land based organic inputs and is an indicator of the level of terrigenous input into a system (Jokiel et al. 2004). The percent of terrigenous material in the sediment sample is an indicator of wave energy, as high wave action, which abrades the basalt boulders shorelines, contributes to the production of terrigenous materials in the sediment. A subsample of mixed sediment was air dried and ground into a fine homogenous material using an IKA A11 analytical mill. Preweighed crucibles were loaded with 10 g of finely ground sediment and placed in a drying oven at 100°C for 10 hours. Crucibles were placed in a desiccator to cool and then reweighed. Crucibles were then placed in a muffle furnace at 500°C for 12 hours, cooled in a desiccator and reweighed to calculate the organic fraction. Finally crucibles were placed in the muffle furnace at 1000°C for 2 hours, cooled and reweighed. The difference in weight after the 1000°C burn is representative of calcium carbonate in the sample and the remaining portion in the crucible is representative of the fraction of the sample that is terrigenous material (Jokiel et al. 2004).

Statistical Analyses

All statistical analyses were conducted in PRIMER v6 and PERMANOVA+ unless otherwise specified. Kruskal-Wallis tests and chi-square tests were performed using Minitab 16.

Investigating differences in disease assemblages

To test differences in disease assemblages among the locations (Hanauma, Pupukea and Waikiki), across protection boundaries, and between the 6 sites, a permutational multivariate analysis of variance (PERMANOVA) was used (Anderson 2006). This analysis was based on a zero-adjusted Bray-Curtis similarity matrix of the abundance (or counts) of the diseased coral colonies (Clarke et al. 2006). The disease abundance data was zero-inflated and therefore a zero-adjusted similarity matrix was used.

To find common diseases that were present at each of the locations, I used a similarity percentages analysis (SIMPER). The SIMPER analysis utilized similarity values from a Bray-Curtis resemblance matrix of the raw disease counts (Clarke 1993).

Linking biological and environmental predictors to indicator diseases

Relationships between five common diseases and lesion types and 17 predictor variables (

Table 3) were investigated through multivariate analysis. Multivariate analysis has proved to be a useful framework to explore connections between biological and environmental variables and disease prevalence (Aeby et al. 2011b). Both prevalence and disease colony counts were used in distance-based linear models (DISTLM) for each of the five common diseases (Anderson et al. 2008). Zero adjusted Bray-Curtis similarity matrices of the response variables (either prevalence or diseased colony counts) and normalized predictor variables were used in all of the models.

Zero-adjusted Bray-Curtis similarity matrices were used in all of the distance-based linear models (DISTLM) due to the large number of zero and near zero values in the disease data. Similarity values in a standard Bray-Curtis matrix remain undefined for two samples containing values of zero and can be highly varied for samples that have values close to zero. A zero-adjusted Bray-Curtis matrix helps to address this problem of highly fluctuating similarity values by adding a dummy variable equal to 1 to the matrix. Instead of two samples containing values of zero being undefined, the zero-adjusted matrix defines these samples as being 100% similar because they share the dummy variable (Clarke et al. 2006).

Table 3. Predictor variables included in the multivariate analysis with units, minimum values, and maximum values. Models using lesions occurring on *Porites lobata* used *Porites lobata* cover and density and models using lesions occurring on *P. meandrina* used *P. meandrina* cover and density. *For the variable "Most common size class *Porites lobata* colonies", the seven size classes were assigned a corresponding number (<5 cm=1, 5-10 cm=2, etc.) and the size class with the greatest number of colonies for that transect was assigned.

Variable	Description and units	Min	Max
Depth	meters	1	15.5
Corallivore density	# corallivores/125 m^2	0	13
Detritivore density	# detritivores/125 m^2	0	28
Herbivore density	# herbivores/125 m^2	0	92
Invertivore (mobile prey) density	# invertivores/125 m^2	0	33
Invertivore (sessile prey) density	# invertivores/125 m^2	0	8
Piscivore density	# piscivores/125 m^2	0	3
Zooplanktivore density	# zooplanktivores/125 m^2	0	55
Macroalgal cover	% cover	0	98.1
Porites lobata cover	% cover	0	34.71
Porites lobata density	# colonies/20 m^2	0	391
Most common size class *Porites lobata* colonies*	Number (1-7) corresponding to a binned size class	1 (<5 cm)	5 (40-80 cm)
Pocillopora meandrina cover	% cover	0	6.4
Pocillopora meandrina density	# colonies/20 m^2	0	122
% organic	% of sediment	2.1	7.81
% carbonate	% of sediment	27.95	97.1
Coarse sediment %	% of sediment from grain size analysis	7.01	89.44
Rubble %	% of sediment from grain size analysis	0.08	25.61
Silt %	% of sediment from grain size analysis	2.86	39.11

The predictor variables were a mixture of biological and environmental variables representing ecosystem health factors. These variables were measured on different scales (abundance, biomass, percent cover, etc.). Variables were normalized and placed on a common scale using PRIMER's method for normalization. The mean for each variable was subtracted from each entry of a single variable and divided by the standard deviation for that variable. This method is applied separately for each variable using that particular variable's mean and standard deviation. After normalization, 92-97% of the values (the % depending on the variable) fell within a range of -2 to +2 (Clarke and Gorley 2006).

Inter-correlations among the predictor variables were examined to look for sets of variables that were highly co-linear. Variables with a correlation value greater than 0.65 were dropped from the list of predictor variables used in the distance-based linear models (DISTLM). Variables with high inter-correlations that were not included in the model included: overall coral cover (correlated with *Porites lobata* cover), overall coral density (correlated with *Porites lobata* density), and fine sand (correlated with gravel and silt). There were 10 missing data values for the variable "rugosity", and so it was also excluded from the list of predictor variables.

Exploring community structure through dominance plots

Dominance plots of coral and fish communities were created for each of the three locations and six sites. Dominance plots are a graphical representation of a community's species evenness, species richness, and ecological dominance (Clarke and Gorley 2006). Averages of abundance were taken for each species at either the location or site level, then species were ranked in decreasing order of abundance and their relative abundances (or the percentage of the total abundance in the sample) were plotted against the increasing rank (x axis). The plots show results for 22 species of coral and 75 species of fish.

Size frequency distributions and relative frequencies of healthy and diseased colonies

Populations of healthy colonies and colonies with signs of disease were compared using relative frequencies calculated from coral colony counts. Relative frequencies were calculated by dividing the total number of colonies in each size class by the total number of colonies. To test the difference between populations of healthy corals and corals with signs of lesions a chi-square test was used.

RESULTS

Disease assemblages among locations and across protective boundaries

Disease assemblages were significantly different between the three locations studied on Oahu (PERMANOVA, *Pseudo-F*=7.369, P=0.0001). Two lesion types, *Porites lobata* growth anomalies and *Porites lobata* trematodiasis, were the strongest contributors to separation in

disease assemblages among the Hanauma, Pupukea, and Waikiki locations (**Figure 12**). There were also significant differences in disease assemblages across protection boundaries (PERMANOVA, *Pseudo-F*=2.821, P=0.0001).

Five Common lesion types used in multivariate analysis

The SIMPER analysis results were used to construct a list of common diseases and lesion types for the island of Oahu (**Table 4**). Five common diseases and lesion types were identified among the three locations: *Porites lobata* growth anomaly, *Porites lobata* trematodiasis, *Porites lobata* tissue loss, *Porites lobata* lesion with red filamentous alga, and *Pocillopora meandrina* tissue loss (**Figure 13**). These indicator diseases and lesion types were identified and named using established coral disease nomenclature (Work and Aeby 2006). Growth anomalies displayed distinct edges with smooth margins and were focal or multifocal (Work and Aeby 2006) (**Figure 13**). Colonies with trematodiasis exhibited multifocal pink swollen nodules. These "coral zits" have distinct edges and smooth margins and are 3-5 mm in size (Work and Aeby 2006) (**Figure 13**). Tissue loss in *Porites lobata* was diffuse with a band of white bare skeleton and a band of tan to brown bare skeleton further from the disease front (Work and Aeby 2006) (**Figure 13**). *Porites lobata* lesion with red filamentous alga was characterized by focal or multifocal tissue loss and the presence of fine filaments of algae that penetrated the coral tissue. Lastly, *Pocillopora meandrina* tissue loss was characterized as having distinct edges and a lesion that left white bare skeleton. This lesion was sometimes associated with the presence of the corallivorous snail *Drupella cornus*.

Two notes should be made about the common diseases and lesion types. First, the red filamentous alga that was associated with tissue loss in *Porites lobata* is suspected to be *Corallophila huysmansii;* however, laboratory tests will be needed to confirm if this is the correct species. Second, *Pocillopora meandrina* tissue loss may be caused by predation by the corallivorous snail *Drupella cornus*. Each *Pocillopora meandrina* showing signs of tissue loss was carefully checked for presence of *Drupella cornus.* While some colonies contained the corallivorous snail, some colonies with signs of tissue loss did not. Field signs indicate that this lesion is most likely attributable to predation but histological analysis is needed to rule out other possible causes including disease.

Porites lobata growth anomalies were most characteristic of the Hanauma location. *Porites lobata* trematodiasis, Porites *lobata* red filamentous alga, and *Pocillopora meandrina* tissue loss and possible predation also typified the location (**Table 4** and **Figure 13**). At Pupukea, there were three common diseases: *Porites lobata* trematodiasis, *Porites lobata* growth anomalies, and *Porites lobata* tissue loss (**Table 4** and **Figure 13**). The disease most characteristic of Waikiki was *Porites lobata* trematodiasis (**Table 4** and **Figure 13**).

Table 4. Common diseases and lesion types of the three locations studied. Results from SIMPER.

Location	Common diseases and lesion types	Order of importance
Hanauma	*Porites lobata* growth anomaly	1
	Porites lobata trematodiasis	2
	Porites lobata lesion with red filamentous alga	3
	Pocillopora meandrina tissue loss	4
Pupukea	*Porites lobata* trematodiasis	1
	Porites lobata growth anomaly	2
	Porites lobata tissue loss	3
Waikiki	*Porites lobata* trematodiasis	1

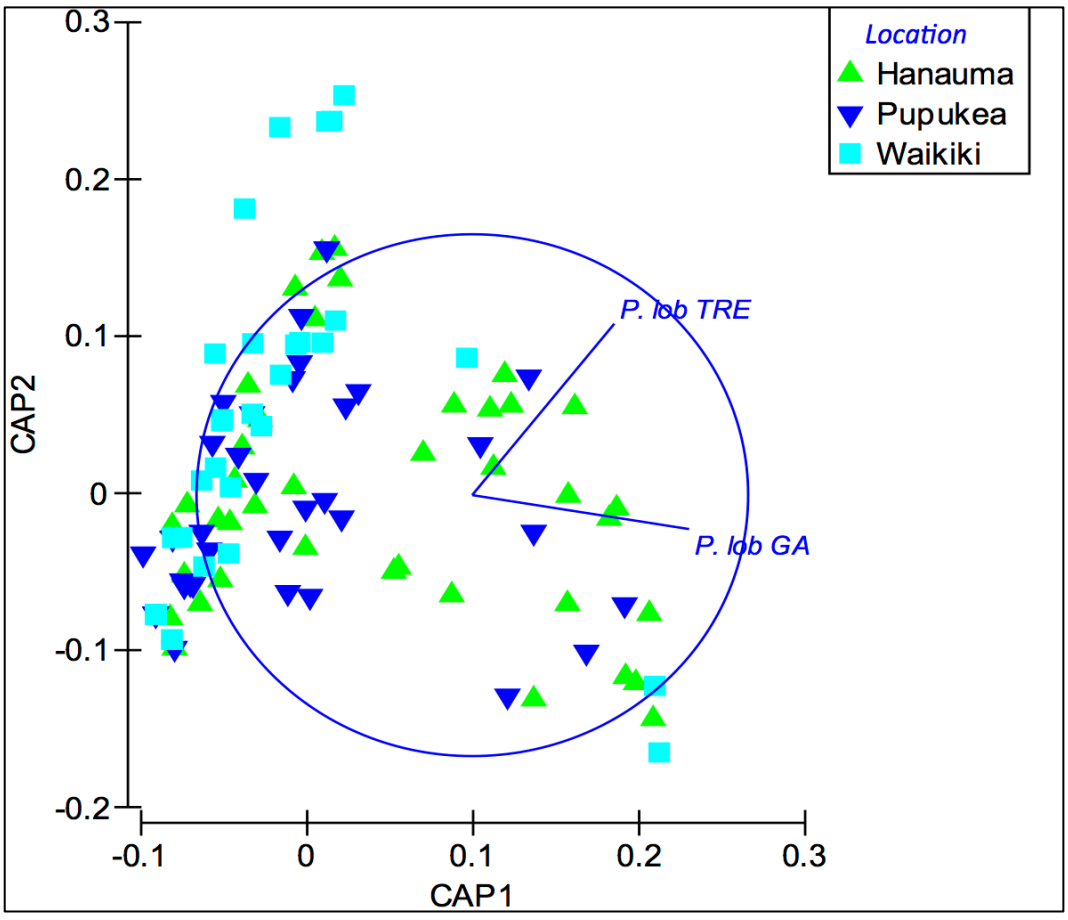

Figure 12. Canonical analysis of principal components (CAP). This is a two-dimensional representation of the multivariate space of all of the disease lesion variables. Points that are closer together are more similar than points that are further apart. The length of the vector shows the strength between the disease lesion variable and the CAP axes.

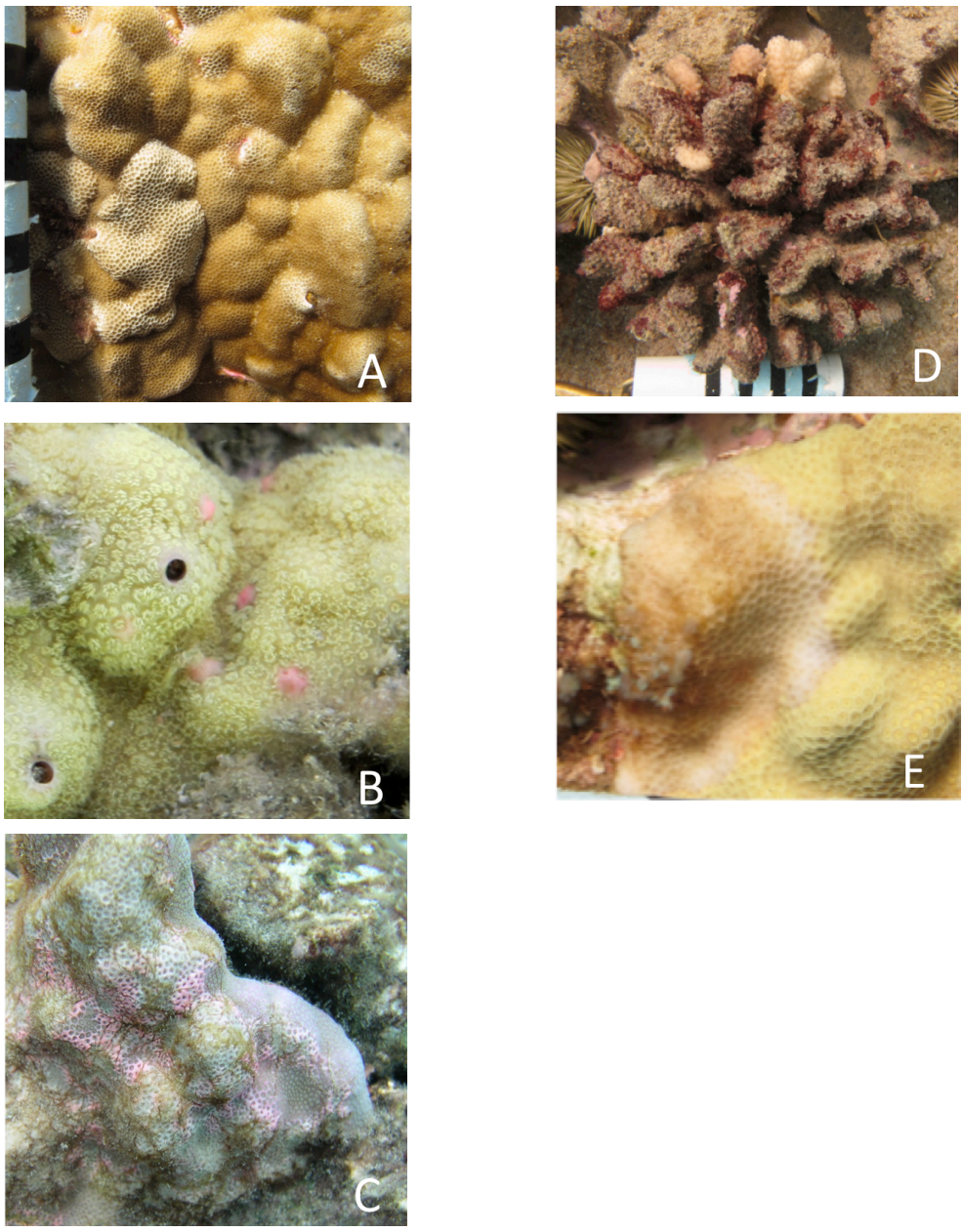

Figure 13. Five common diseases that are characteristic of the locations studied. A) *Porites lobata* growth anomalies B) *Porites lobata* trematodiasis C) *Porites lobata* lesion with red filamentous alga D) *Pocillopora meandrina* tissue loss and E) *Porites lobata* tissue loss.

Comparisons of mean prevalence for the five most common lesion types across protective boundaries at each of the three locations revealed varying results. *Porites lobata* lesion with red filamentous alga at the Hanauma location was the only lesion type to show significantly lower disease prevalence in the MLCD compared to the adjacent unprotected area (Table 5). Two out of five lesion types at the Hanauma location, two out of five lesion types at the Pupukea location, and four out of five lesion types at the Waikiki location had no significant difference in prevalence across protective boundaries (Table 5). The Hanauma location had two out of five lesion types that showed significantly higher prevalence in the MLCD compared to the adjacent control site: *Porites lobata* growth anomaly and *Porites lobata* tissue loss (Table 5). The Pupukea location had three out of five lesion types that showed significantly higher prevalence in the MLCD compared to the unprotected site: *Porites lobata* trematodiasis, *Porites lobata* tissue loss, and *Pocillopora meandrina* tissue loss (Table 5). The Waikiki location had only one lesion type with significantly higher prevalence in the MLCD: *Porites lobata* growth anomaly (Table 5).

Table 5. Mean prevalence of five common diseases across protection boundaries at the three study locations. Standard errors in parentheses. * indicates a significant difference across the protection boundary based on a Kruskal-Wallis test ($p<0.05$).

Hanauma

Lesion type	Protected	Unprotected
Porites lobata growth anomaly*	16.47 (1.79)	0.85 (0.36)
Porites lobata trematodiasis	10.83 (2.62)	2.77 (0.72)
Porites lobata tissue loss*	1.72 (0.50)	0.07 (0.04)
Porites lobata lesion with red filamentous alga*	3.64 (0.94)	5.67 (4.97)
Pocillopora meandrina tissue loss	3.04 (1.37)	3.62 (0.91)

Pupukea

Lesion type	Protected	Unprotected
Porites lobata growth anomaly	2.89 (0.90)	0.77 (0.29)
Porites lobata trematodiasis*	3.47 (0.77)	0.94 (0.34)
Porites lobata tissue loss*	1.33 (0.47)	0.41 (0.17)
Porites lobata lesion with red filamentous alga	1.86 (0.13)	0
Pocillopora meandrina tissue loss*	1.48 (0.54)	0.25 (0.25)

Waikiki

Lesion type	Protected	Unprotected
Porites lobata growth anomaly*	8.55 (4.64)	0.417 (0.42)
Porites lobata trematodiasis	19.69 (4.35)	20.44 (5.89)
Porites lobata tissue loss	0	0.35 (0.35)
Porites lobata lesion with red filamentous alga	0	0.56 (0.56)
Pocillopora meandrina tissue loss	0	2.00 (2.00)

Relationships between common diseases and predictors

For each of the five common disease and lesion types both the prevalence and abundance of colonies presenting that lesion were modeled against 17 predictor variables, for a total of ten models. Data for the statistical models utilized all of the data from the 119 completed surveys at the six sites.

Porites lobata growth anomalies

The prevalence of growth anomalies on *Porites lobata* was optimally predicted by silt levels, and explained 10.89% of the variation in the model (Table 6). However, the model produced using the abundance of *Porites lobata* colonies affected by growth anomalies showed that *Porites lobata* percent cover was one of the best predictors, explaining 36.45% of the variation in abundance (Table 6). This model was also able to explain almost half (46.16%) of the total variation and was the second best performing model out of the ten models (Table 6). Density of *Porites lobata* colonies was positively associated with higher levels of *Porites lobata* growth anomaly prevalence and abundance, explaining 3.85% and 3.66% respectively in each model (Table 6). Macroalgal cover (explaining 2.64%), corallivore density (explaining 3.93%), and rubble (explaining 2.84%) were also positively associated with this lesion type in the model using *Porites lobata* growth anomaly prevalence (Table 6).

Table 6. Results of distance-based linear models for association between *Porites lobata* growth anomaly prevalence and abundance with 17 predictor variables. Model selection was based on Akaike's Information Criterion (AICc) and a step-wise selection.

***Porites lobata* growth anomalies**

Response	Predictor	AICc	Pseudo-F	P value	% variability	% total
Prevalence	Silt %	341.47	14.299	0.0023	10.89%	
	Porites lobata density	338.32	5.2365	0.0277	3.85%	
	Porites lobata cover	327.76	12.951	0.0020	8.63%	
	Macroalgal cover	325.76	4.0743	0.0459	2.64%	
	Corallivore density	321.48	6.3427	0.0262	3.93%	
	Rubble %	318.81	4.7382	0.0318	2.84%	32.79%
Counts	Porites lobata cover	772.54	67.104	0.0001	36.45%	
	Porites lobata density	767.59	7.0897	0.0039	3.66%	
	Rubble %	760.1	9.688	0.0006	4.65%	
	Invertivore (mobile prey) density	759.23	2.9617	0.0632	1.40%	46.16%

Porites lobata trematodiasis

Trematodiasis on *Porites lobata* was best predicted by macroalgal cover, which explained17.28% of the variation in prevalence (Table 7). *Porites lobata* percent cover explained the most variation (5.52%) in the model using trematodiasis abundance (Table 7). Trematodiasis prevalence was also influenced by depth, which explained 2.88% of the variation and the most frequent size class of *Porites lobata* colonies, explained 2.78% of the variation. Host cover explained 5.52% of the variation and corallivore density explained 2.69% of the variation in the model using abundance of trematodiasis on *Porites lobata*.

Table 7. Results of distance-based linear models for association between *Porites lobata* trematodiasis prevalence and abundance with 17 predictor variables. Model selection was based on Akaike's Information Criterion (AICc) and a step-wise selection.

***Porites lobata* trematodiasis**

Response	Predictor	AICc	Pseudo-F	P value	% variability	% total
Prevalence	Macroalgal cover	423.44	24.441	0.0002	17.28%	
	Depth	421.32	4.1898	0.0422	2.88%	
	Most common size class *Porites lobata* colonies	419.24	4.1506	0.0421	2.78%	
	Detritivore density	418.75	2.5866	0.1066	1.71%	24.65%
Counts	Porites lobata cover	831.17	6.9568	0.0044	5.52%	
	Corallivore density	829.79	3.4573	0.0432	2.69%	
	Detritivore density	835.99	2.97	0.0673	2.48%	
	Most common size class *Porites lobata* colonies	829.72	2.172	0.1202	1.67%	12.35%

Porites lobata tissue loss

Porites lobata tissue loss prevalence and abundance (counts) were optimally predicted by *Porites lobata* percent cover and explained 19.89% and 15.72% of the variation in the model responses, respectively (**Table 8**). The amount of rubble in the sediment samples as well as the % organics, or the proportion of organic material in the sediment sample, were also relatively good predictors of *Porites lobata* tissue loss prevalence explaining 4.04% and 3.81% of the variation in the model respectively (**Table 8**).

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Table 8. Results of distance based linear models for association between *Porites lobata* tissue loss and 17 predictor variables. Model selection was based on Akaike's Information Criterion (AICc) and a step-wise selection.

***Porites lobata* tissue loss**

Response	Predictor	AICc	Pseudo-F	P value	% variability	% total
Prevalence	*Porites lobata* cover	-95.346	29.046	0.0001	19.89%	
	Rubble %	-106.84	6.6876	0.0120	4.04%	
	Organics %	-99.035	5.7879	0.0234	3.81%	
	Porites lobata density	-102.24	5.2848	0.0272	3.35%	
	Detritivore density	-110.25	4.4752	0.0439	2.58%	
	Zooplanktivore density	-107.85	3.1019	0.0733	1.84%	35.51%
Counts	*Porites lobata* cover	905.59	21.825	0.0001	15.72%	
	Porites lobata density	904.18	3.4829	0.0043	2.46%	
	Rubble %	903.38	2.8783	0.0150	2.00%	
	Detritivore density	902.63	2.7726	0.0140	1.88%	
	Most common size class *Porites lobata* colonies	903.29	2.1888	0.0469	1.50%	23.56%

Porites lobata lesion with red filamentous alga

Prevalence of *Porites lobata* lesions with red filamentous alga was best predicted by the most frequent size class of the host species and explained 3.79% of the variation (Table 9). The model using prevalence was only able to explain 15.85% of the total variation whereas the model using abundance of this lesion type was the best performing model out of the ten models made for all five common disease and lesion types. The statistical model built using the abundance of *Porites lobata* lesions with red filamentous alga explained 48.88% of the total variation (Table 9). Abundance of this lesion type was optimally predicted by *Porites lobata* cover and explained 43.46% of the variation (Table 9).

Table 9. Results of distance based linear models for association between *Porites lobata* lesion with red filamentous alga and 17 predictor variables. Model selection was based on Akaike's Information Criterion (AICc) and a step-wise selection.

***Porites lobata* lesion with red filamentous alga**

Response	Predictor	AICc	Pseudo-F	P value	% variability	% total
Prevalence	Most common size class *Porites lobata* colonies	277.14	4.6078	0.0341	3.79%	
	% calcium carbonate	274.93	4.2900	0.0592	3.43%	
	Porites lobata density	273.58	3.4229	0.0455	2.68%	
	Invertivore (sessile prey) density	273.00	2.6735	0.0924	2.06%	
	Depth	272.40	2.7045	0.1142	2.06%	
	Zooplanktivore density	272.11	2.4297	0.0756	1.83%	15.85%
Counts	*Porites lobata* cover	642.11	89.9180	0.0001	43.46%	
	Rubble (%)	637.60	6.6310	0.0084	3.06%	
	Corallivore density	636.86	2.8200	0.0834	1.28%	
	Porites lobata density	636.53	2.4302	0.1044	1.09%	48.88%

Pocillopora meandrina tissue loss

Piscivore densities explained 3.55% of the variation in the model for *P. meandrina* tissue loss (**Table 10**). The model using *Pocillopora meandrina* tissue loss prevalence did not perform well and was only able to explain 3.55% of the total variation. The model using abundance, on the other hand, was able to explain 30.65% of the total variation. Abundance of this lesion type was optimally predicted by *P. meandrina* density and explained 22.92% of the variation (**Table 10**).

Table 10. Results of distance based linear models for association between *P. meandrina* tissue loss and 17 predictor variables. Model selection was based on Akaike's Information Criterion (AICc) and a step-wise selection.

***Pocillopora meandrina* tissue loss**

Response	Predictor	AICc	Pseudo-F	P value	% variability	% total
Prevalence	Piscivore density	184.62	4.3068	0.0424	3.55%	3.55%
Count	*P. meandrina* density	695.32	34.798	0.0001	22.92%	
	Piscivore density	690.93	6.5063	0.009	4.09%	
	Depth	689.45	3.5533	0.0472	2.19%	
	Herbivore density	689.17	2.3786	0.1139	1.45%	30.65%

Model Performance

The five common diseases were modeled using both prevalence and abundance of the disease lesions type (total of ten statistical models). Model performance ranged from explaining 3.55% to 48.88% of the total variation. *Porites lobata* lesions with red filamentous algae and Porites lobata growth anomalies using abundance were the most effectively modeled out of the 5 common diseases (48.8% and 46.16% of the variation explained respectively).

Coral and fish community structure

Coral and fish species richness and evenness was similar across the three locations (Figure 14 and Figure 15). The Pupukea location had slightly lower coral species richness compared to the other two locations (Figure 14). Comparisons across protective boundaries showed coral species richness to be higher in protected sites for the Hanauma and Pupukea locations and lower in protected areas for the Waikiki location (Figure 16). Fish species richness was lower in protected areas for the Hanauma and Pupukea locations and higher in the protected areas in the Waikiki location (Figure 17).

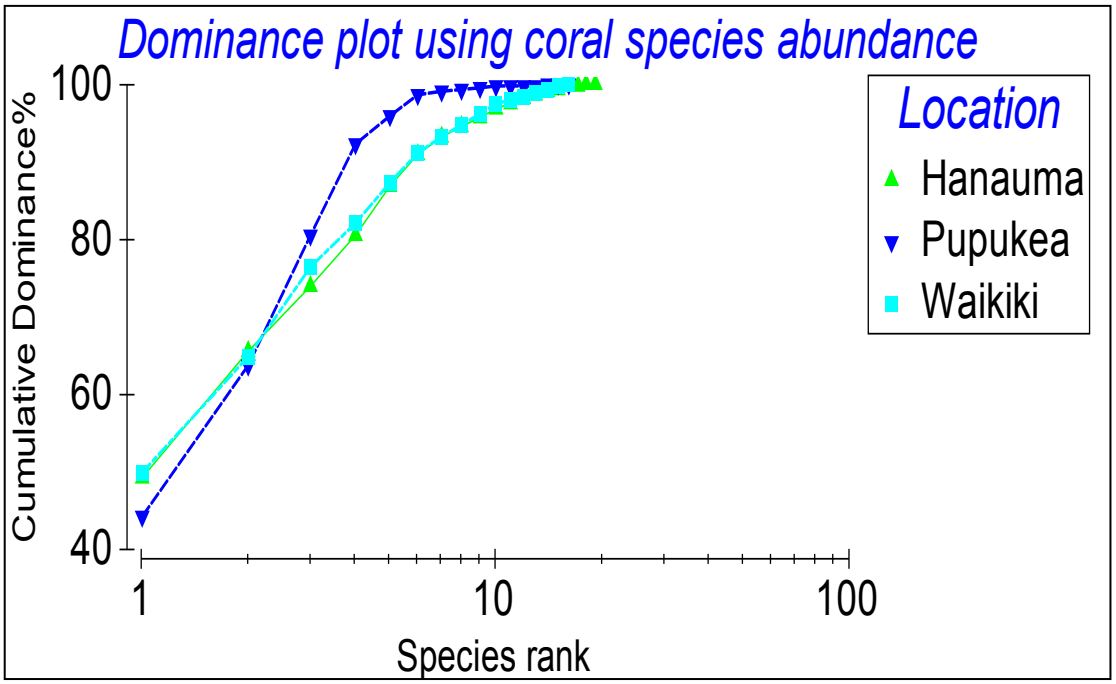

Figure 14. Coral species richness and evenness using location averages of coral species abundance.

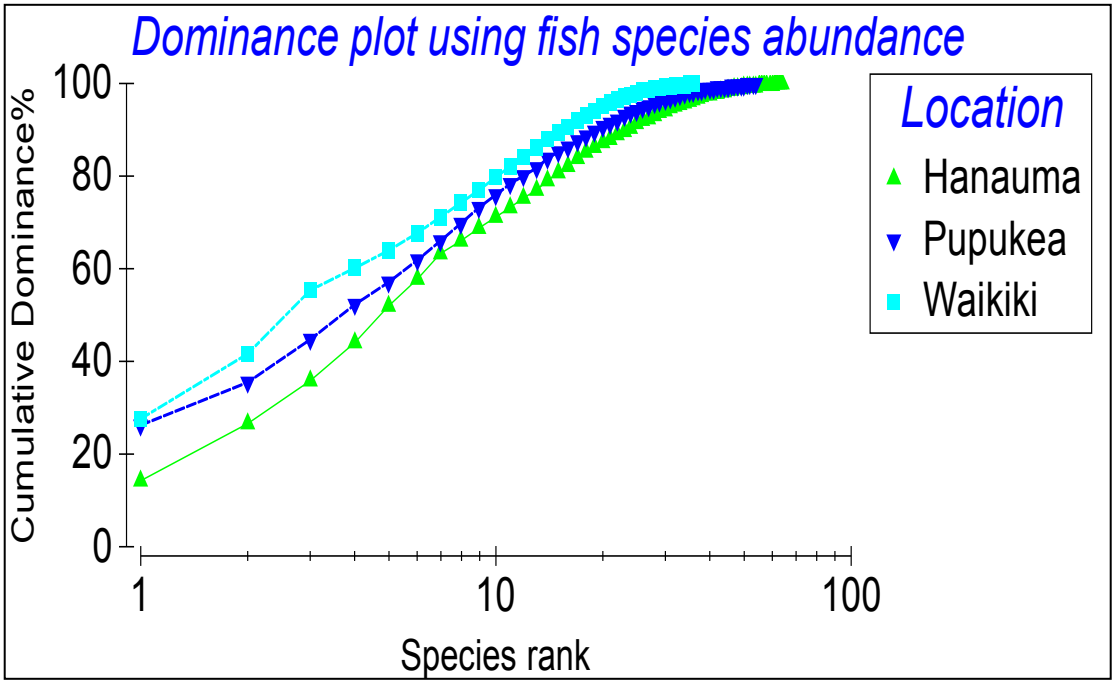

Figure 15. Fish species richness and evenness using location averages of coral species abundance.

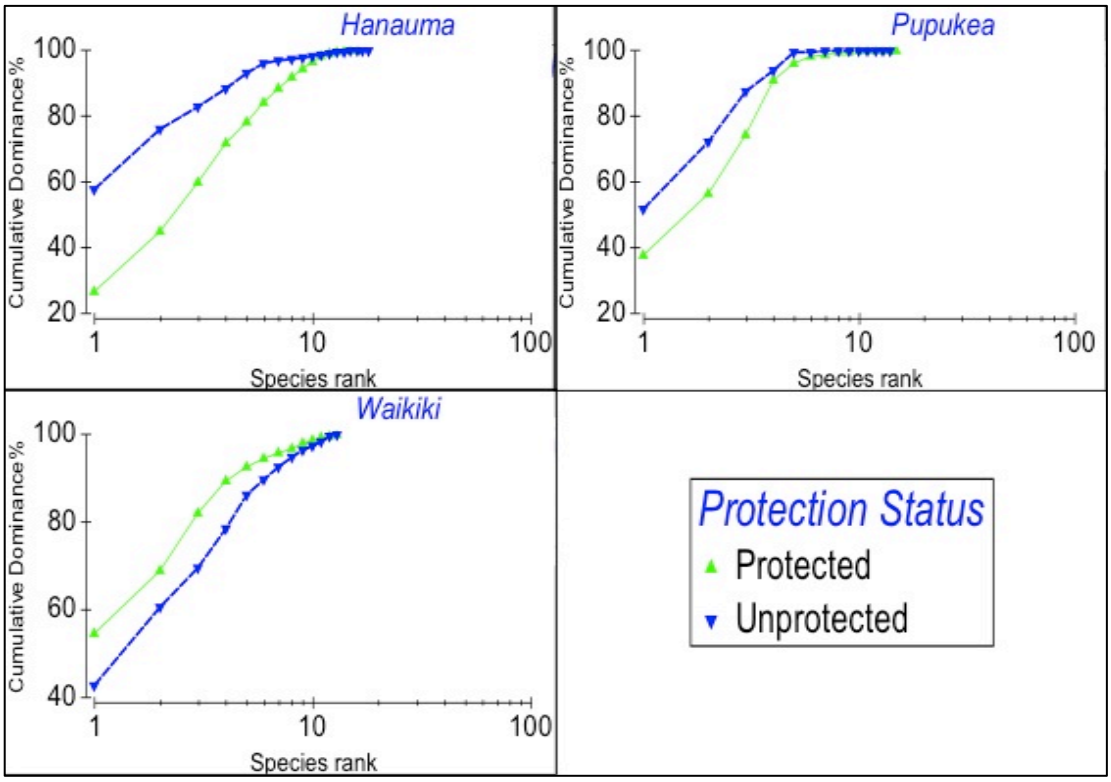

Figure 16. Coral species richness comparisons across protective boundaries for each location.

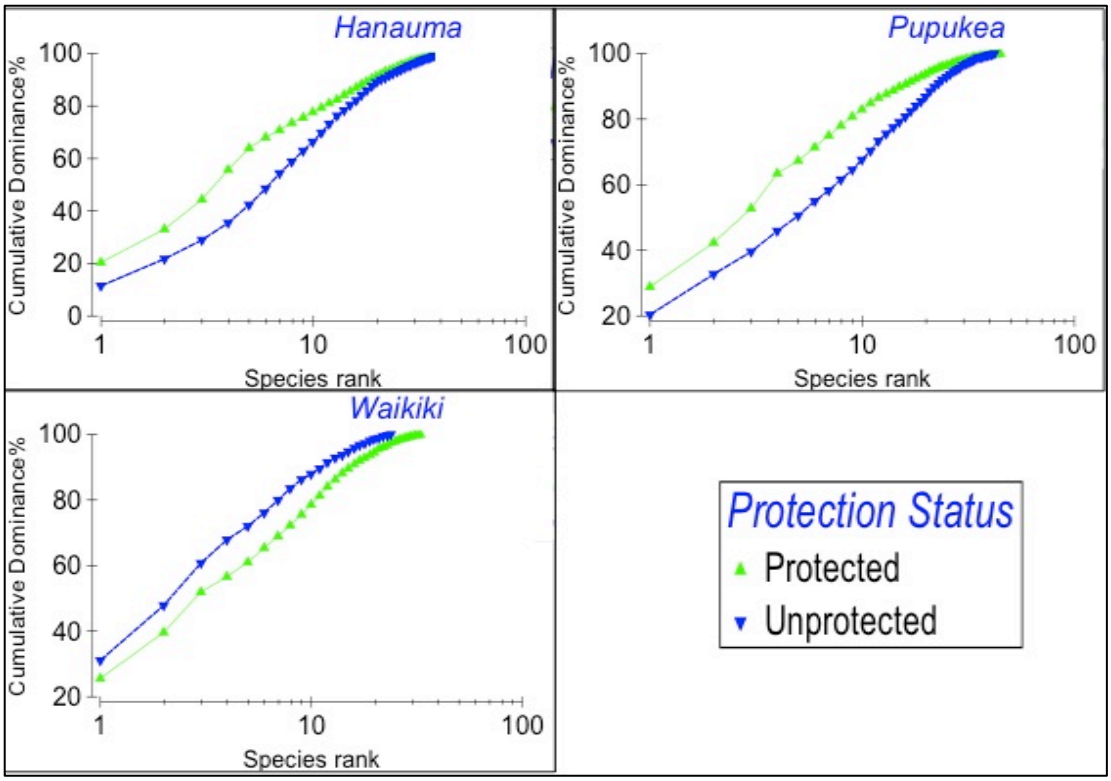

Figure 17. Fish species richness comparisons across protective boundaries for each location.

Coral community size structure and prevalence of *Porites lobata* growth anomaly

Growth anomalies on *Porites lobata* were more frequently found on larger colonies than on smaller colonies at all six sites (Figure 18). Using the Hanauma-Protected site as an example of this trend, healthy *Porites lobata* were distributed among size classes ranging from < 5 cm to 80-160 cm with most of the healthy individuals falling under the 10-20 cm size class (Figure 18). *Porites lobata* with growth anomalies ranged from the 5-10 cm to 80-160 cm size class with the majority of individuals falling under the 80-160 cm size class (Figure 18).

Community size structure, however, did not play a strong role for all lesion types on *Porites lobata.* The distribution of healthy *Porites lobata* and *Porites lobata* with growth anomalies were significantly different in the Hanauma Bay MLCD (Chi-square test, $p<0.0001$) (Figure 18). Similarly when populations of healthy *Porites lobata* and *Porites lobata* with trematodiasis were compared they also showed a statistically significant difference in the Hanauma Bay MLCD (Chi-square test, $p<0.0001$) (Figure 19). However, when populations of healthy *Porites lobata* and *Porites lobata* with tissue loss were compared at the Hanauma-Protected site there was no detectable difference, indicating that community size structure does not play a role in this disease process (Figure 20).

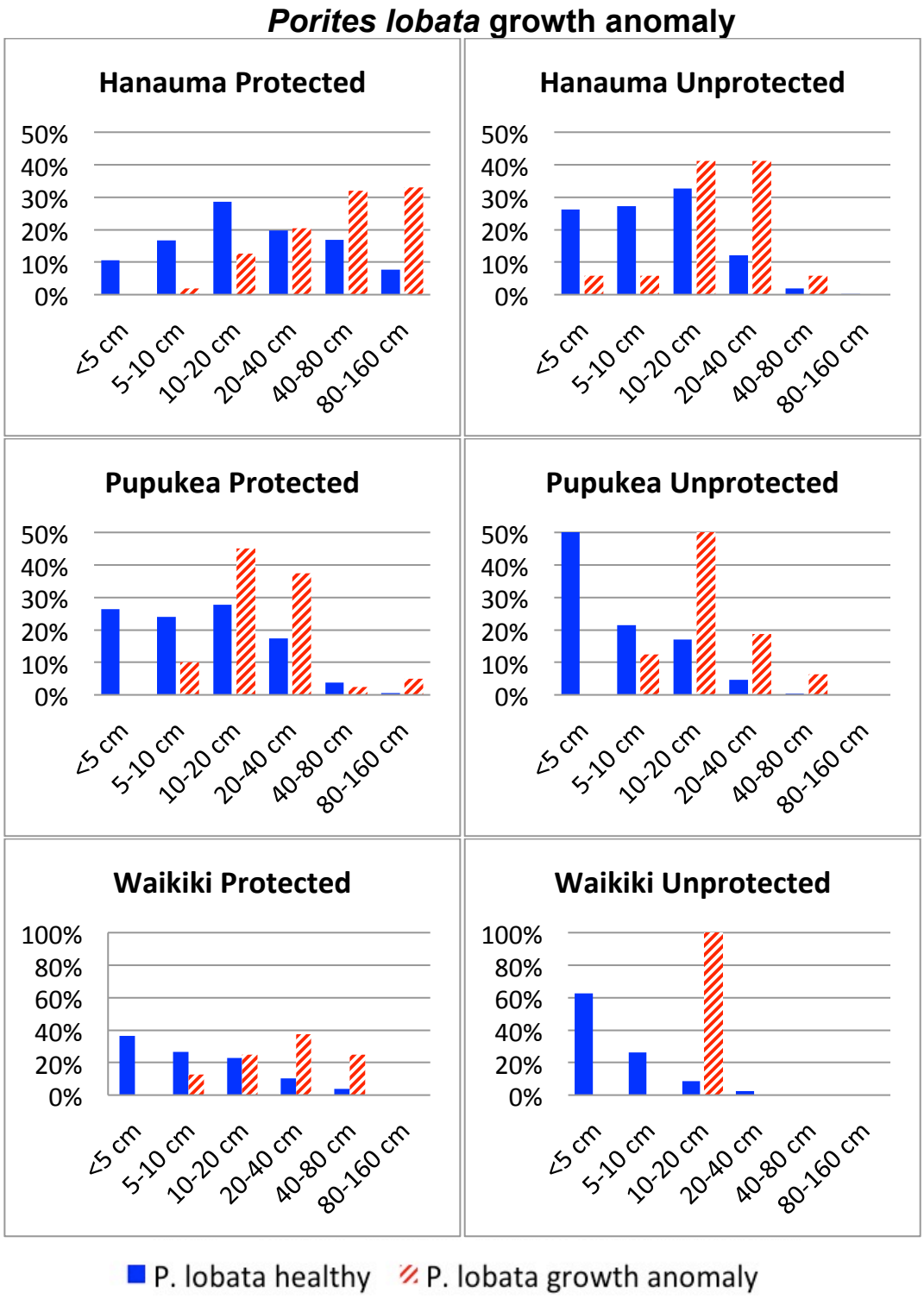

Figure 18. Relative frequencies of healthy *Porites lobata* and *Porites lobata* with growth anomalies at each of the six sites. Relative frequency shown as % on y-axis and size classes shown in cm on x-axis.

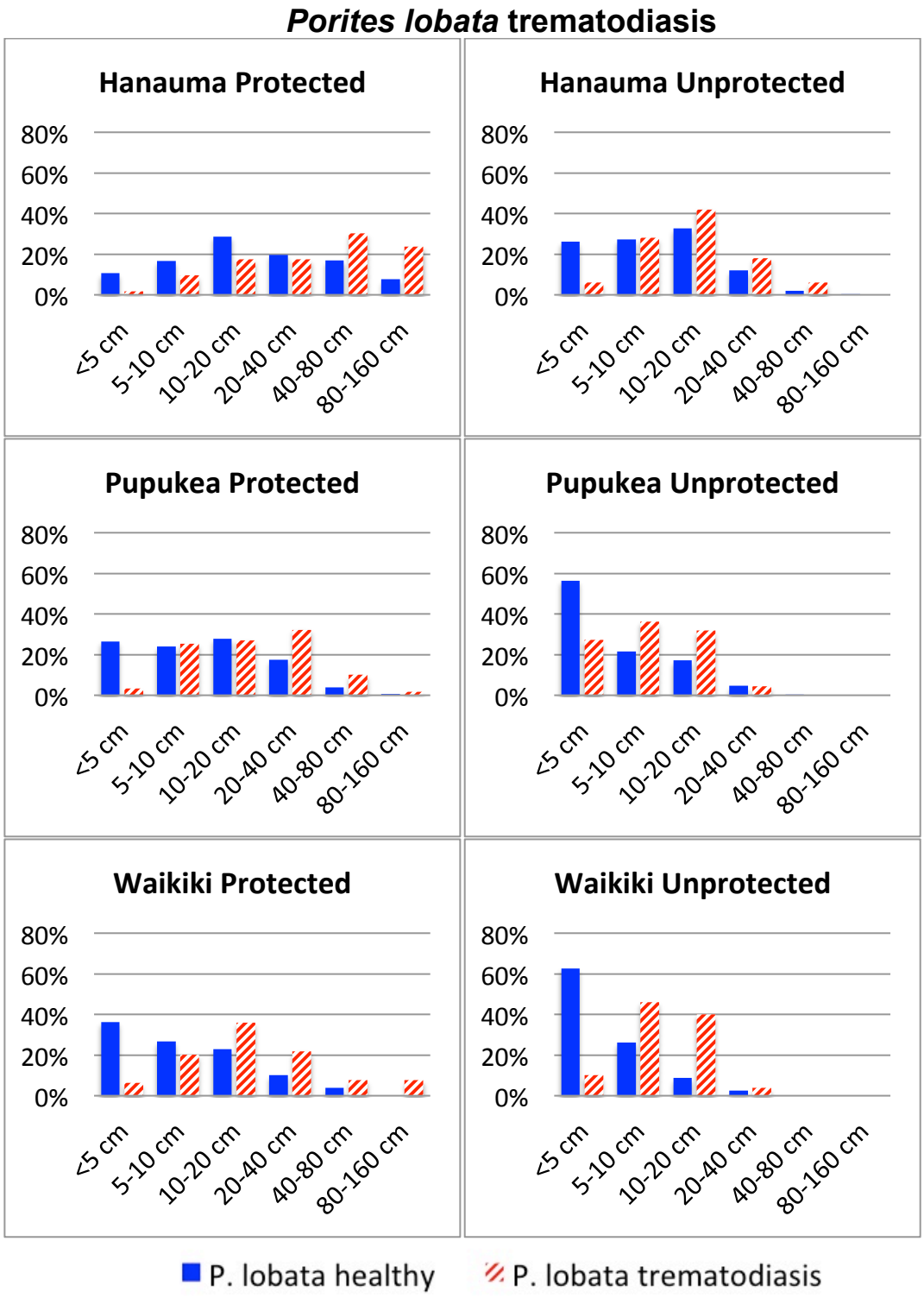

Figure 19. Relative frequencies of healthy *Porites lobata* and *Porites lobata* with trematodiasis at each of the six sites. Relative frequency shown as % on y-axis and size classes shown in cm on x-axis.

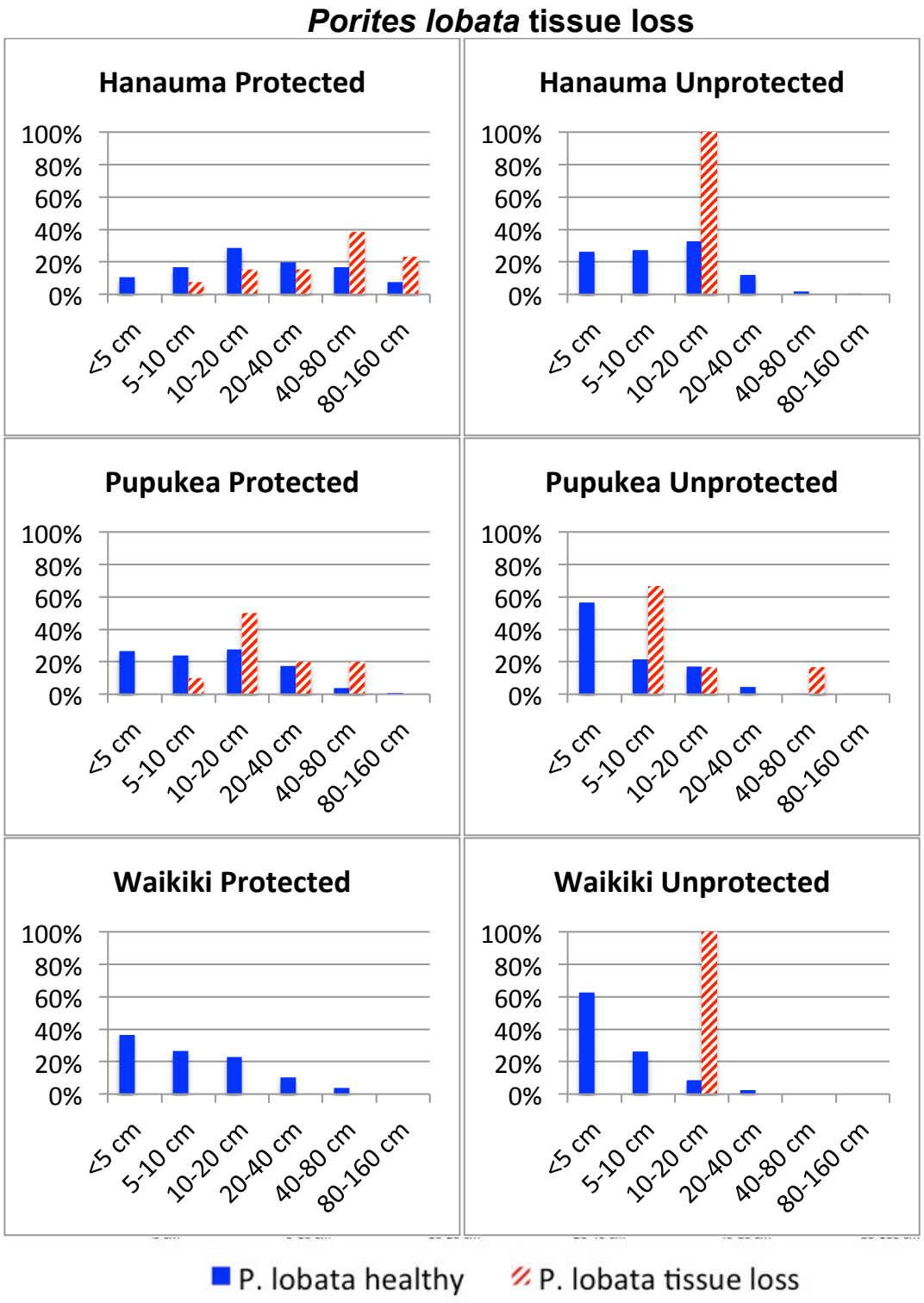

Figure 20. Relative frequencies of healthy *Porites lobata* and *Porites lobata* with tissue loss at each of the six sites. Relative frequency shown as % on y-axis and size classes shown in cm on x-axis.

Sediment composition and grain-sizes

Sediment composition varied slightly among the three locations but was similar among sites within a given location (Figure 21). Sites showed similar mean proportions of sediment composition across protection boundaries (Figure 21). Calcium carbonate made up the largest proportion in sediment samples across all sites ranging from 76.4% to 94.7% of the sample. Terrigenous (non-organic) materials were highest at the two Pupukea sites (Table 11). All six sites had low organic matter proportions ranging from 2.9% to 4.0% (Table 11).

Table 11. Proportion (%) of organic, carbonate, and terrigenous materials. Sample statistics are overall mean ± standard deviation for each site.

Site	Organic	Carbonate	Terrigenous
Hanauma - Protected	3.1 ± 1.2	91.8 ± 7.7	5 ± 7.1
Hanauma - Unprotected	2.9 ± 0.5	84.9 ± 21.6	12.2 ± 21.5
Pupukea - Protected	4.0 ± 1.3	76.4 ± 17.2	19.7 ± 17
Pupukea - Unprotected	3.0 ± 0.6	76.8 ± 22.1	20.1 ± 21.7
Waikiki - Protected	3.0 ± 0.5	94.7 ± 1.5	2.3 ± 1.4
Waikiki - Unprotected	3.1 ± 0.5	94.6 ± 1.7	2.3 ± 1.6

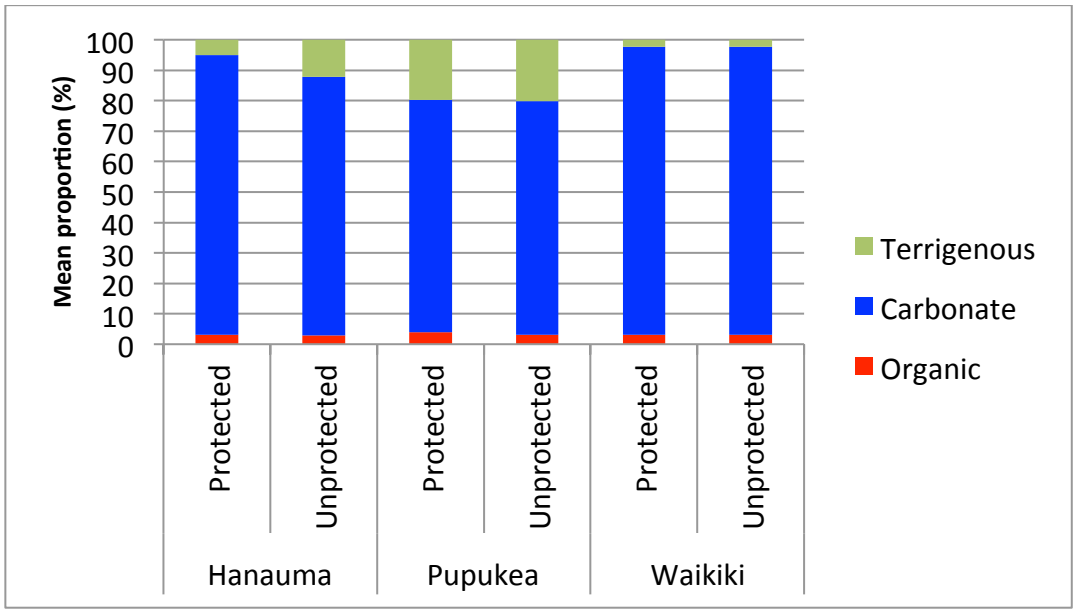

Figure 21. Mean proportion of sediment composition (%) for the six sites.

Gravel and coarse sand were the dominant grain size fractions for sediment samples from all six sites (Figure 22). Gravel ranged from 24.6% to 40.9% of site proportions and coarse sand ranged from 30.3% to 43.3% (Table 12). The mean proportion of silt was highest for the

Hanauma Protected site (15.3%) and lowest at the Pupukea Protected and Pupukea Unprotected sites (5.9% and 6.0% respectively) (Table 12).

Table 12. Proportion (%) of sediment grain-size categories. Sample statistics are overall mean ± standard deviation for each site.

Site	Rubble	Gravel	Coarse sand	Fine sand	Silt
Hanauma - Protected	5.4 ± 2.0	24.6 ± 13.1	33.5 ± 9.0	21.2 ± 12.7	15.3 ± 9.7
Hanauma - Unprotected	8.7 ± 4.5	32.2 ± 9.4	34.5 ± 6.0	13.9 ± 8.8	10.7 ± 5.3
Pupukea - Protected	3.3 ± 2.1	40.6 ± 5.7	43.3 ± 4.2	7.0 ± 4.8	5.9 ± 3.6
Pupukea - Unprotected	4.0 ± 1.7	40.9 ± 2.9	42.8 ± 2.7	6.3 ± 2.1	6.0 ± 2.5
Waikiki - Protected	10.8 ± 5.1	36.4 ± 5.1	34.3 ± 5.0	8.9 ± 4.8	9.6 ± 2.1
Waikiki - Unprotected	12.9 ± 5.7	35.3 ± 5.4	30.3 ± 9.5	11.1 ± 6.7	10.7 ± 2.7

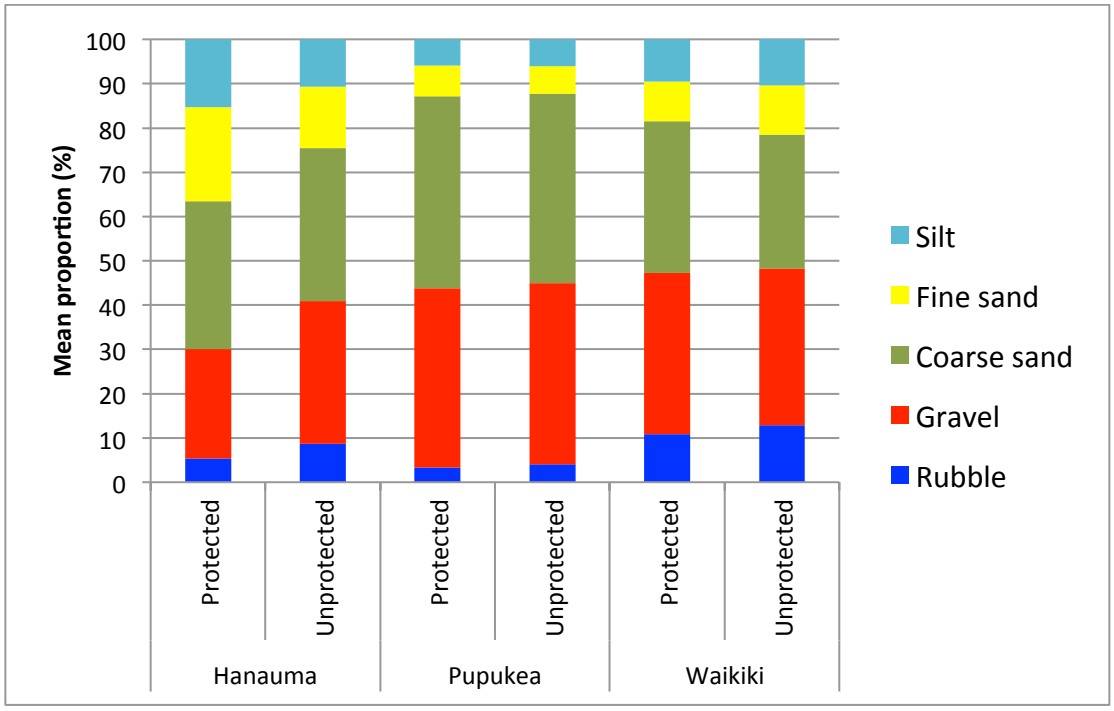

Figure 22. Mean proportion of sediment grain size (%) for six sites.

Ecosystem health factors and protection status

Fish populations had significantly higher densities at the Pupukea Protected site compared to its adjacent unprotected site (Kruskal-Wallis test, n=39, p=0.002; Figure 23). While the Hanauma and Waikiki locations showed a trend towards more dense fish populations in their protected sites the difference was not significant. Fish density examined through trophic guilds showed herbivores to be the most abundant taxa at the three protected sites (

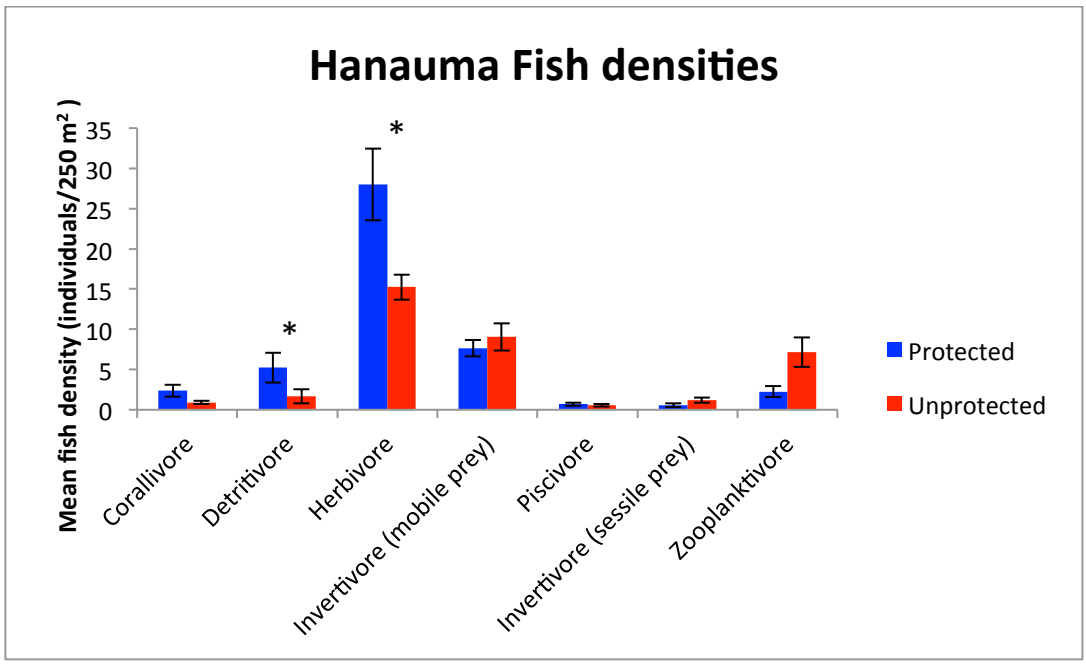

Figure 24, Figure 25, and Figure 26). Herbivore abundance was significantly higher in the Pupukea and Hanauma MLCDs compared to their adjacent unprotected sites (Kruskal-Wallis test, Pupukea $p<0.0001$, Hanauma $p=0.011$;

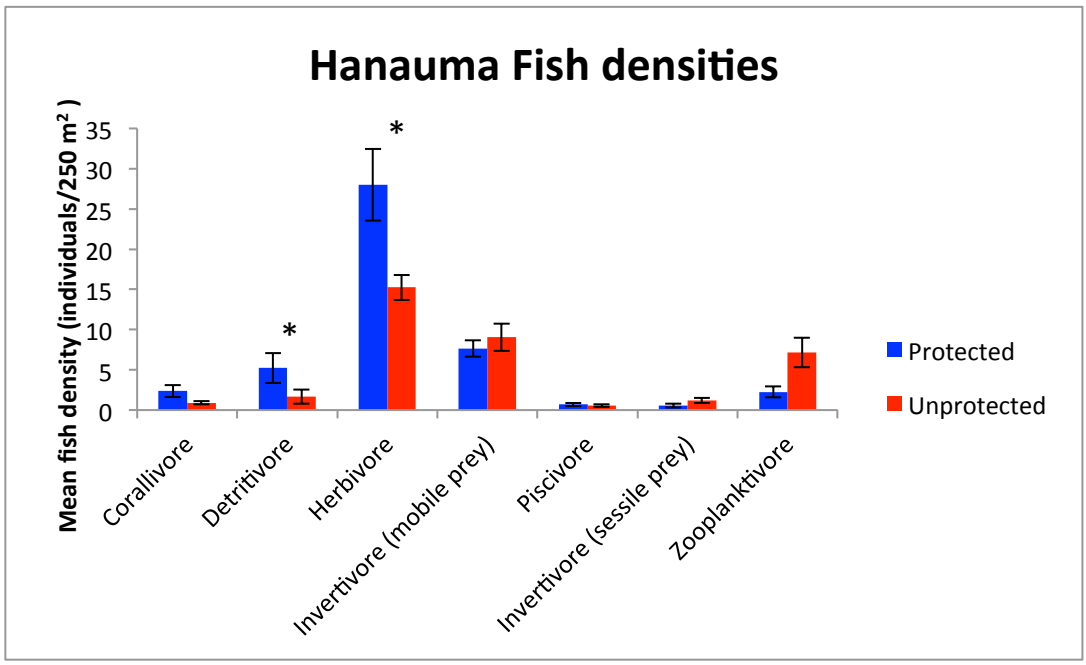

Figure 24, and Figure 25). There were also significantly different densities of detritivores at the Hanauma sites (Kruskal-Wallis test, $p=0.014$;

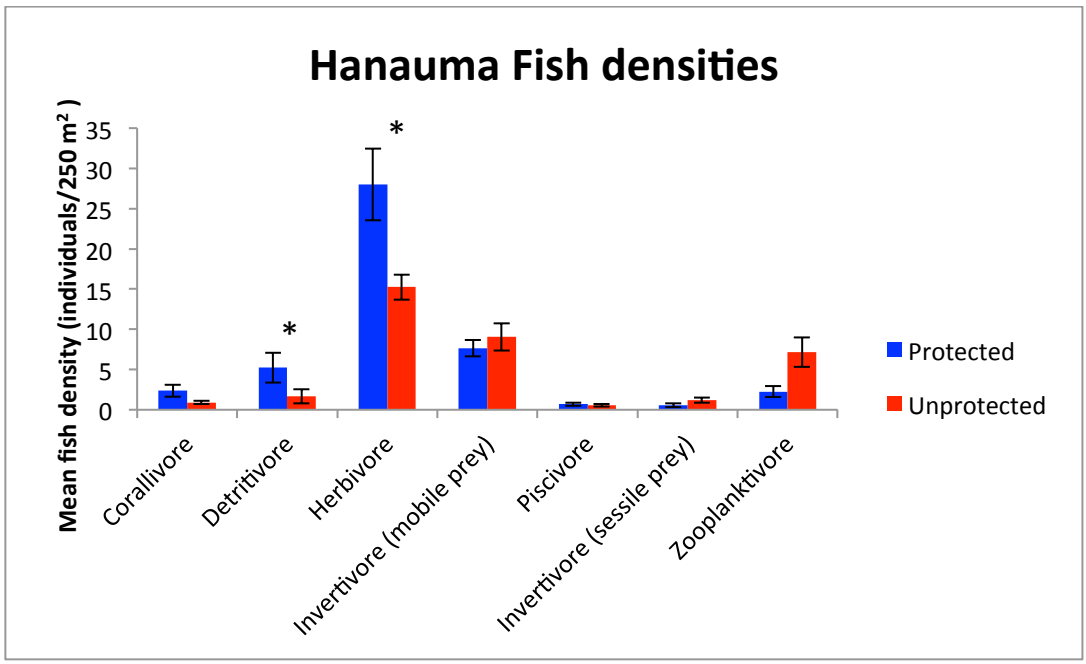

Figure 24). While Waikiki had comparatively less total fish abundance than the other two locations piscivore and zooplanktivore abundance was significantly different between the MLCD and the Fisheries Managed Area (Kruskal-Wallis test, piscivore p=0.038, zooplanktivore p=0.021; Figure 26). Piscivore populations remained largely absent from all six sites (

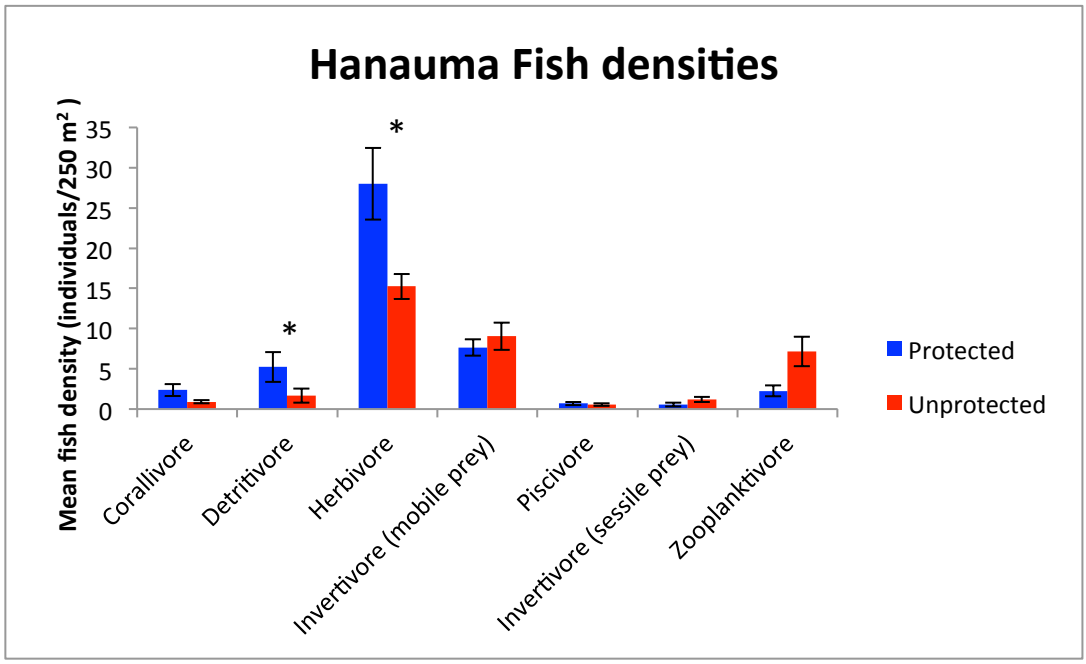

Figure 24, Figure 25, and Figure 26). Macroalgae levels varied spatially at the location level but there were no detectable differences in macroalgae levels across protection boundaries (Figure 27). There was substantial variability in total coral cover among sites (Figure 28). Coral cover was significantly higher in protected areas compared to adjacent unprotected sites in the Hanauma

(Kruskal-Wallis test, n=40, p<0.0001) and Pupukea locations (Kruskal-Wallis test, n=39, p<0.0001) (Figure 28). There was no detectable difference in coral cover at the Waikiki sites (Figure 28). *Porites lobata* was the most dominant coral species at all three locations in both density and cover (Figure 29).

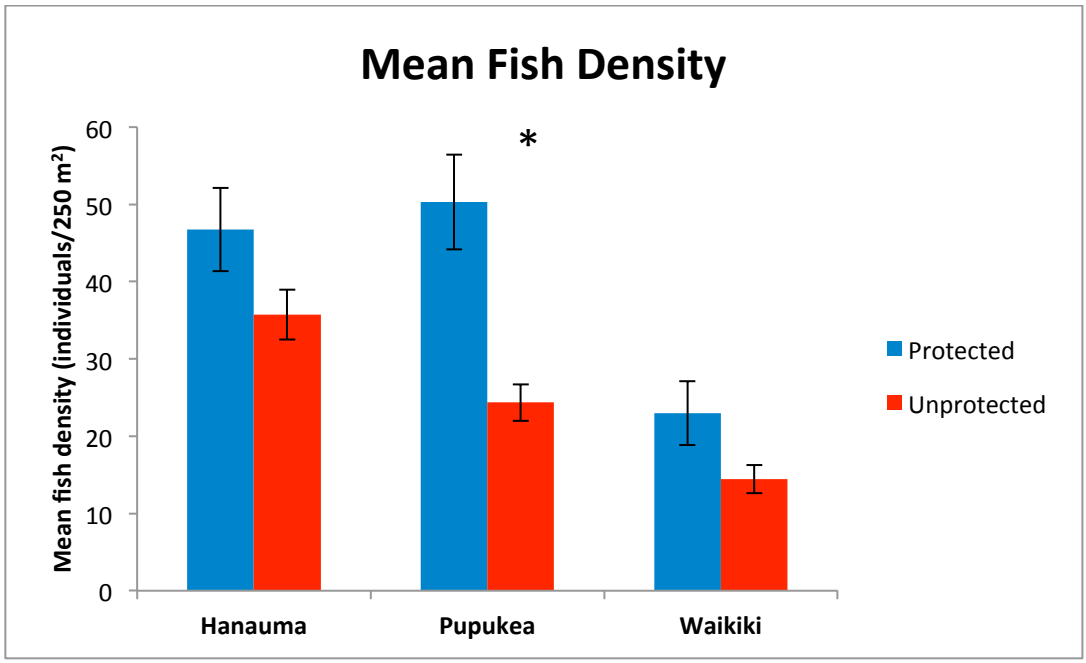

Figure 23. Blue and red bars represent mean fish density at each of the locations. Black lines indicate standard error and * indicates significant difference between protected and unprotected sites for that location (Kruskal-Wallis test, p<0.0001).

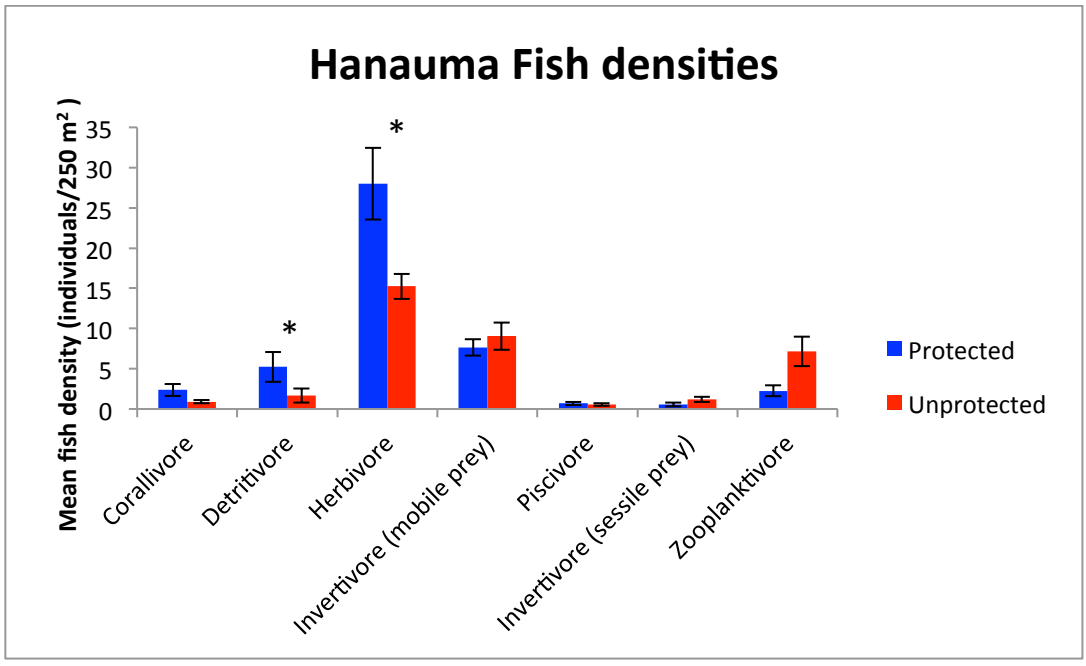

Figure 24. Blue and red bars represent mean fish density at the Hanauma sites for 7 different

trophic guilds. Black lines indicate standard error and * indicates significant difference between protected and unprotected sites for that location (Kruskal-Wallis test, p<0.05).

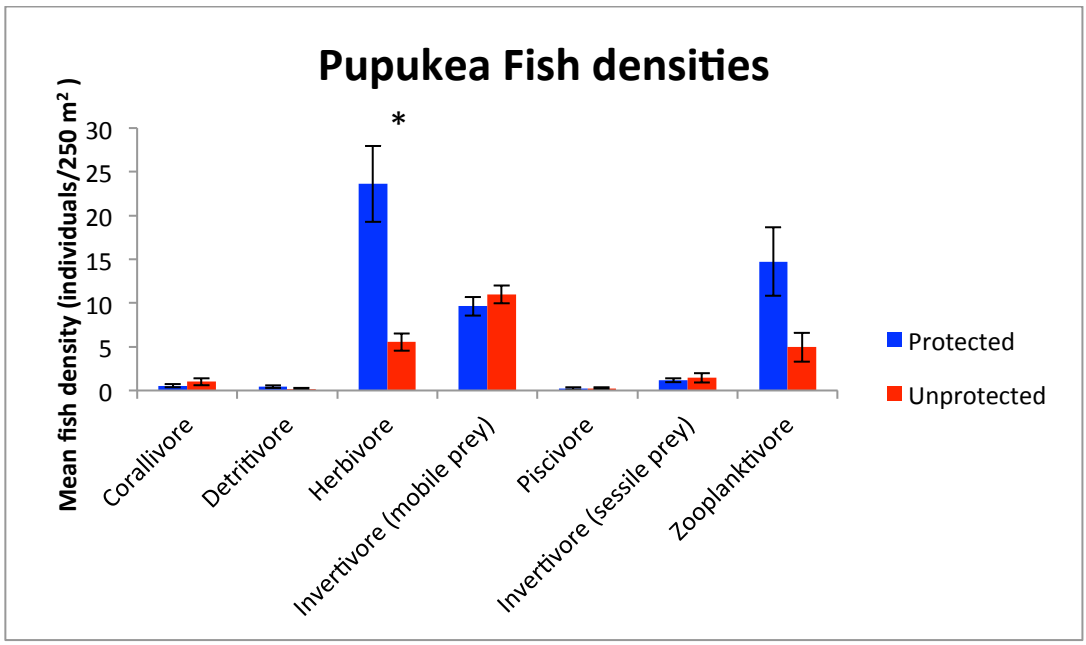

Figure 25. Blue and red bars represent mean fish density at the Pupukea sites for 7 different trophic guilds. Black lines indicate standard and * indicates significant difference between protected and unprotected sites for that location (Kruskal-Wallis test, p<0.05).

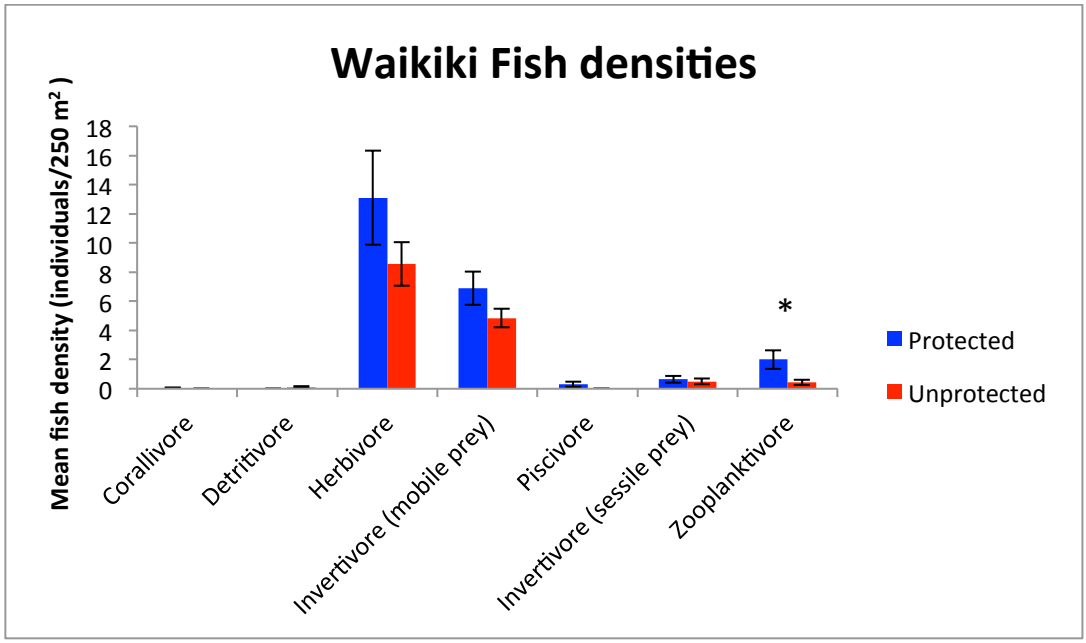

Figure 26. Blue and red bars represent mean fish density at the Waikiki sites for 7 different trophic guilds. Black lines indicate standard error and * indicates significant difference between protected and unprotected sites for that location (Kruskal-Wallis test, p<0.05).

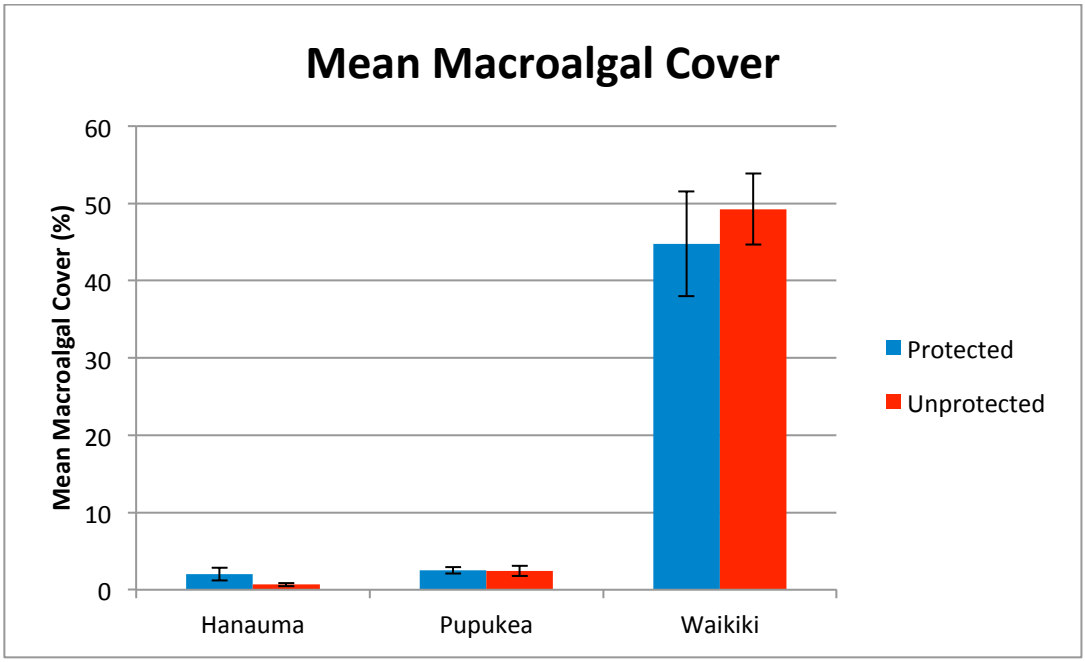

Figure 27. Blue (protected) and red (unprotected) bars represent mean percent macroalgal cover at each of the locations. Black lines show standard error.

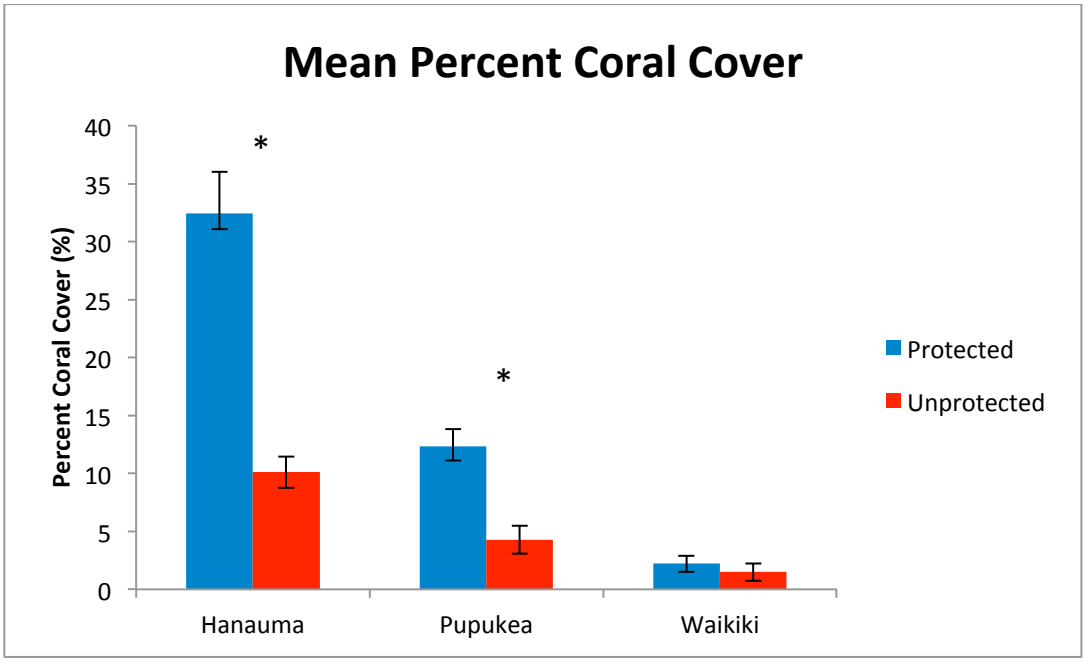

Figure 28. Blue (protected) and red (unprotected) bars represent mean percent coral cover at each of the locations. Black lines show standard error and * indicates significant difference between protected and unprotected sites for that location (Kruskal-Wallis test, $p<0.05$).

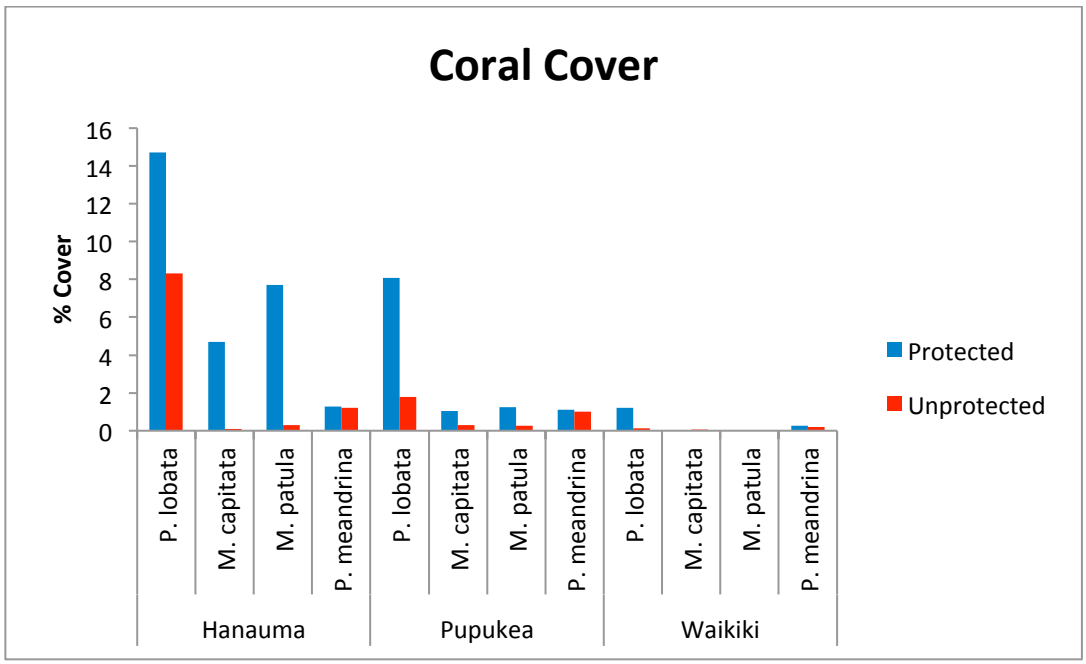

Figure 29. Blue (protected) and red (unprotected) bars represent mean percent coral cover for four of the most common coral species at each of the locations.

DISCUSSION

Disease assemblages, in other words the types of diseases present and how prevalent the diseases were, differed significantly between locations. Differences in disease assemblages are most likely not due to differences in the coral species present at each of the three locations. Dominance plots showed species richness to be similar at the three locations (Figure 14) and *Porites lobata* to be the most dominant species at all six sites (Figure 29). However, it is possible that differences in disease assemblages among the three locations are partly due to site-level differences in oceanographic conditions and land-based inputs at each of the sites.

These location level differences are also reflected in the results from the sediment analyses that serve as an indicator of wave action regimes and terrigenous runoff at each of the sites. The two Pupukea sites had high mean proportions of terrigenous (non-organic) materials. Pupukea sites experience high wave energy in the winter through exposure to north swells. High wave action, which abrades the basalt boulders on the shoreline, contributes to the production of new terrigenous materials in the sediment. Sites on the south shore of Oahu, such as the sites studied in the Hanauma and Waikiki locations, are exposed to lower levels of wave energy and their wave regimes are reflected in the lower amounts of terrigenous material in their sediment composition (Macdonald et al. 1983). Proportions of grain size fractions also varied slightly among locations and were reflective of each location's exposure to wave action. Locations that have less exposure to high surf are generally characterized by sediment samples with higher proportions of silt and fine sand. The Hanauma Protected site showed the highest levels of silt in the sediment samples compared to the other sites. This site is an enclosed embayment and has relatively low exposure to high surf, and therefore has lower rates of sediment and nutrient removal compared to other sites. This difference in sites on north facing and south facing shores is consistent with results from a study which found the link between coral reef health and watershed health to be stronger on the south shores of islands than on the north shores (Rodgers et al. 2012). The researchers concluded that high wave action on north facing shores helps to flush land based materials such as silt and sediment away from the shoreline (Rodgers et al. 2012).

Disease assemblages also showed significant differences across protective boundaries. Further exploration of the mean prevalence of five common lesion types across protective boundaries showed three outcomes: significantly lower disease prevalence in the MLCD, no significant difference across protective boundaries, and significantly higher disease prevalence in the MLCD. The result of lower disease prevalence in the MLCD, was found for one lesion type (*Porites lobata* lesion with red filamentous alga) at the Hanauma location and this result is consistent with results for a study conducted in the Philippines by Raymundo and colleagues (Raymundo et al. 2009). For other lesion types there was no detectable difference in prevalence across protective boundaries. This was consistent with results from Page and colleagues in Palau (Page et al. 2009). Interestingly, for some lesion types at some locations there was significantlu

higher prevalence inside the Marine Life Conservation District and lower levels in unprotected sites. This was a new and somewhat unexpected result that was explored more deeply through multivariate analysis.

Results from multivariate analyses of the five common lesion types revealed that prevalence and abundance of each lesion type was most optimally explained by different sets of explanatory variables. This different groupings of explanatory variables which best explained the variation in the models for each of the lesion types, not only highlights the importance of analyzing coral disease data by separate lesion types (Williams et al. 2010), but is also reflective of the difference in disease etiologies for the five lesion types that were modeled. In fact, four out of the five lesion types that were explored through statistical models occurred on the same species, *Porites lobata,* and the results further support how different disease etiologies acting on the same host species can reveal different patterns in prevalence across sites. It should be noted, however, that while the predictor variables were able to explain some of the variation in each of the models, more than half of the variation in all of the models was unexplained. Disease processes are complex, and while some of this complexity was captured in the variables used in the models, there may be other parameters that were not incorporated in these models that help to shape these particular disease dynamics.

The model for *Porites lobata growth* anomaly prevalence showed silt % and host density to be the best performing explanatory variables and the model using abundance for this same lesion type showed host cover to be the best performing variable. There have been several studies investigating environmental and biological factors that are correlated with the prevalence of growth anomalies. Results from this study showed the silt sediment fraction to be one of the best performing variables in the model. Higher fractions of silt in sediment samples may be linked to lower rates of sediment removal and longer residence times of land-based pollutants. The potential connection between silt levels, length of exposure to pollution, and prevalence of growth anomalies should be further explored to clarify the role that water quality plays in this disease process. Past studies have also shown prevalence of growth anomalies to be positively correlated with nearby human population size, with results showing growth anomalies on *Porites* to be more common in the densely populated Main Hawaiian Islands than on the nearly uninhabited North Western Hawaiian Islands (Aeby et al. 2011a). This may be evidence for an indirect effect from humans on the environment or water quality that may contribute to *Porites lobata growth* anomaly levels.

Host density and host abundance (% cover of host species) also explained a large amount of the variation in the statistical models for *Porites lobata* growth anomalies. To date the disease causing agent and modes of transmission for this lesion type still remains undetermined. There is evidence that growth anomalies on *Porites lobata* are transmissible between colonies (Kaczmarsky and Richardson 2007) suggesting the potential role of an infectious agent in the

disease process. One potential hypothesis is with higher density and abundance of *Porites lobata* there may be higher levels of transmission with decreased distance between individuals or a higher chance of pathogens landing on coral tissue. In addition to host abundance, host density, and silt being good predictors for growth anomalies there were also strong connections between growth anomaly prevalence and coral community size structure. Growth anomalies were more commonly observed on larger colonies (colonies in the 80-160 cm size class) than on smaller colonies (especially in the Hanauma MLCD). Growth anomalies are known to be a chronic lesion and it is possible that growth anomalies accumulate on coral colonies as they grow larger, which may contribute to the connection between size and prevalence. The higher prevalence of growth anomalies on larger colonies may also suggest a potential connection to long-term chronic stressors that persist at sites over long periods of time, such as poor water quality and high levels of sedimentation. The average prevalence of *Porites* growth anomalies across the Pacific is < 1% (Aeby et al. 2011a). While the unprotected sites in this study had similar values of mean prevalence ranging from 0.42%-0.85%, the prevalence of *Porites lobata* growth anomalies ranged from 2.89%-16.57% within the Marine Life Conservation Districts of Oahu.

Statistical models for *Porites lobata* trematodiasis showed macroalgal percent cover to be the best performing predictor for prevalence of the lesion and host cover to be the best performing predictor for trematodiasis abundance. Trematodiasis in *Porites sp.* is caused by a digenetic parasitic trematode whose lifecycle involves *Porites sp.* coral, a coral feeding fish, and a probable mollusk. The parasite is transmitted to corals through contact with feces from infected fish, which contain the eggs of the trematode. One potential explanation for macroalgal cover as the best performing explanatory variable is that macroalgae may serve as a habitat for a mollusk that may act as an intermediate host for the trematode. In fact many micro-molluscs have been found to use macroalgae as a habitat (Minton 2000). The model utilizing trematodiasis abundance showed host cover to be a high performing predictor variable and this is consistent with results from a study conducted observing levels of the same lesion type in Kaneohe Bay, Oahu (Williams et al. 2010). Williams and colleagues hypothesize that in areas with high host cover there may be a higher likelihood of corals coming into contact with infected feces containing the parasite. Intriguingly, corallivores, which are the final host of the trematode, explained a small amount of the variation (2.69%) in the model using abundance of colonies with signs of trematodiasis. While at first glance we might expect corallivore densities to be more tightly linked with prevalence and abundance of trematodiasis, corallivores while territorial, display large home ranges and are highly motile (Hourigan 1989). Additionally, the Waikiki sites, which had the highest mean prevalence of trematodiasis, also had the lowest mean coral cover and it is probable that sites dominated by macroalgae, like the sites at Waikiki, may be unsuitable habitat for corallivores.

Host cover was the best performing variable for both models (the model using prevalence and the model using abundance) for *Porites lobata* tissue loss. This result is consistent with a study investigating *Porites* tissue loss syndrome for the entire Hawaiian archipelago, that found overall coral cover to be positively associated with cases of this lesion (Aeby et al. 2011b). Tissue loss in other species, such as in *Montipora capitata,* is induced by bacteria (Ushijima et al. 2012). It is possible that tissue loss in *Porites lobata* may also be linked to a bacterial pathogen but further studies and laboratory analysis will be needed to identify the pathogen. This lesion type had low mean prevalence at all six sites, ranging from 0%-1.72%, and it seems that *Porites lobata* colonies at these sites are more likely to show signs of the other lesion types like growth anomalies and trematodiasis.

The model using prevalence of *Porites lobata* lesion with red filamentous alga showed the most common size class of *Porites lobata* colonies to be the best performing predictor variable. It should be noted that the six variables in this model all explained relatively equal amounts of variation in the model and it would be difficult to say if any of the six outperformed the other variables to a great extent. Interestingly, the model utilizing abundance for *Porites lobata* lesion was a higher performing model overall, and host cover was the variable that explained the most variation in the model. This lesion type at the Hanauma location was also the only lesion to have significantly lower prevalence in the MLCD compared to the adjacent unprotected area. Other studies have suggested that grazing pressure from herbivores may help to keep the alga, *Corallophila huysmansii,* cropped back (Jompa and McCook 2003) and it is plausible that inside the MLCD where there is a higher density of herbivores that we might also see lower levels of the red filamentous alga and lower levels of the lesion.

The last lesion type that was explored through statistical models was *Pocillopora meandrina* tissue loss. The model using prevalence of this lesion was only able to explain 3.55% of the total variation in the data and was the worst performing model of the ten that were used in this study. Results from the model using abundance showed host density to be the best performing predictor variable. Colonies with *Pocillopora meandrina* with tissue loss were sometimes associated with the presence of the corallivorous snail *Drupella cornus* and the tissue loss lesion was most apparent in the crevices of the colony where the snails are most likely to reside. While field signs point to snail predation further histological analysis could be used to confirm this result. Past studies have shown a higher abundance of the corallivorous snail, *Drupella cornus,* in unprotected areas compared to MPAs (McClanahan 1994). *Drupella cornus* abundance displayed a negative relationship with biomass of fish from the families Balistidae (triggerfish) and Lutjanidae (snappers) (McClanahan 1994). One potential future direction of research is examining whether fishing pressure impacts the density of these potential predator groups and in turn effects abundance of *Drupella cornus* and snail predation on *Pocillopora meandrina.* There may also be links between snail population growth and water quality. One

study documented population growth of *Drupella cornus* in conjunction to a siltation event in the Gulf of Eilat (Shafir et al. 2008). The east side of Maunalua Bay, where the Hanauma-Unprotected site for this study is located, is characterized by a permanent layer of suspended sediment (Wolanski et al. 2009). Future research should investigate if poor water quality at the Hanauma-Unprotected site contributes to the growth of *Drupella cornus* populations and in turn the prevalence of tissue loss lesions observed in *Pocillopora meandrina*.

Investigation of ecosystem health factors revealed that while some factors were preserved and even enhanced by protection status others showed little to no change across protection boundaries. Fish populations showed a trend of higher densities in MLCDs compared to adjacent unprotected sites. The Pupukea location was the only location to have statistically significant higher fish densities in the MLCD compared to adjacent unprotected sites. This site is also unique in the high level of community involvement in the MLCD from the grass roots organization Malama Pupukea Waimea. It is possible that educational outreach and reporting of poaching through the organization has translated into greater compliance with MLCD fishing regulations at the Pupukea-Protected site and in turn higher densities of fish within the MLCD. Further examination of fish density through specific trophic guilds revealed significantly higher herbivore abundance in the Hanauma and Pupukea MLCD compared to adjacent unprotected sites. Herbivores such as parrotfish (*Scarus sp.)* and surgeonfish (*Acanthurus sp.)* are highly sought after in Hawaiian near-shore environments (Williams et al. 2008) and these results indicate the effectiveness of MLCDs in protecting targeted fish species. Macroalgae levels, however, showed no detectable differences across protection boundaries despite the higher densities of herbivores in MLCDs. Biomass of herbivores is significantly lower in the Main Hawaiian Islands compared to the comparatively pristine Northwestern Hawaiian Islands (Friedlander and DeMartini 2002) and perhaps even though herbivore densities in Oahu's MLCDs are higher than unprotected areas these densities could still be below what is necessary to see a difference in macroalgae levels. Waikiki also had the lowest mean density of herbivores of the three locations studied, which is commensurate with it also having the highest mean macroalgal percent cover.

CHAPTER 3: Recommendations for management strategies to address coral disease in Marine Life Conservation Districts

There are several trends that emerged in this dataset that may be useful take home messages for managers concerned with addressing the threat of coral disease within MLCDs and other MPAs. First, while higher prevalence inside MLCDs than unprotected areas for some lesion types was unexpected, this result makes sense in light of the high level of coral cover and coral density in these protected sites. Percent cover of host species was the strongest predictor for four out of five models using coral disease abundance and one out of five models using coral disease prevalence for the five common lesion types that were investigated through multivariate analysis. Results from this study are also consistent with other studies that show coral host abundance to be one of the strongest drivers of disease levels (Aeby 2007; Aeby et al. 2010; Williams et al. 2010). Furthermore data on mean coral cover at the three locations showed significantly higher levels of coral in the Hanauma Bay and Pupukea MLCDs compared to adjacent control sites. MLCDs were historically placed in sites with high levels of coral cover and given the results from this study and others that show a strong connection between host abundance and disease prevalence it will be important to continue to regularly monitor for disease inside MLCDs.

Second, many of the results suggest that water quality plays a strong role in disease dynamics. Reduced water quality (Wooldridge and Done 2009) and increased sediment stress (Fabricius 2005) can compromise the health of coral reefs. Additionally higher prevalence of *Montipora* white syndrome and *Porites* growth anomalies in Kaneohe Bay, Hawaii have been linked to reduced water quality, as measured through chlorophyll a levels (Williams et al. 2010). In this study, multivariate analyses showed that silt sediment fractions, which are a proxy for terrigenous runoff, were the best predictor for prevalence of *Porites lobata* growth anomalies. Providing further evidence for the potential connection between the prevalence of certain lesion types, levels of terrigenous runoff, and low water quality. Sediment grain size also showed the Pupukea sites to have the he lowest mean proportion of silt in their sediment samples, and interestingly these sites also had some of the lowest mean prevalences of the three locations studied on Oahu.

Third, while human use was not a direct point of study for this research, the link between human use and coral reef ecosystem healthy may be a potential future direction for research within MLCDs. Particularly on the highly populated south shore of Oahu, high levels of human use within the Waikiki MLCD and Hanauma Bay MLCD may be an additional stressor impacting the health of corals and the behavior of fish. Furthermore, there are other ways in which the human dimension intersects with the success of meeting MLCD aims. Managers should continue to support programs, which foster community involvement and community support for MLCD regulations. Again, Malama Pupukea Waimea is an excellent example of how the efforts of an

organization can contribute to building an educated and engaged public who is willing to stand behind regulations that can enhance coral reef ecosystem health.

In conclusion, with our understanding of host cover as one of the strongest drivers of coral disease prevalence, and MLCDs as sites with dense coral populations, MLCDs should continue to be regularly monitored for disease and other signs of reduced coral reef ecosystem health. The high host abundance in MLCDs may make them vulnerable to more frequent and more severe disease outbreaks compared to other locations. Also, since protected areas like Hanauma Bay contain larger and presumably older colonies, these populations may be exposed to long-term and chronic stressors, which in turn may contribute to disease levels. One of the MLCDs surveyed in this project (Pupukea), as well as MLCDs outside of Oahu have shown to have significantly more abundant fish populations (Friedlander et al. 2007). Currently, however, less than 1% of the coastline in the Main Hawaiian Islands is protected from fishing efforts and many areas may benefit from the establishment of new MPAs. Lastly, while MLCDs may act as a refuge for fish, the current regulations offer no protection against changes in water quality or sedimentation that act as stressors on corals reefs. The link between land-use practices, watershed conditions, and reef health are especially strong on south facing shores of Hawaii (Rodgers et al. 2012), where lower wave energy can lead to longer residency time of land-based sources of pollution and sediment. Integration of effective watershed management, into coral reef ecosystem management, may be an effective addition for facilitation more comprehensive protection and ensuring coral reef ecosystem health in MLCDs.

APPENDICES

Appendix A: Description of common lesion types

Appendix A is a literature review of the five diseases that were used in each of the statistical models. Current knowledge of the etiologies, associated biological and environmental factors, and the impacts that the lesions can have on the health and fitness of the coral colony is discussed for each of the five modeled diseases.

Porites growth anomalies

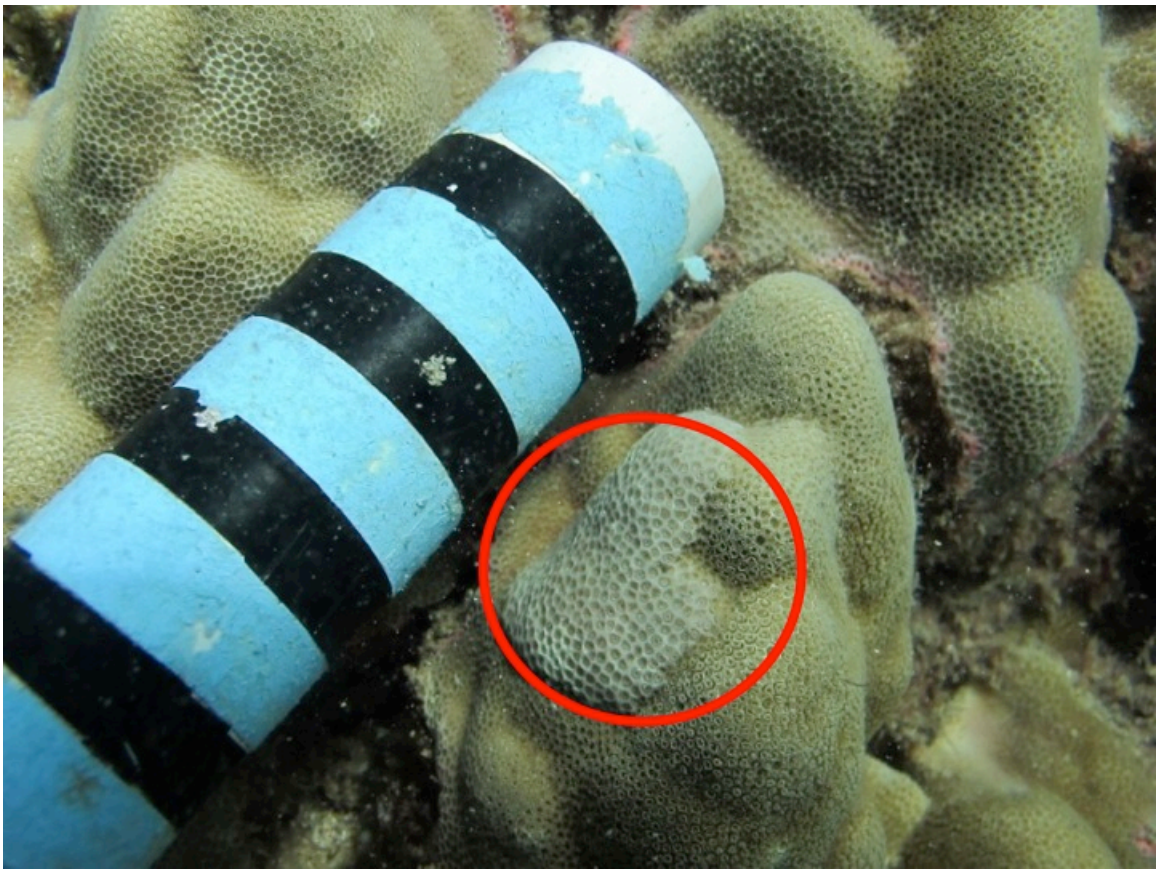

Figure 30. *Porites lobata* growth anomaly circled in red.

The first report of “tumors” on *Porites lobata* in the Hawaiian islands was made in Hanauma Bay in 1992 (Hunter 1999). The tumors from this study were characterized by larger polyps and lighter pigmentation than surrounding healthy tissue and closely match the description of growth anomalies in the genus *Porites* (Stimson 2010b). The etiology and pathogenesis of this disease lesion, however, is still unknown.

Although the etiology of the disease is not clear there have been numerous studies investigating environmental and biological factors that are correlated with the prevalence of growth anomalies (Table 13). A study centered in the Indo-Pacific found that *Porites* growth anomalies were positively correlated with host density and human population size (Aeby et al.

2011a). Human population size may be a proxy for other environmental co-factors such as pollution, environmental degradation or direct introduction of a pathogen (Aeby et al. 2011a). There is also evidence that growth anomalies on *Porites lobata* are transmissible between colonies (Kaczmarsky and Richardson 2007) suggesting the potential role of an infectious agent in the disease process. Research utilizing statistical models has shown a negative correlation between abundance of colonies with growth anomalies and turbidity and depth. A study testing UV as a causative factor found no detectable difference in prevalence of growth anomalies on *Porites compressa* colonies exposed to UV and shaded colonies (Stimson 2010b).

Table 13. Factors associated with *Porites sp.* growth anomalies.
***Porites* growth anomalies**

Factor	Relationship	Source
Bleaching	Positive	(McClanahan et al. 2009)
Host density	Positive	(Aeby et al. 2011a)
Human population size	Positive	(Aeby et al. 2011a)
UV	No relationship	(Stimson, 2010)
Turbidity	Negative	(Williams et al. 2010)
Depth	Negative	(Williams et al. 2010)

Multiple studies have also investigated the impact that growth anomalies have on the health and fitness of *Porites* corals (**Table 14**). Branches with growth anomalies grow more slowly than branches without the lesion (Stimson 2010b). The number of oocytes and gonads per polyp was reduced by 60% compared to healthy corals (Hunter and Field 1997). Growth anomalies on *Porites sp.* can also experience partial mortality (Hunter 1999).

Table 14. Evidence of reduced fitness in *Porites sp.* colonies affected by growth anomalies.
Reduced fitness in *Porites sp.* with growth anomalies

Impact on coral colony	Source
Slower growth rates	(Stimson, 2010)
Partial mortality	(Hunter 1999; Aeby et al. 2011a)
Reduced reproduction	(Hunter and Field 1997).

Hypotheses have been proposed outlining the etiology and pathogenesis of growth anomalies on *Porites*. A study examining bleaching and growth anomalies proposes a model whereby bleached colonies with reduced calcification are more susceptible to pathogens and fungi that create growth anomalies (McClanahan et al. 2009).

The average prevalence of *Porites* growth anomalies across the Pacific is < 1% (Aeby et al. 2011a). While the unprotected sites in this study had similar values of mean prevalence ranging from 0.42%-0.85%, the prevalence of *Porites lobata* growth anomalies ranged from 2.89%-16.57% within the Marine Life Conservation Districts of Oahu.

Porites tissue loss

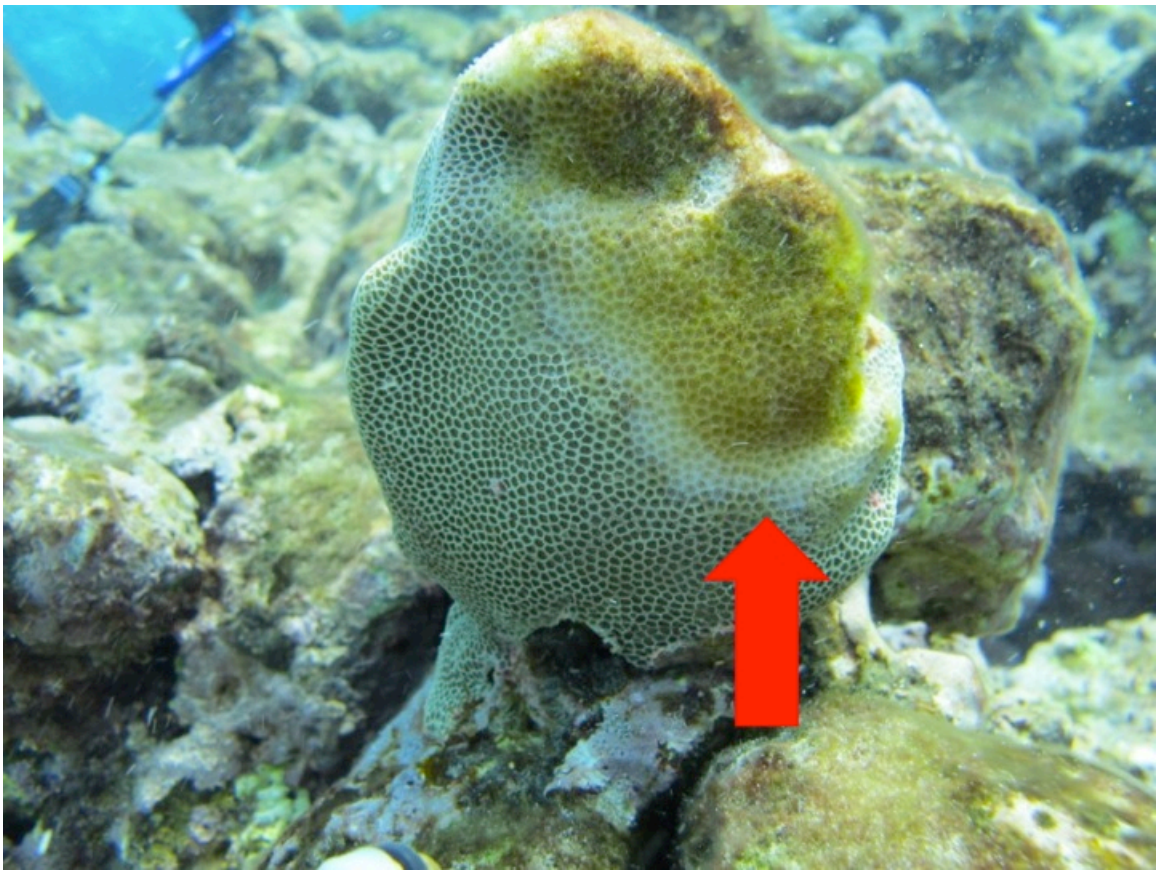

Figure 31. *Porites lobata* tissue loss. Disease front is at the tip of the red arrow.

The etiology and pathogenesis of *Porites lobata* tissue loss is also unknown. Tissue loss in other species, such as in *Montipora capitata,* is induced by bacteria (Ushijima et al. 2012). It is possible that tissue loss in *Porites,* similar to tissue loss in other species, may also be linked to a bacterial pathogen. Interestingly, extracts from *Porites* corals were shown to have antibacterial properties against known coral pathogens and potential pathogens from human waste (Gochfeld and Aeby 2008). Therefore, while *Porites* corals may be susceptible to bacterial pathogens that cause tissue loss, their bacterial constituents may also aid them in resisting infection. Overall coral cover has been found to be positively correlated with *Porites* tissue loss (Aeby et al. 2011b) (Table 15). Weekly sea surface temperature anomalies were found to be negatively correlated with *Porites lobata* tissue loss (Aeby et al. 2011b) (Table 15).

Table 15. Factors associated with *Porites sp.* tissue loss.
Porites lobata tissue loss

Factor	Relationship	Source
Overall coral cover	Positive	(Aeby et al. 2011b)
Weekly sea surface temperature anomalies	Negative	(Aeby et al. 2011b)

Porites trematodiasis

Figure 32. *Porites lobata* trematodiasis.

Trematodiasis in Porites is caused by *Podocotyloides stenometra*, a species of digenetic trematode (Aeby 1998). This lesion was first described as being caused by a metacercaria of *Plagioporus sp.* on *Porites compressa* and *Porites lobata* in Kaneohe Bay (Cheng and Wong 1974). There are two intermediate hosts: molluscs (species not yet confirmed) and corals in the genus *Porites*. Coral-feeding fish act as the final host, and the butterflyfish *Chaetodon multicinctus* has been confirmed to feed on and carry the parasite (Aeby 1998).

The disease does not show changes in levels across seasons (Aeby 2007) (Table 16). Trematodiasis is positively correlated with host cover and butterflyfish abundance (Williams et al. 2010; Aeby et al. 2011c) (Table 16). Human population size, survey area, weekly sea surface temperature anomalies, and depth are negatively correlated (Williams et al. 2010; Aeby et al. 2011c) (Table 16). This lesion can also impact host fitness through slower growth rates (Aeby 1991).

Table 16. *Porites* trematodiasis

Factor	Relationship	Source
Host cover	Positive	(Aeby et al. 2011c)

Butterfly fish abundance	Positive	(Williams et al. 2010)
Host density	Positive	(Williams et al. 2010)
Seasonality	No relationship	(Aeby 2007)
Human population size	Negative	(Aeby et al. 2011c)
Survey area	Negative	(Aeby et al. 2011c)
Host density	Negative	(Aeby et al. 2011c)
Weekly sea surface temperature anomalies	Negative	(Aeby et al. 2011c)
Depth	Negative (weak)	(Williams et al. 2010)

Table 17. Evidence of reduced fitness in *Porites sp.* colonies affected by trematodiasis.
Reduced fitness in *Porites sp.* with trematodiasis

Impact on coral colony	**Source**
Slower growth rates	(Aeby 1991)

Porites lesion with red filamentous alga

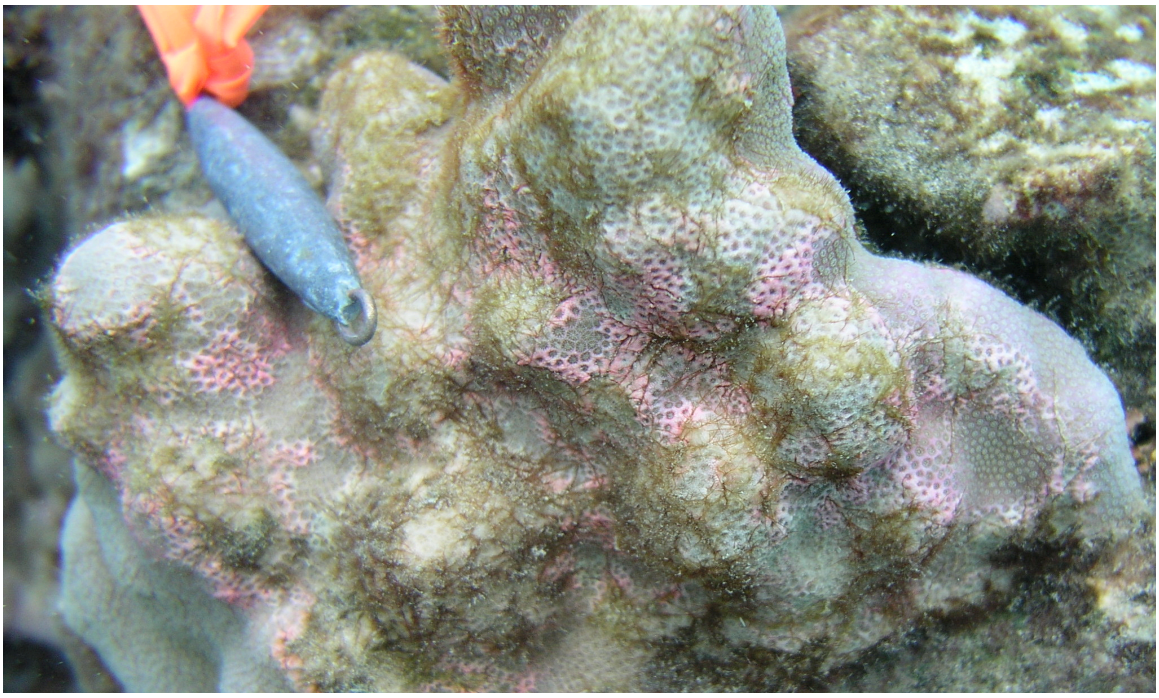

Figure 33. *Porites lobata* lesion with red filamentous alga.

The red filamentous turf alga *Corallophila huysmansii* was associated with tissue loss on two species of coral in this study: *Porites lobata and Porites evermanni. Corallophila huysmansii* has been observed to overgrow and kill live coral tissue and production of allelochemicals has been suggested to be the main mechanism supporting its establishment in coral (Jompa and McCook 2003). They found that *Corallophila huysmansii* caused initial bleaching and swelling of *Porites cylindrica* tissue and eventually tissue mortality in affected areas. Experiments comparing the amount of coral tissue death in fragments exposed to *Corallophila huysmansii* in aquaria showed no difference in the impact of the alga on coral across seasons (Jompa and McCook

2003). The aquaria study also revealed that the filaments were able to grow for longer (up to six months) in aquaria than in the field. The lack of grazing pressure from herbivores may account for the longer lifespan of *Corallophila huysmansii* in an experimental setting but further studies are needed to confirm which species feed on this alga and whether herbivory can limit its ability to colonize coral tissue.

Pocillopora meandrina tissue loss

Figure 34. *Pocillopora meandrina* tissue loss.

Tissue loss on *Pocillopora meandrina* was observed and recorded in this study. The Hanauma-Unprotected site had the highest prevalence (3.62%) of *Pocillopora meandrina* tissue loss out of the six sites surveyed in this study. Some colonies of *Pocillopora meandrina* with tissue loss were associated with the presence of the corallivorous snail *Drupella cornus* and the tissue loss lesion was most apparent in the crevices of the colony where the snails are most likely to reside. In contrast, other predators such as *Acanthaster* are associated with tissue loss that occurs mostly on the tips of branches and does not reach into the cracks and crevices of a colony because the stomach of the animal is not able to make contact with these areas.

It is possible that the tissue loss lesion that was observed on *Pocillopora meandrina* were the result of predation by a corallivorous snail but this cannot be confirmed without appropriate analysis in a laboratory. The snail, however, can pose a threat to corals as it is known to graze at a rate of 0.27 cm^2/ day and can graze at rates of up to 1.31 cm^2/ day when temperatures are elevated to 30 ºC (Al-horani et al. 2011).

Past studies have shown a higher abundance of the corallivorous *Drupella cornus* in unprotected areas compared to MPAs (McClanahan 1994). *Drupella cornus* abundance displayed a negative relationship with biomass of fish from the families Balistidae (triggerfish) and Lutjanidae (snappers) (McClanahan 1994). Potential predators of the snail include *Coris aygula* (Shafir et al. 2008) and fish from the families Balistidae, Labridae, and Diodontidae (Dr. Ken Longenecker, Bishop Museum, pers. comm.). One potential future direction of research is examining whether fishing pressure impacts the density of these potential predator groups and in turn effects abundance of *Drupella cornus* and snail predation on *Pocillopora meandrina.*

Predation by *Drupella cornus* has also been linked to the presence of white band disease in the Red Sea (Antonius and Riegl 1997). Researchers found *Drupella* snails feeding directly on the interface of the disease lesion but were unsure of whether white syndrome attracted snails to feed on the coral or if snail predation promoted infection with white syndrome (Antonius and Riegl 1997).

There may also be links between snail population growth and water quality. Population growth of *Drupella cornus* occurred during a siltation event in the Gulf of Eilat (Shafir et al. 2008). The east side of Maunalua Bay, where the Hanauma-Unprotected site for this study is located, is characterized by a permanent layer of suspended sediment (Wolanski et al. 2009). Future research should investigate if poor water quality at the Hanauma-Unprotected site contributes to the growth of *Drupella cornus* populations and in turn the prevalence of tissue loss lesions observed in *Pocillopora meandrina*.

Appendix B: Comparisons with historical data

Historical data can indicate how biological data varies temporally. I have used multiple sources to show long-term trends in coral disease prevalence, mean coral cover, and macroalgal cover at my study sites.

Data collected for this study from 2012 to 2013 revealed similar levels of coral cover in Hanauma Bay compared to historical studies. Mean coral cover for 2012-2013 was 32.43% and is similar to levels reported for transects at a depth of 30 feet from 1992 (34.65 %) and 1976 (37.65%) (Table 21) (Hunter 1999). Prevalence of growth anomalies has declined in Hanauma Bay, shifting from prevalence ranging from 35-60% in 1992 (Hunter 1999) to a mean prevalence of 16.47% in 2013 (**Table 18**). Mean trematodiasis prevalence for Oahu in 2004 was 0.77% (Aeby et al. 2011c; **Table 18**) which is comparable to levels of trematodiasis found at Hanauma-Unprotected, Pupukea-Protected, and Pupukea Unprotected sites. Hanauma-Protected (10.83%),

Waikiki-Protected (19.69%), and Waikiki Unprotected (20.44%) had much higher mean prevalence than what was reported in 2004 (**Table 18**). *Porites* tissue loss mean prevalence in 2013 ranged from 0%-1.72%, and was consistent with prevalence of 0.77% found in 2004 (**Table 18**).

The Coral Reef Assesment and Montioring Program (CRAMP) also has permanent transects in the Hanauma MLCD at depths of 3 meters and 10 meters. The majority of the points that were surveyed for this study were at similar depths. CRAMP data showed a decline in mean coral cover from 23.61% in 1999 to 9.55% in 2012 at the 3 meter depth permanent transect (Figure 37) and an increase in mean coral cover from 26.74% in 1999 to 30% in 2012 at the 10 meter depth (Figure 37. Coral cover from the Coral Reef Assessment and Monitoring Project (CRAMP) for the 3-meter depth permanent transect in the Hanauma MLCD from 1999-2012. Red solid arrow indicates a statistically significant decrease in coral cover from 1999-2012 (Paired T-test, $p<0.001$). Black bars show standard error.

Mean coral cover assessed in this study in 2012-2013 in the Pupukea MLCD was 12.31% and surveys covered areas ranging in depth from 5 meters to 15 meters. CRAMP reported similar mean coral cover of 14.5% at the 4-meter transect and 12.24% at the 8-meter transect in 2012, increased from the 1999 values of 10.32 % (4 meter depth) and 8.30% (8 meter depth) (

Figure 38. Coral cover from the Coral Reef Assessment and Monitoring Project (CRAMP) for the 10-meter depth permanent transect in the Hanauma MLCD from 1999-2012. Green open arrow indicates a non-significant increase in coral cover from 1999-2012 (Paired T-test, $p=0.550$). Black bars show standard error.

Table 18. Comparison with historical prevalence data from (Hunter 1999; Aeby et al. 2011c) for Hanauma sites. Prevalence is shown as a percentage followed by the standard error in parentheses where available.

Hanauma

	Porites Trematodiasis	*Porites* Growth anomaly	*Porites* Tissue loss
Hunter (Hanauma- Protected) 1992	N/A	41.7% (4.41)	N/A
Hunter (Hanauma- Protected) 1994	N/A	28.8% (8.98)	N/A
Hunter (Hanauma-Protected) 1998	N/A	35.0% (3.00)	N/A
Aeby (Hanauma Protected Deep) 2004-2005	0%	3.7%	1.1%
Aeby (Hanauma Protected Shallow) 2004-2005	1.4%	1.4%	1.4%
Aeby (Hanauma Unprotected) 2004-2005	4.4%	8.7%	1.6%
Walton (Hanauma-Protected) 2012-2013	10.8% (2.62)	16.5% (1.79)	1.7% (0.50)
Walton (Hanauma-Unprotected) 2012-2013	2.8% (0.72)	0.9% (0.36)	0.1% (0.04)

Table 19. Comparison with historical prevalence data from (Aeby et al., 2011c) for Pupukea sites. Prevalence is shown as a percentage followed by the standard error in parentheses where available.

Pupukea

	Porites Trematodiasis	*Porites* Growth anomaly	*Porites* Tissue loss
Aeby (Pupukea 1 -Protected) 2004-2005	1.50%	0.14%	0.40%
Aeby (Pupukea 2 -Protected) 2004-2005	0.28%	0.28%	NA
Walton (Pupukea-Protected) 2012	3.47% (0.77)	2.89% (0.90)	1.33% (0.47)
Walton (Pupukea-Unprotected) 2012	0.94% (0.34)	0.77% (0.29)	0.41 (0.17)

Table 20. Comparison with historical prevalence data for Oahu from (Aeby et al., 2011c) and prevalence data for Waikiki sites from 2012-2013. Prevalence is shown as a percentage followed by the standard error in parentheses where available

Waikiki

	Porites Trematodiasis	*Porites* Growth anomaly	*Porites* Tissue loss
Aeby (Oahu) 2004-2005	0.77% (0.2)	0.89% (0.4)	0.24% (0.09)
Walton (Waikiki-Protected) 2012-2013	19.69% (4.35)	8.55% (4.64)	0%
Walton (Waikiki-Unprotected) 2012-2013	20.44% (5.89)	0.42% (0.42)	0.35% (0.35)

Table 21. Coral cover from Hanauma Bay taken from (Hunter 1999).

Table 4. Comparison of percent coral and algal abundance data from present study to data from previous studies. * refers to site designations of previous studies

Hanauma Bay

	Anderson, 1978*	present study
Mean Coral Abundance	Sep-76	Oct-92
Area:		
10', p.293-94*, 4	28.10	33.90
25', p.254-55*, 7	36.30	30.22
30', p.301-02*, 8	37.65	34.65
35', p.277-78*, 6	64.76	45.51
Mean Algal Abundance		
Area:		
10', p.293-94*, 4	29.00	64.07
25', p.254-55*, 7	31.50	66.67
30', p.301-02*, 8	29.00	49.78
35', p.277-78*, 6	17.00	45.58

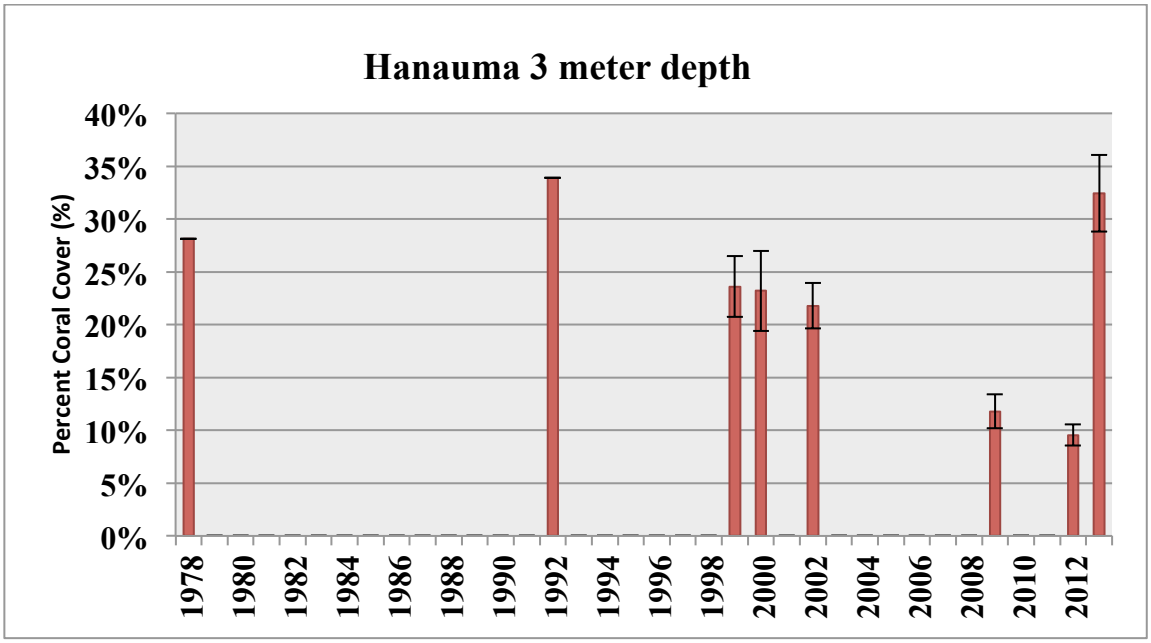

Figure 35. Historical data on mean coral cover at Hanauma Bay for a 3-meter depth spanning from 1978-2013. Data from 1978 (Anderson 1978), 1999 (Hunter 1999), 1999-2012 (CRAMP, unpublished), and 2013 (Walton, 2013). Where available standard error is shown with black bars. The data from (Walton, 2013) reports mean coral cover for surveys conducted at a mean depth of 5.5 meters.

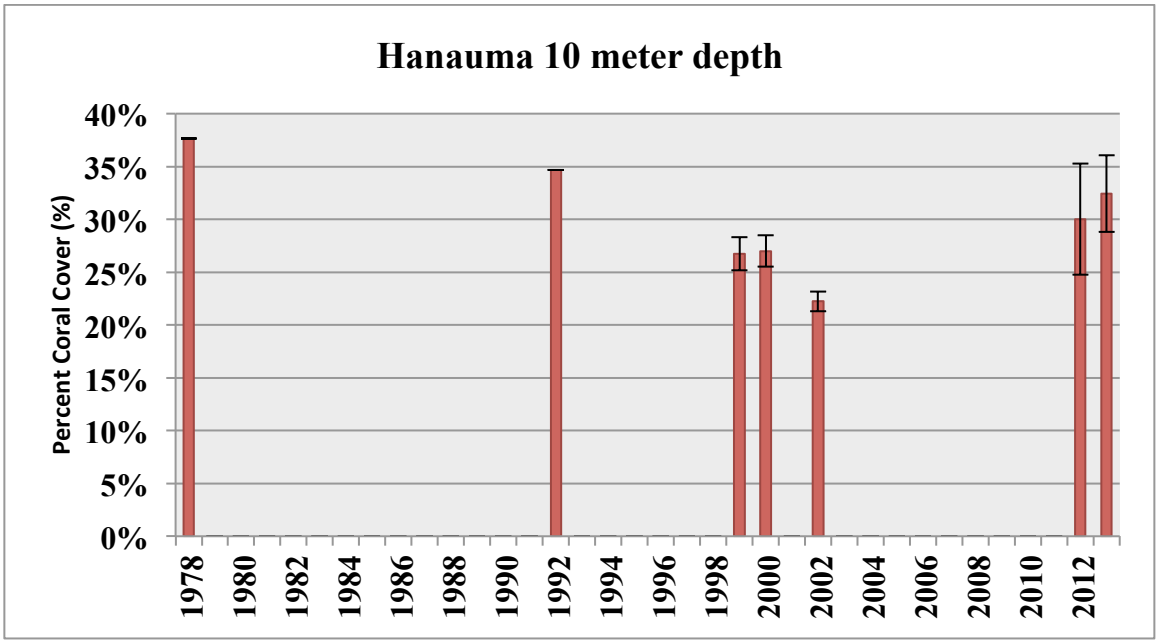

Figure 36. Historical data on mean coral cover at Hanauma Bay for a 10-meter depth spanning from 1978-2013. Data from 1978 (Anderson 1978), 1999 (Hunter 1999), 1999-2012 (CRAMP, unpublished), and 2013 (Walton, 2013). Where available standard error is shown with black bars. The data from (Walton, 2013) reports mean coral cover for surveys conducted at a mean depth of 5.5 meters.

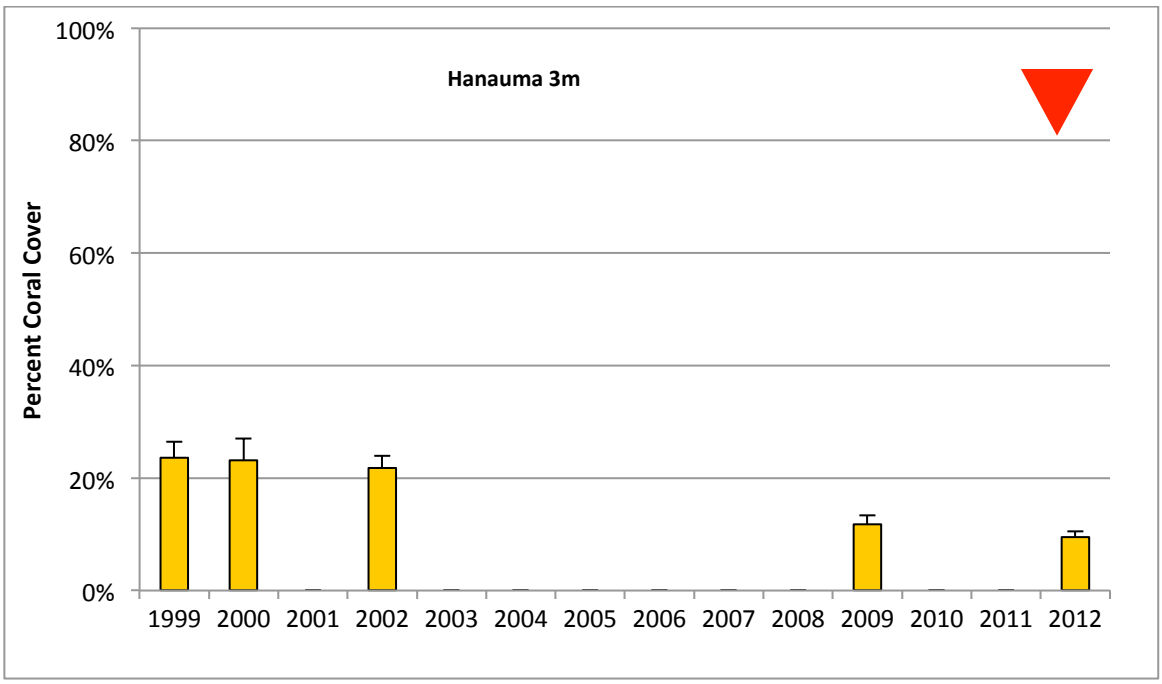

Figure 37. Coral cover from the Coral Reef Assessment and Monitoring Project (CRAMP) for the 3-meter depth permanent transect in the Hanauma MLCD from 1999-2012. Red solid arrow indicates a statistically significant decrease in coral cover from 1999-2012 (Paired T-test, $p<0.001$). Black bars show standard error.

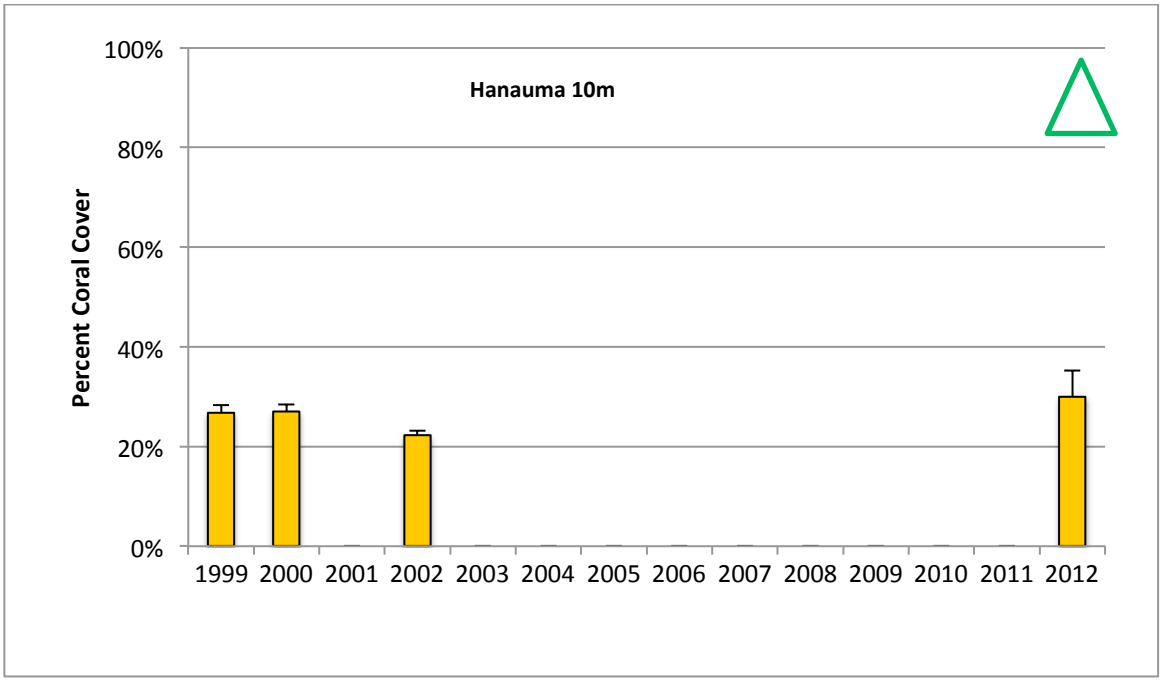

Figure 38. Coral cover from the Coral Reef Assessment and Monitoring Project (CRAMP) for the 10-meter depth permanent transect in the Hanauma MLCD from 1999-2012. Green open arrow indicates a non-significant increase in coral cover from 1999-2012 (Paired T-test, $p=0.550$). Black bars show standard error.

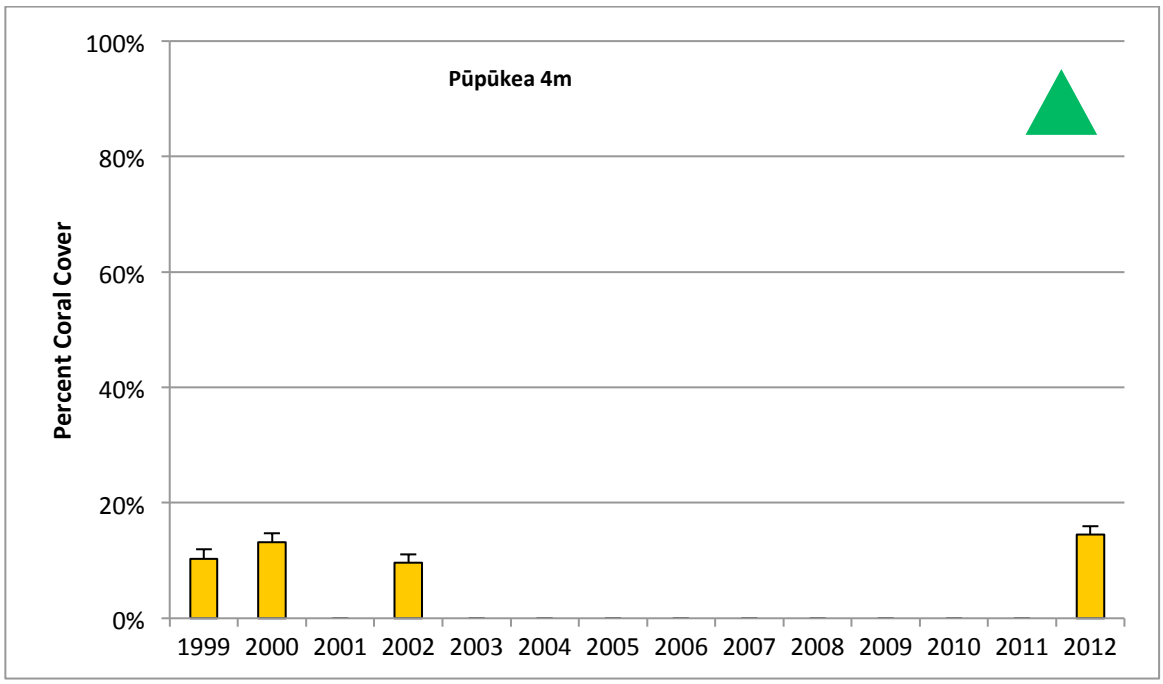

Figure 39. Coral cover from the Coral Reef Assessment and Monitoring Project (CRAMP) for the 4-meter depth permanent transect in the Pupukea MLCD from 1999-2012. Green solid arrow indicates a statistically significant increase in coral cover from 1999-2012 (Paired T-test, p=0.003). Black bars show standard error.

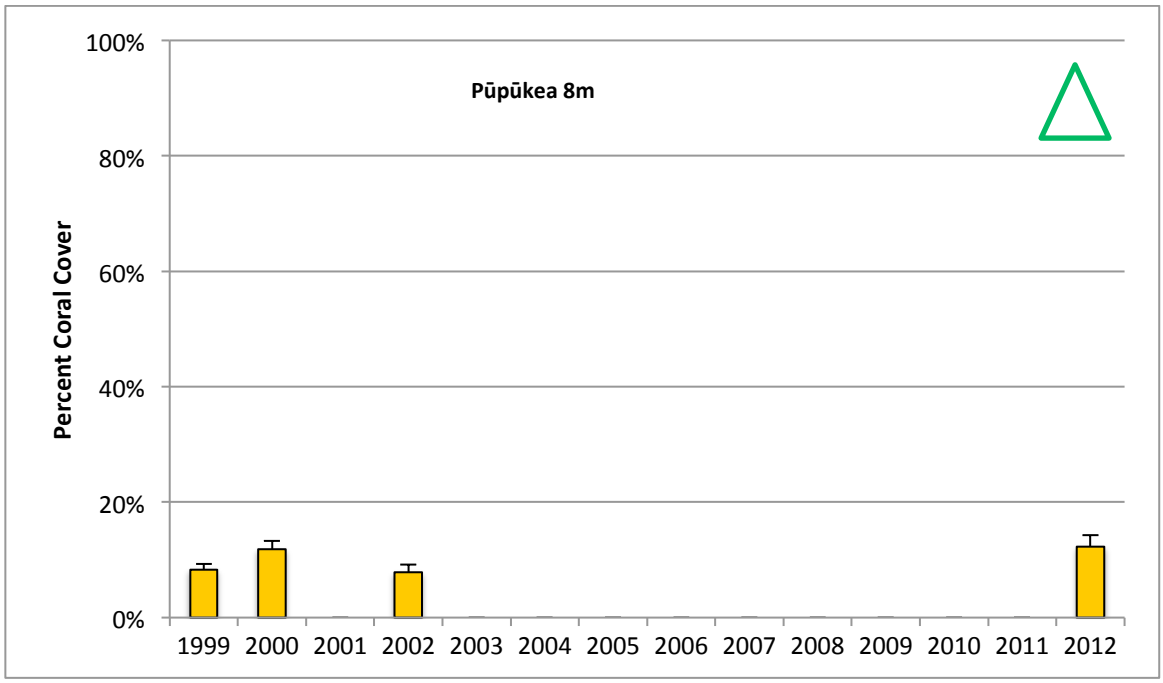

Figure 40. Coral cover from the Coral Reef Assessment and Monitoring Project (CRAMP) for the 8-meter depth permanent transect in the Pupukea MLCD from 1999-2012. Green open arrow indicates a non-significant increase in coral cover from 1999-2012 (Paired T-test, p=0.068). Black bars show standard error.

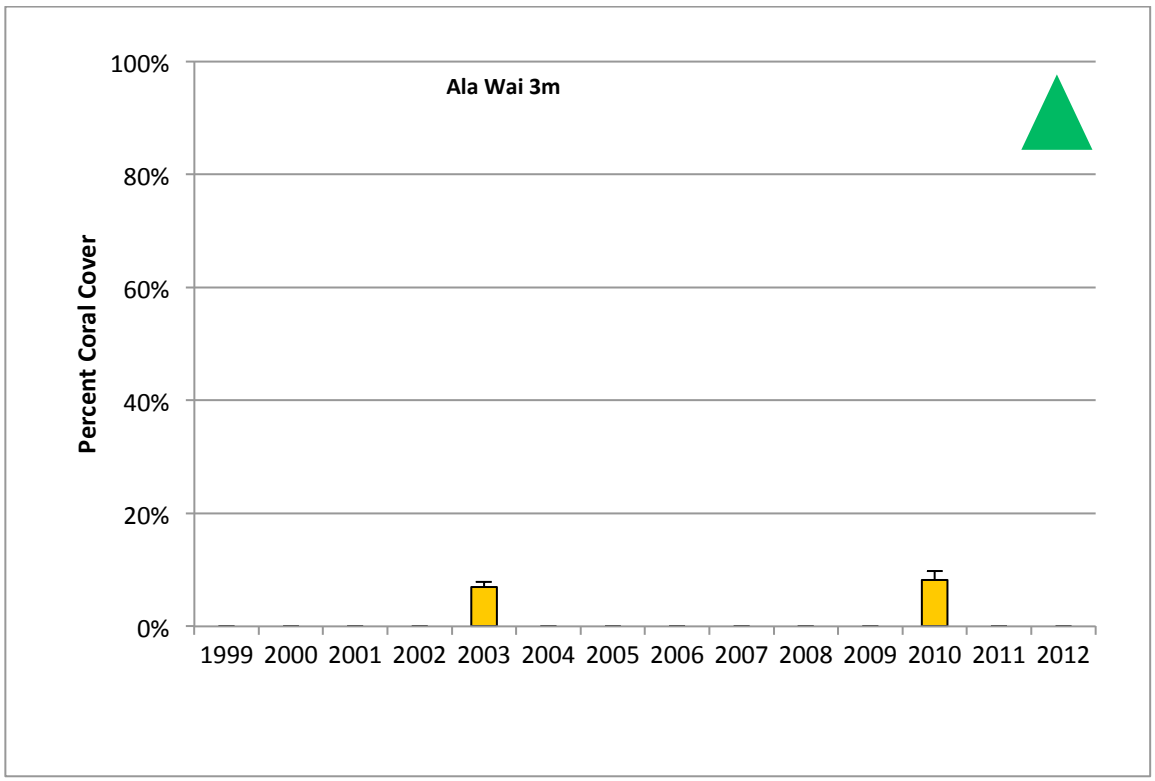

Figure 41. Coral cover from the Coral Reef Assessment and Monitoring Project (CRAMP) for the 3-meter depth permanent transect at the Ala Wai site from 2003 and 2010. Green solid arrow indicates a statistically significant increase in coral cover from 2003-2010 (Paired T-test, p=0.002). Black bars show standard error.

Mean coral cover at the Waikiki sites was 2.25% in the MLCD and 1.49% in the unprotected area. Historical data from 1975-2005 showed similar levels of coral cover ranging between close to 0% to 10% (Kinzie 2008) (**Figure 6**). The closest CRAMP permanent transect to the Waikiki MLCD is located near the Ala Wai harbor, 2.82 Km to the west of the MLCD. The CRAMP data reports mean coral cover ranging from 6.94-8.2% (**Figure 41**). The difference, however, between the mean coral cover that reported for this study and what CRAMP reports may be purely due to the distance between the sites that were monitored, as the depth and exposure to waves is similar at both sites.

Appendix C: Disease Prevalence Maps

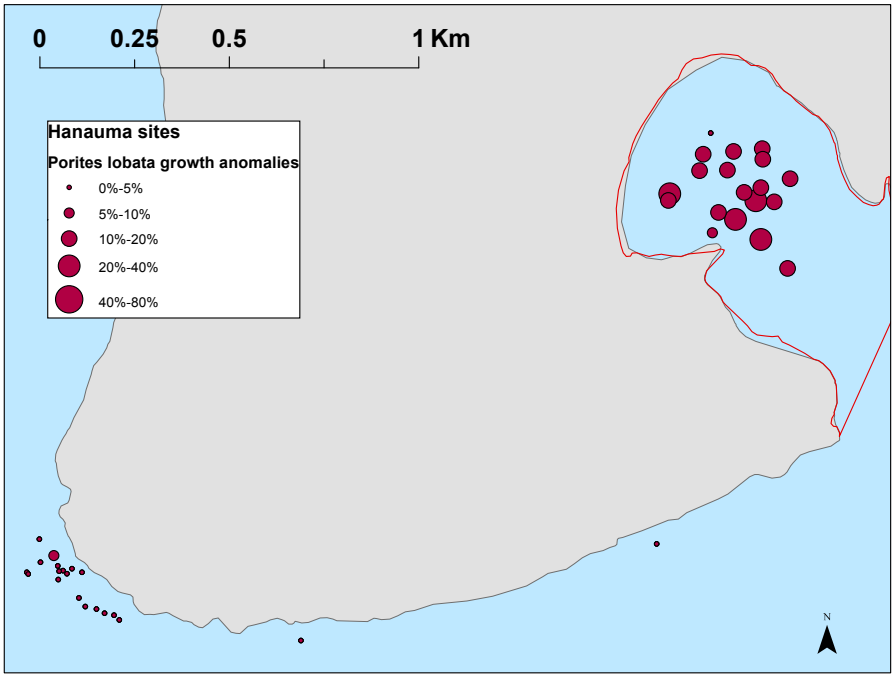

Figure 42. Prevalence of *Porites lobata* growth anomalies at the Hanauma sites. Red lines mark the boundary of the MLCD.

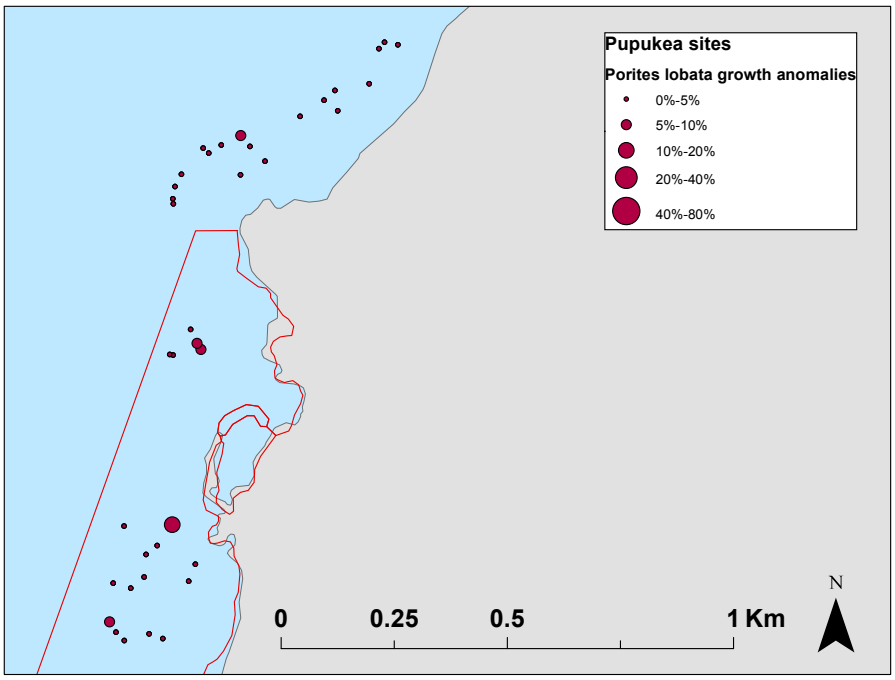

Figure 43. Prevalence of *Porites lobata* growth anomalies at the Pupukea sites. Red lines mark the boundary of the MLCD.

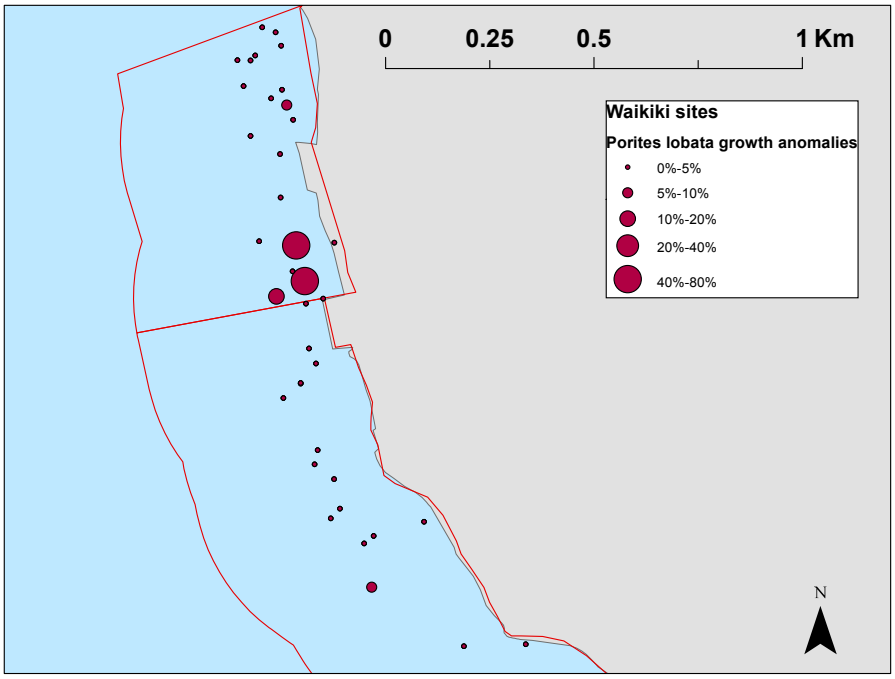

Figure 44. Prevalence of *Porites lobata* growth anomalies at the Waikiki sites. Red lines mark the boundary of the MLCD.

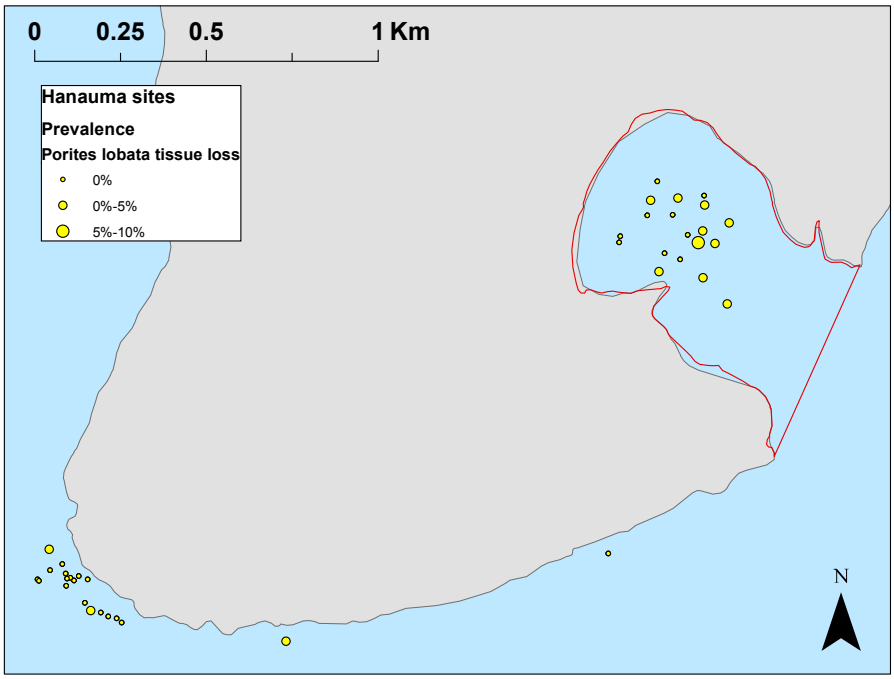

Figure 45. Prevalence of *Porites lobata* tissue loss at the Hanauma sites. Red lines mark the boundary of the MLCD.

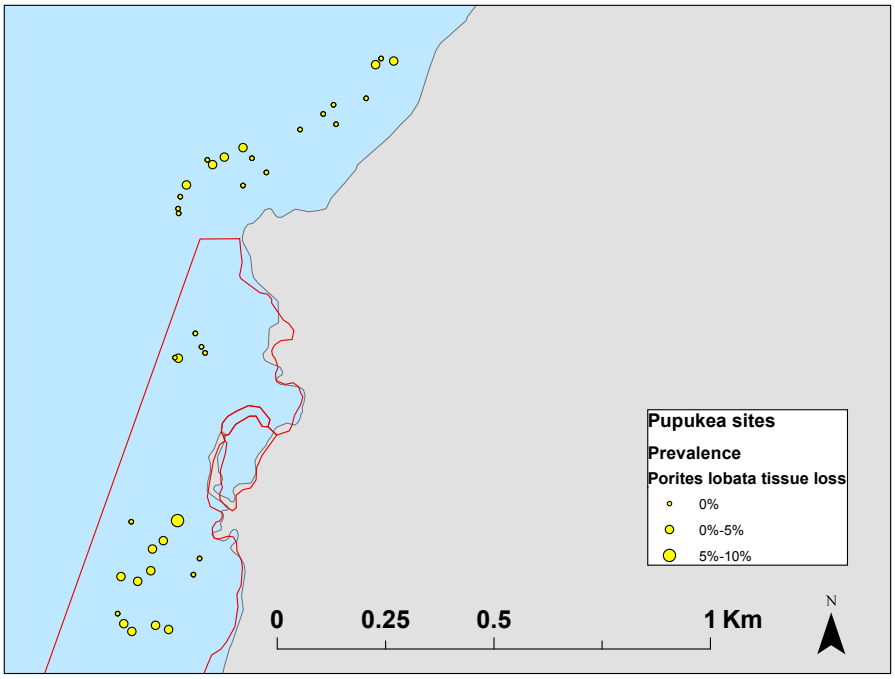

Figure 46. Prevalence of *Porites lobata* tissue loss at the Pupukea sites. Red lines mark the boundary of the MLCD.

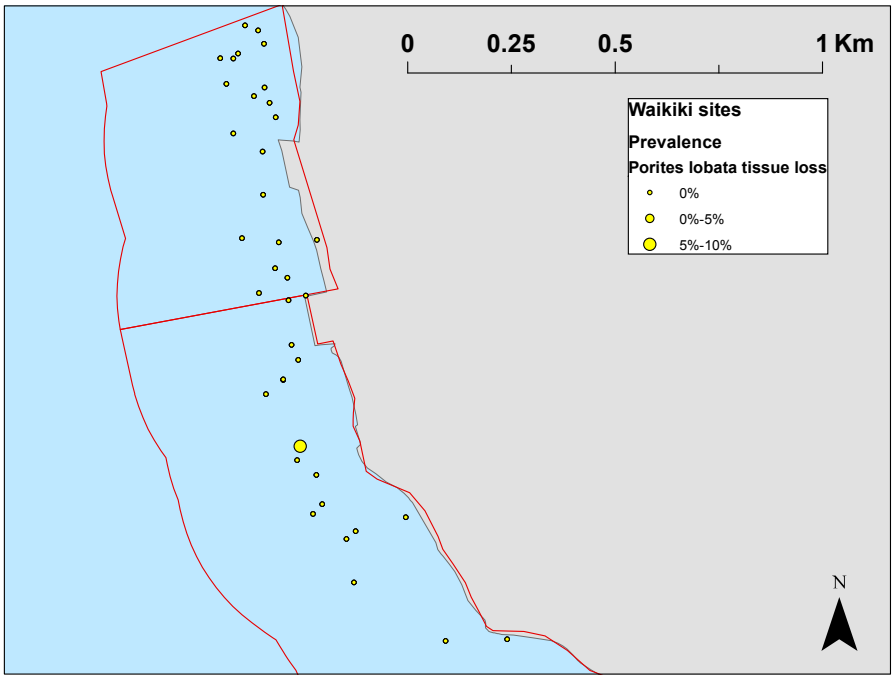

Figure 47. Prevalence of *Porites lobata* tissue loss at the Waikiki sites. Red lines mark the boundary of the MLCD.

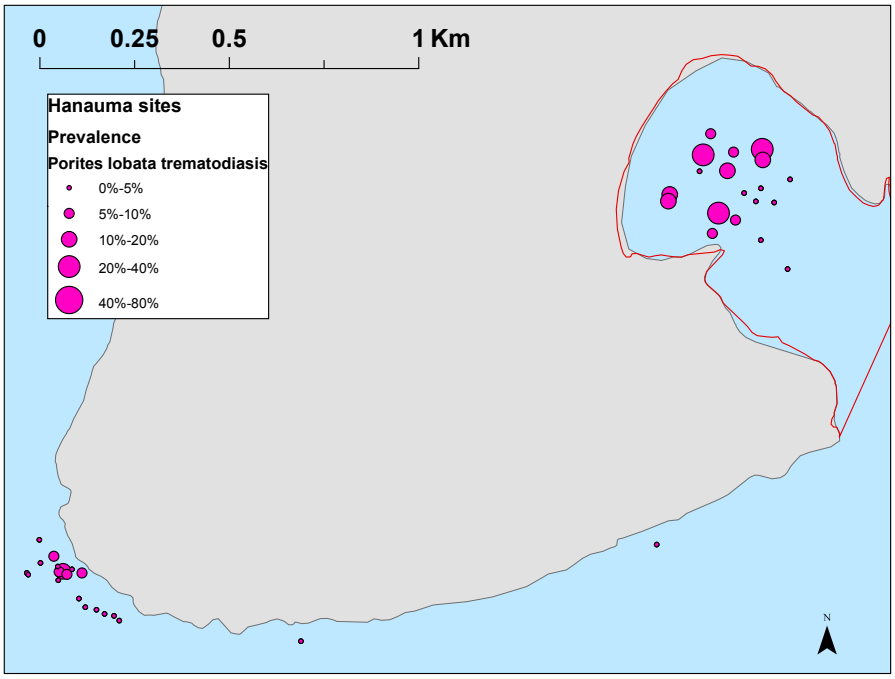

Figure 48. Prevalence of *Porites lobata* trematodiasis at the Hanauma sites. Red lines mark the boundary of the MLCD.

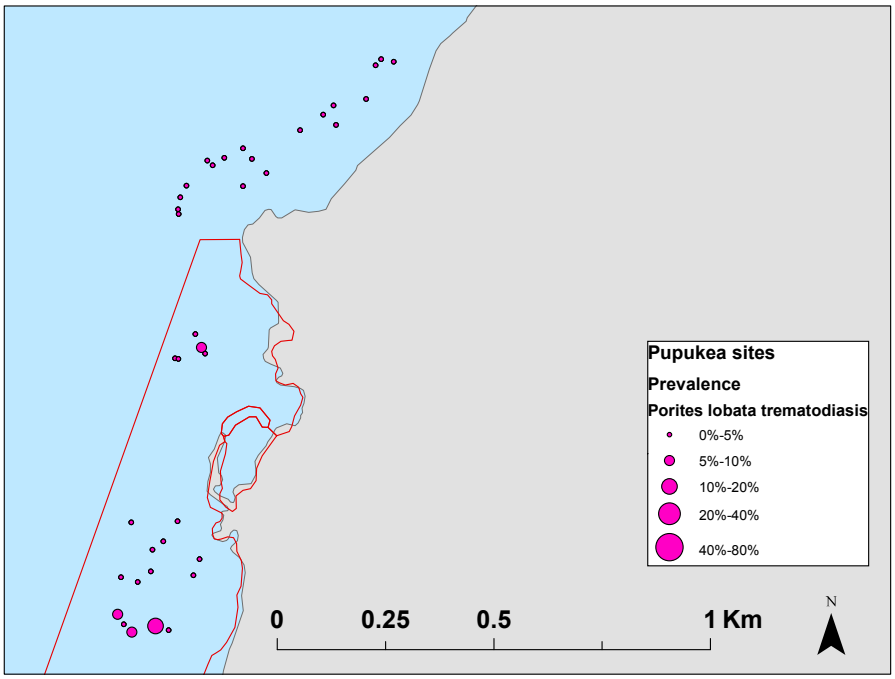

Figure 49. Prevalence of *Porites lobata* trematodiasis at the Pupukea sites. Red lines mark the boundary of the MLCD.

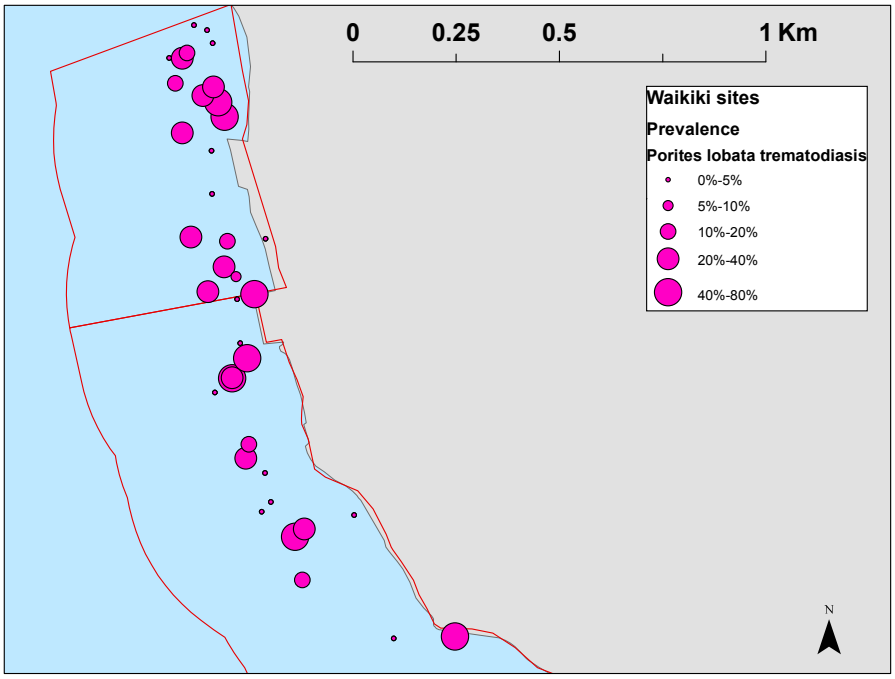

Figure 50. Prevalence of *Porites lobata* trematodiasis at the Waikiki sites. Red lines mark the boundary of the MLCD.

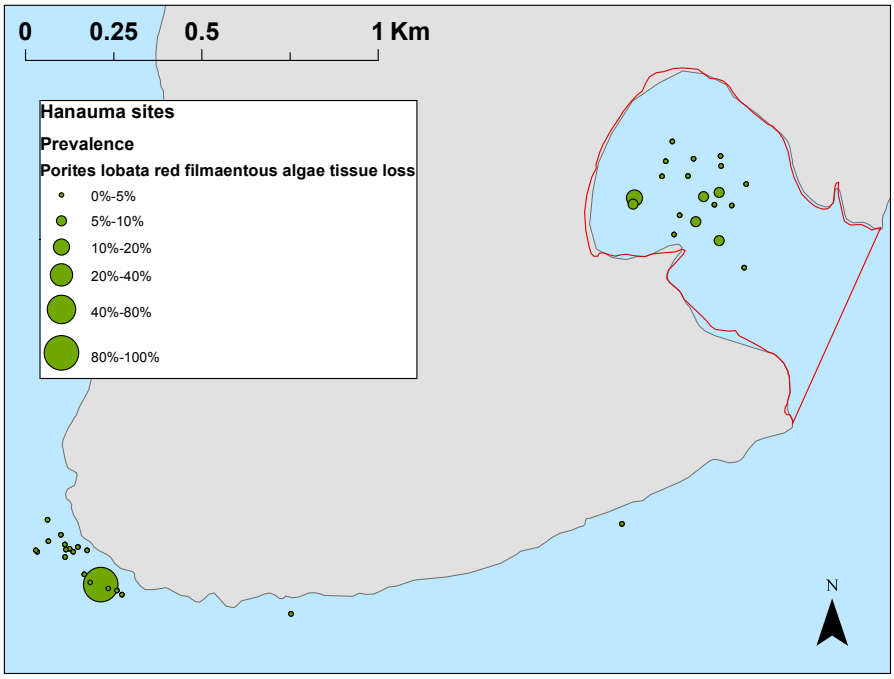

Figure 51. Prevalence of *Porites lobata* red filamentous algae tissue loss at the Hanauma sites. Red lines mark the boundary of the MLCD.

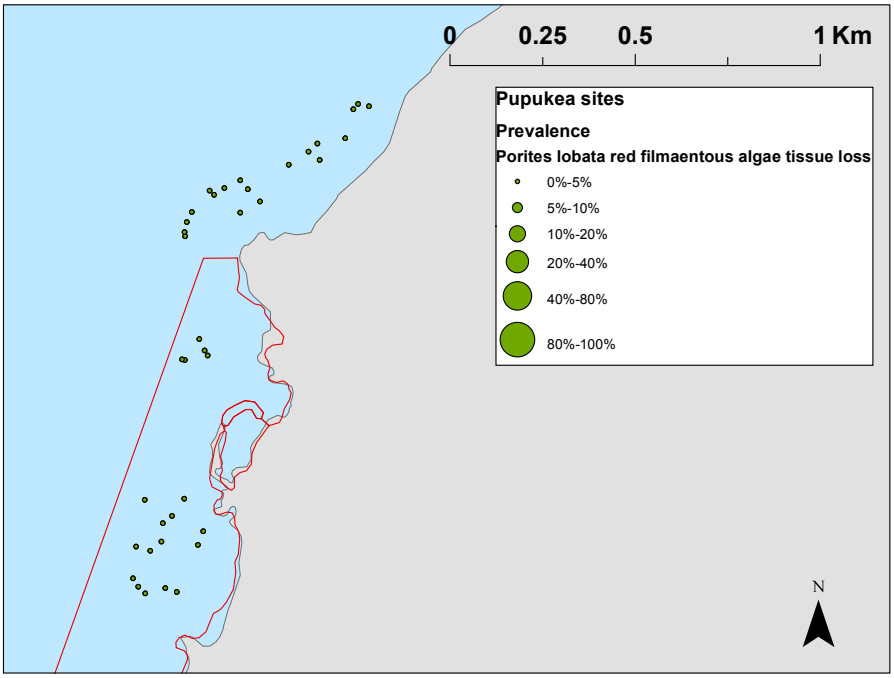

Figure 52. Prevalence of *Porites lobata* red filamentous algae tissue loss at the Pupukea sites. Red lines mark the boundary of the MLCD.

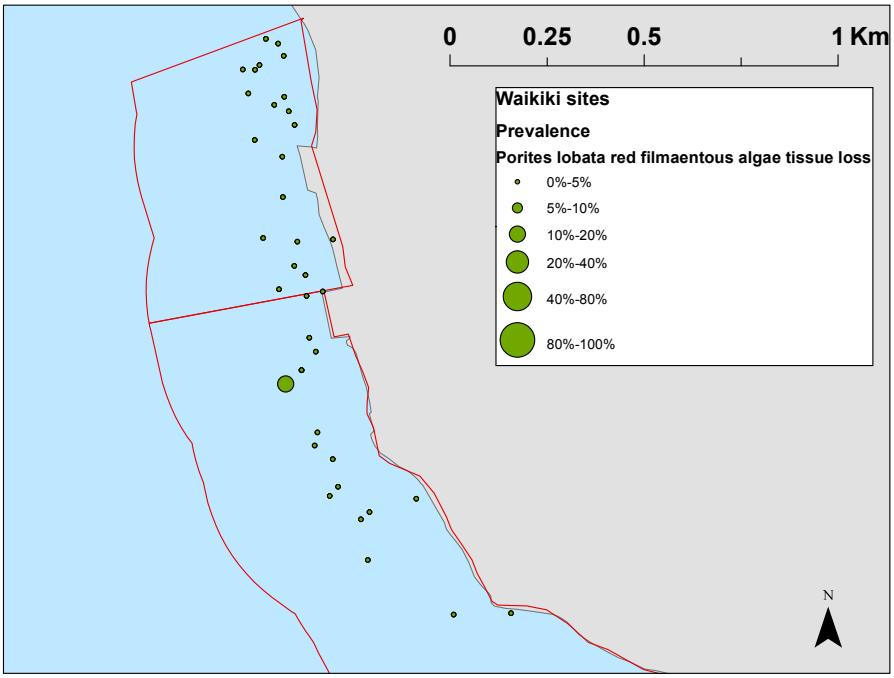

Figure 53. Prevalence of *Porites lobata* red filamentous algae tissue loss at the Waikiki sites. Red lines mark the boundary of the MLCD.

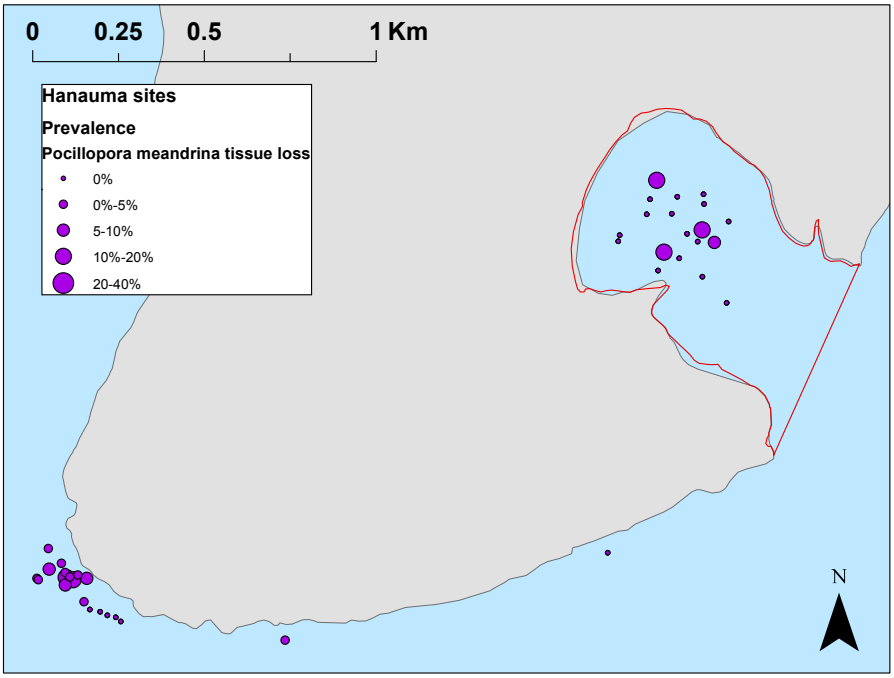

Figure 54. Prevalence of *Pocillopora meandrina* tissue loss at the Hanauma sites. Red lines mark the boundary of the MLCD.

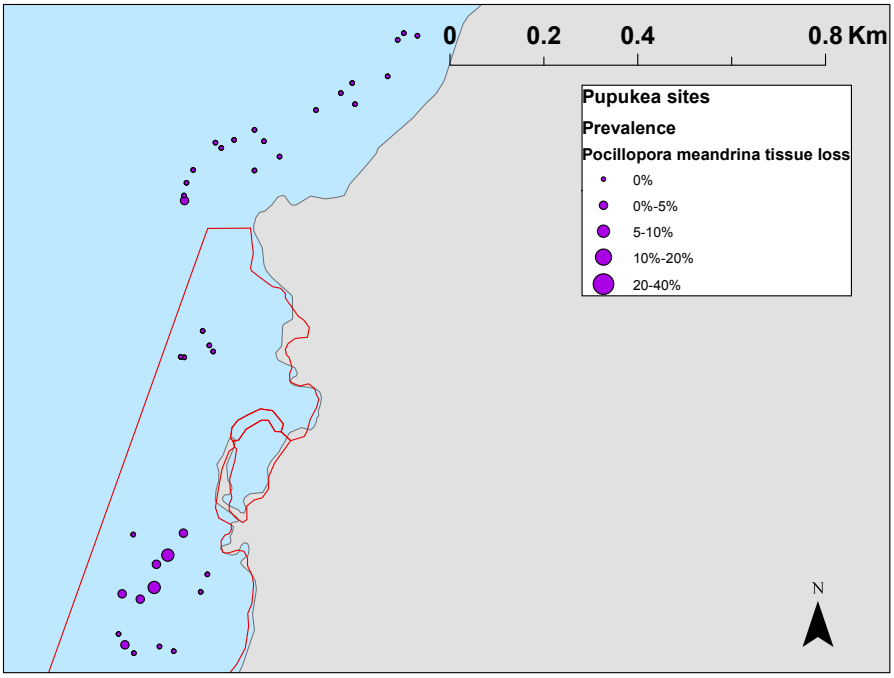

Figure 55. Prevalence of *Pocillopora meandrina* tissue loss at the Pupukea sites. Red lines mark the boundary of the MLCD.

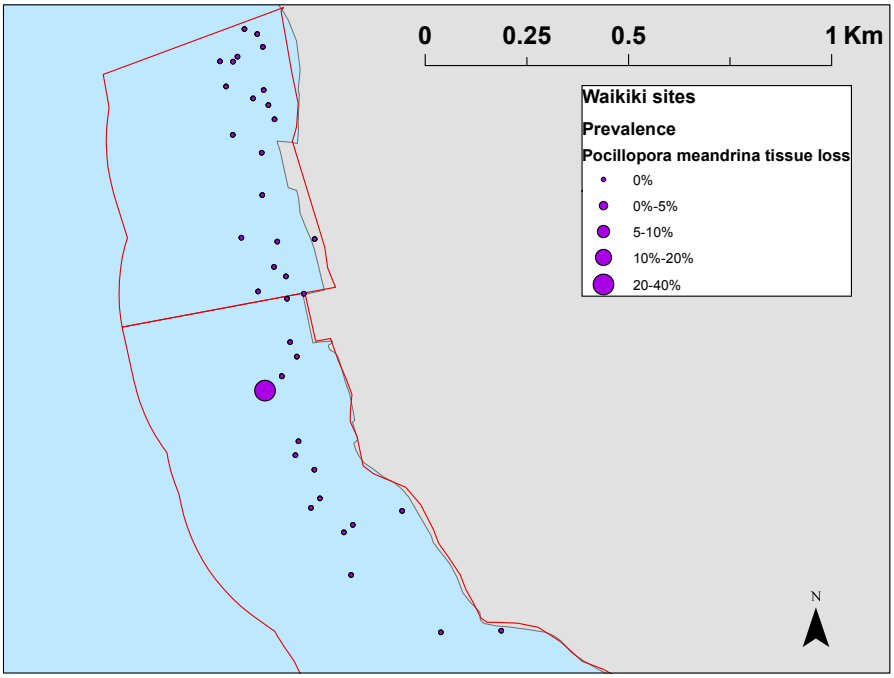

Figure 56. Prevalence of *Pocillopora meandrina* tissue loss at the Waikiki sites. Red lines mark the boundary of the MLCD.

Appendix D: Fish species lists

Table 23. Mean density was calculated from abundance of fish species on completed surveys for each site. Cells where MINITAB was unable to calculate standard error are shown as (*).

Hanauma-Protected

Trophic guild	Species Name	Mean density (#individuals /250m^2)	Standard error
Corallivore	*Chaetodon multicinctus*	2.50	0.50
	Chaetodon ornatissimus	2.33	0.33
	Chaetodon quadrimaculatus	1.50	0.29
	Chaetodon unimaculatus	3.25	1.60
	Plectroglyphidodon johnstonianus	1.50	0.50
Detritivore	*Ctenochaetus strigosus*	7.00	2.33
Herbivore	*Acanthurus blochii*	1.00	0.00
	Acanthurus guttatus	1.00	*
	Acanthurus leucopareius	1.00	0.00
	Acanthurus nigrofuscus	6.32	1.01
	Acanthurus olivaceus	1.92	0.33
	Acanthurus triostegus	6.24	1.42
	Canthigaster amboinensis	1.00	0.00
	Canthigaster jactator	1.75	0.25
	Melichthys vidua	1.11	0.11
	Naso lituratus	1.22	0.15
	Naso unicornis	1.00	*
	Scarus sp.	10.50	3.39
	Stegastes fasciolatus	2.11	0.75
	Zebrasoma flavescens	3.36	0.65
	Zebrasoma veliferum	3.67	1.67
Invertivore (mobile prey)	*Chaetodon ephippium*	2.00	*
	Gomphosus varius	1.27	0.20
	Halichoeres ornatissimus	2.50	0.50
	Lutjanus fulvus	1.00	*
	Lutjanus kasmira	2.00	0.58
	Macropharyngodon geoffroy	1.00	*
	Monotaxis grandoculis	1.00	*
	Paracirrhites arcatus	1.00	0.00
	Parupeneus multifasciatus	1.36	0.15
	Rhinecanthus aculeatus	2.29	0.42
	Rhinecanthus rectangulus	1.00	0.00
	Sufflamen bursa	1.00	0.00
	Thalassoma duperrey	3.95	0.65
Piscivore	*Aulostomus chinensis*	1.00	*

	Cephalopholis argus	1.43	0.20
	Fistularia commersonii	1.00	*
	Labroides phthirophagus	1.00	*
	Paracirrhites forsteri	1.00	*
Invertivore (sessile prey)	*Chaetodon auriga*	1.00	*
	Chaetodon lunula	1.33	0.33
	Forcipiger flavissimus	2.00	1.00
	Zanclus cornutus	1.00	0.00
Zooplanktivore	*Abudefduf abdominalis*	7.00	2.00
	Abudefduf vaigiensis	1.00	*
	Chromis hanui	1.50	0.50
	Chromis vanderbilti	5.00	1.30
	Dascyllus albisella	1.00	*
	Naso hexacanthus	1.00	*

Table 24. Mean density was calculated from abundance of fish species on surveys for each site. Cells where MINITAB was unable to calculate standard error are shown as (*).

Hanauma-Unprotected

Trophic guild	Species Name	Mean density (#individuals /250m^2)	Standard error
Corallivore	*Chaetodon multicinctus*	1.75	0.16
	Chaetodon quadrimaculatu	2.00	0.00
Detritivore	*Ctenochaetus strigosus*	4.71	2.11
Herbivore	*Acanthurus blochii*	1.25	0.25
	Acanthurus leucopareius	1.00	*
	Acanthurus nigrofuscus	5.06	1.12
	Acanthurus olivaceus	2.27	0.49
	Acanthurus triostegus	4.80	1.08
	Canthigaster jactator	1.33	0.24
	Centropyge potteri	1.00	*
	Kyphosus species	6.00	*
	Melichthys vidua	1.46	0.21
	Naso lituratus	1.25	0.25
	Naso unicornis	1.00	*
	Scarus	3.00	0.83
	Stegastes fasciolatus	1.60	0.40
	Zebrasoma flavescens	3.64	0.61
Invertivore (mobile prey)	*Cirrhitus pinnulatus*	1.00	*
	Coris flavovittata	4.00	3.00
	Coris gaimard	2.00	1.00
	Gomphosus varius	1.00	0.00
	Halichoeres ornatissimus	3.25	2.25
	Macropharyngodon geoffro	1.00	*
	Mulloidichthys vanicolen	30.00	*
	Paracirrhites arcatus	1.00	0.00
	Parupeneus multifasciatu	2.00	0.35
	Rhinecanthus aculeatus	1.33	0.33
	Rhinecanthus rectangulus	1.83	0.30
	Stethojulis balteata	3.00	*
	Sufflamen bursa	1.43	0.20
	Thalassoma duperrey	3.00	0.58
	Thalassoma trilobatum	1.50	0.50
Piscivore	*Aulostomus chinensis*	1.20	0.20
	Caranx melampygus	1.00	0.00
	Gymnothorax meleagris	1.00	*

	Scorpaenopsis diabolus	1.00	*
Invertivore (sessile prey)	*Canthigaster coronata*	1.00	*
	Chaetodon fremblii	1.00	*
	Forcipiger flavissimus	1.50	0.29
	Ostracion meleagris	1.50	0.50
	Zanclus cornutus	1.86	0.34
Zooplanktivore	*Abudefduf abdominalis*	12.00	2.00
	Chaetodon miliaris	4.00	*
	Chromis vanderbilti	9.25	2.74
	Dascyllus albisella	1.00	*
	Naso hexacanthus	20.00	0.00

Table 25. Mean density was calculated from abundance of fish species on surveys for each site. Cells where MINITAB was unable to calculate standard error are shown as (*).

Pupukea-Protected

Trophic guild	Species Name	Mean density (#individuals /250m^2)	Standard error
Corallivore	*Chaetodon ornatissimus*	1.50	0.50
	Chaetodon quadrimaculatus	1.50	0.29
	Chaetodon unimaculatus	1.00	*
Detritivore	*Ctenochaetus strigosus*	1.33	0.21
Herbivore	*Abudefduf sordidus*	1.00	*
	Acanthurus blochii	2.67	0.67
	Acanthurus leucopareius	6.73	1.68
	Acanthurus nigrofuscus	6.00	0.91
	Acanthurus olivaceus	4.25	1.56
	Acanthurus triostegus	11.55	4.77
	Canthigaster jactator	1.67	0.31
	Kyphosus species	1.75	0.48
	Melichthys niger	1.00	*
	Melichthys vidua	1.00	*
	Naso lituratus	1.00	0.00
	Naso unicornis	2.00	*
	Scarus	2.57	0.84
	Stegastes fasciolatus	1.83	0.54
	Zebrasoma flavescens	1.00	*
Invertivore (mobile prey)	*Bodianus bilunulatus*	1.00	0.00
	Coris flavovittata	3.75	0.80
	Coris gaimard	6.00	*
	Halichoeres ornatissimus	1.25	0.25
	Macropharyngodon geoffro	3.00	*
	Mulloidichthys flavoline	1.00	*
	Paracirrhites arcatus	1.33	0.21
	Parupeneus multifasciatus	2.24	0.33
	Rhinecanthus aculeatus	1.75	0.48
	Rhinecanthus rectangulus	1.69	0.18
	Stethojulis balteata	4.00	*
	Sufflamen bursa	2.00	0.63
	Thalassoma duperrey	2.92	0.55
	Thalassoma trilobatum	1.00	0.00
Piscivore	*Cephalopholis argus*	2.00	*
	Paracirrhites forsteri	1.00	*
	Scorpaenopsis diabolus	1.00	*

Invertivore (sessile prey)	*Canthigaster coronata*	1.38	0.18
	Chaetodon auriga	3.00	*
	Forcipiger flavissimus	2.00	*
	Ostracion meleagris	1.00	*
	Zanclus cornutus	1.25	0.25
Zooplanktivore	*Abudefduf vaigiensis*	1.00	*
	Chromis hanui	1.00	0.00
	Chromis vanderbilti	19.71	4.54
	Xanthichthys auromargina	1.00	*

Table 26. Mean density was calculated from abundance of fish species on surveys for each site. Cells where MINITAB was unable to calculate standard error are shown as (*).

Pupukea-Unprotected

Trophic guild	Species Name	Mean density (#individuals /250m^2)	Standard error
Corallivore	*Chaetodon multicinctus*	2.50	1.50
	Chaetodon ornatissimus	2.00	0.00
	Chaetodon quadrimaculatu	1.40	0.25
Detritivore	*Ctenochaetus strigosus*	1.50	0.50
Herbivore	*Acanthurus blochii*	2.00	1.00
	Acanthurus leucopareius	3.50	1.50
	Acanthurus nigrofuscus	3.67	0.93
	Acanthurus olivaceus	2.14	0.63
	Acanthurus triostegus	2.25	0.63
	Canthigaster jactator	1.67	0.33
	Kyphosus species	7.00	*
	Melichthys vidua	1.00	0.00
	Naso unicornis	1.00	*
	Scarus sp.	2.00	0.71
	Stegastes fasciolatus	2.67	1.20
Invertivore (mobile prey)	*Bodianus bilunulatus*	1.00	0.00
	Coris flavovittata	3.14	0.71
	Coris gaimard	1.00	*
	Diodon hystrix	1.00	*
	Halichoeres ornatissimus	2.80	1.11
	Macropharyngodon geoffroy	2.20	0.58
	Monotaxis grandoculis	1.00	0.00
	Mulloidichthys flavoline	1.50	0.50
	Novaculichthys taeniouru	6.00	*
	Paracirrhites arcatus	2.13	0.55
	Parupeneus multifasciatus	1.91	0.34
	Rhinecanthus aculeatus	1.00	*
	Rhinecanthus rectangulus	1.50	0.27
	Stethojulis balteata	8.00	*
	Sufflamen bursa	3.53	0.46
	Thalassoma duperrey	2.29	0.34
	Thalassoma trilobatum	1.00	0.00
Piscivore	*Aulostomus chinensis*	1.00	*
	Caranx ignobilis	1.00	*
	Caranx melampygus	1.00	*

	Fistularia commersonii	2.00	*
Invertivore (sessile prey)	*Canthigaster coronata*	1.75	0.31
	Chaetodon fremblii	2.00	*
	Forcipiger flavissimus	1.50	0.50
	Ostracion meleagris	1.50	0.50
	Zanclus cornutus	1.75	0.48
Zooplanktivore	*Chromis vanderbilti*	11.00	2.51

Table 27. Mean density was calculated from abundance of fish species on surveys for each site. Cells where MINITAB was unable to calculate standard error are shown as (*).

Waikiki-Protected

Trophic guild	Species Name	Mean density (#individuals /250m^2)	Standard error
Corallivore	*Chaetodon quadrimaculatu*	1.00	*
Herbivore	*Abudefduf sordidus*	1.00	0.00
	Acanthurus blochii	1.00	0.00
	Acanthurus leucopareius	1.71	0.18
	Acanthurus nigrofuscus	6.33	3.15
	Acanthurus olivaceus	1.00	*
	Acanthurus triostegus	7.80	1.94
	Canthigaster jactator	1.75	0.48
	Chanos chanos	1.00	*
	Naso lituratus	1.86	0.55
	Naso unicornis	2.10	0.50
	Scarus sp.	2.33	0.55
	Stegastes fasciolatus	1.33	0.33
Invertivore (mobile prey)	*Diodon holocanthus*	1.00	*
	Gomphosus varius	1.67	0.33
	Halichoeres ornatissimus	1.60	0.27
	Parupeneus multifasciatus	1.33	0.33
	Rhinecanthus aculeatus	4.50	1.50
	Rhinecanthus rectangulus	1.50	0.22
	Stethojulis balteata	1.75	0.31
	Thalassoma duperrey	5.00	0.73
	Thalassoma trilobatum	1.33	0.33
Piscivore	*Aulostomus chinensis*	1.00	0.00
	Caranx melampygus	3.00	*
	Fistularia commersonii	1.00	*
Invertivore (sessile prey)	*Chaetodon auriga*	2.00	*
	Chaetodon lunula	1.00	0.00
	Ostracion meleagris	1.00	0.00
	Zanclus cornutus	1.50	0.50
Zooplanktivore	*Abudefduf abdominalis*	4.00	1.76
	Chromis hanui	1.00	*
	Chromis ovalis	2.00	0.00
	Chromis vanderbilti	2.14	0.77

Table 28. Mean density was calculated from abundance of fish species on surveys for each site. Cells where MINITAB was unable to calculate standard error are shown as (*).

Waikiki-Unprotected

Trophic guild	Species Name	Mean density (#individuals /250m^2)	Standard error
Detritivore	*Ctenochaetus strigosus*	1.00	0.00
Herbivore	*Acanthurus blochii*	1.00	0.00
	Acanthurus leucopareius	1.00	0.00
	Acanthurus nigrofuscus	4.00	1.03
	Acanthurus triostegus	5.63	1.14
	Canthigaster jactator	1.50	0.50
	Naso lituratus	1.25	0.25
	Naso unicornis	1.50	0.50
	Scarus 2	0.00	
	Stegastes fasciolatus	2.00	0.78
Invertivore (mobile prey)	*Coris flavovittata*	1.00	*
	Halichoeres ornatissimus	1.38	0.26
	Parupeneus multifasciatus	1.71	0.47
	Rhinecanthus rectangulus	1.75	0.25
	Stethojulis balteata	2.00	0.63
	Thalassoma duperrey	2.47	0.38
	Thalassoma trilobatum	1.50	0.50
Invertivore (sessile prey)	*Chaetodon auriga*	1.00	*
	Ostracion meleagris	1.67	0.67
	Zanclus cornutus	2.00	0.00
Zooplanktivore	*Abudefduf abdominalis*	1.00	*
	Chromis ovalis	2.00	*
	Chromis vanderbilti	1.25	0.25
	Dascyllus albisella	1.00	*

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