**Community structure and demographic drivers of partial mortality in corals throughout the Papahānaumokuākea Marine National Monument.**

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PMNM: Papahanaumokuakea Marine National Monument

NWHI: Northwestern Hawaiian Islands

FFS: French Frigate Shoals

LIS: Lisianski Island

LAY: Laysan Island

MAR: Maro Reef

PHR: Pearl and Hermes Atoll

MID: Midway Atoll

KUR: Kure Atoll

General Introduction

Coral reefs are some of the most diverse and valuable ecosystems on Earth. The dynamic habitat created by corals provides complex structure that supports more species per unit area than any other marine ecosystem (Reaka- Kudla 1997). Unfortunately, coral disease is a growing problem on reefs throughout the global ocean (Goldberg and Wilkins 2004). The prevalence, severity, and distribution of diseases have increased within the last two decades (Aeby 2006; Ruiz-Moreno et al 2012, Maynard et al. 2015). The increase of anthropogenic stressors such as nutrient input, overfishing, and climate change have all been linked to coral diseases (Friedlander et al. 2005; Aeby 2006; Aeby et al 2011).) Consequently, diseases have contributed to large-scale coral mortality and caused dramatic reductions to important ecosystem services (Pratchett et al. 2012, Holbrook et al. 2015). Despite the documented impacts of coral disease, there is still a gap in knowledge pertaining to how coral community structure and demographics can influence coral disease. More than half of all coral reefs have either been lost, placed in critical state, or are now seriously threatened with loss in the years to come (Hoegh-Geuldberg et al. 2007; Harvell et al. 2007; Wilkinson 2008; Maynard et al. 2015). Understanding how coral community structure and demographics are associated with coral disease and their impacts is important in light of the projected increases in the occurrence and prevalence of diseases in the future.

While disease is often viewed as a detrimental occurrence, it is a fundamental characteristic of a functional ecosystem. Organisms, populations and communities are constantly undergoing changes driven by mortality and natality of individuals (Connell 1961; Caughley 1966: Bak and Meester 1998; Hughes and Tanner 2000). Live corals create complex calcium carbonate reef structures that provide the structural foundation of tropical reefs, which are capable of supporting high productivity and biodiversity (Reaka-Kudla, 1997). Unfortunately, corals are highly vulnerable to an array of local and global stressors that can result in disease and mortality. While diseases occur naturally in corals, combinations of environmental stressors (i.e., elevated sea surface temperatures and local pollutants) can result in large-scale mortality events that dramatically impair ecosystem function (Ainsworth et al. 2007; Sweet and Bythell 2012). Globally, increasing amounts of carbon dioxide and greenhouse gases in the atmosphere are leading to both rising sea surface temperatures and acidification (Goldberg and Wilkins 2004; Hoegh-

Geuldberg et al. 2007; Harvell et al. 2007). On local scales, corals are impacted by anthropogenic disturbances such as pollution, runoff, sedimentation, coastal development, recreational overuse, and overfishing (Aeby et al. 2011). Understanding baselines levels of coral disease prevalence is important for identifying when stressors may be causing reductions in coral health that may lead to harmful disease outbreaks and mortality.

Corals are sessile cnidarians that exhibit a mutualistic relationship with endosymbiotic dinoflagellates from the genus *Sybiodinium* (Hughes and Connell 1987). In addition to *Symbiodinium*, corals have biological associations with other microorganisms including as fungi, bacteria, thus the term 'coral holobiont' is used to refer to this assemblage of different species that form an ecological unit (Muller-Parker et al. 2015). The coral holobiont exists in a dynamic equilibrium and differs between individual colonies. Environmental stressors can cause disturbances to the holobiont equilibrium and lead to disease and reduced health conditions. Despite the intense research recording the impacts of corals diseases and disturbances, little is known about the association and interplay between coral community structure and coral health (Richmond and Wolanski 2011). More research is needed to adequately understand how diseases impact the biology and ecology of corals. Considering the lack of understanding of coral disease, one critical epizootiological component to study is the link between the demographics of coral community structure and disease. When studying coral demographics, ecologists often use size rather than age to account for the large amounts of variability in population structure (Hughes and Connell 1987; Hughes and Tanner 2000). Corals are constantly experiencing partial mortality, tissue lesions, fusion, and fission (Hughes and Connell 1987; Hughes and Tanner 2000), all of which can be affected by demographics, environment, competition, reduced health, disease, and natural disturbances. Corals exhibit varying responses to environmental stressors, and one condition commonly used to assess the general health of corals is 'partial mortality', which is the proportion of colony surface area that has succumbed to mortality. Tracking partial mortality is useful for quantifying changes in the general health of coral communities. It is important to understand how demographic factors, such as size, are associated with partial mortality in order to develop accurate baseline assessments of coral health.

Coral disease is especially concerning for isolated regions like the Hawaiian Archipelago, which naturally foster low levels of biodiversity and high levels of species endemism (Friedlander and De Martini 2002). The Papahanaumokuakea Marine National Monument (PMNM) encompasses the Northwestern Hawaiian Islands (NWHI). It is a unique and pristine marine ecosystem that is exposed to minimal anthropogenic influences (Friedlander and De Martini 2002; Aeby et al. 2011). Over the last few decades, scientists have worked to develop comprehensive baseline data pertaining to coral community structure and coral health throughout the NWHI. This work has included characterization of the relative density, diversity, size, morphology, and depth of coral communities at sites throughout the Monument (Friedlander et al. 2005). There still remains a need to quantitatively examine the relationships of coral demographics and levels of coral disease. This research uses long-term monitoring data and statistical modeling to predict relationships between demographics of coral communities and populations, thus, providing an example of how long-term monitoring data can be used in mixed-effect modeling in order to enhance future management decisions.

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## COMMUNITY STRUCTURE AND DEMOGRAPHIC DRIVERS OF PARTIAL MORTALITY IN CORALS THROUGHOUT THE PAPAHĀNAUMOKUĀKEA MARINE NATIONAL MONUMENT.

Abstract

Understanding the association between coral reef community demographics and coral health is critical in the face of increasing environmental stressors driven by an ever-expanding human population. Within the last several decades, coral reefs around the globe have experienced substantial increases in levels of coral disease as well as large-scale outbreaks and mortality. Corals can experience partial mortality lesions because they are colonial organisms. A coral colony is constantly experiencing partial mortality lesion, fission and fusion. Corals exhibit highly variable levels of partial mortality, which is a useful indicator of overall coral health, thus it is important to identify drivers of this condition. This study examines monitoring data on coral health and disease from surveys (n= 4449) conducted throughout the Papahānaumokuākea Marine National Monument for the Reef Assessment and Monitoring Program (RAMP). Linear mixed-effects models were used to identify coral community demographic parameters that were associated with coral partial mortality. Significant variability in mean coral colony size, density, diversity, morphology, and partial mortality of corals was found among the sites in the NWHI. Mean coral size, density, and diversity decreased with increasing latitude. Mean values of coral partial mortality were also found to be statistically greater at sites in the high latitude atolls. The twelve morphologies identified in this study exhibited statistically significant differences in mean values of partial mortality. The results from the linear mixed-effects models showed coral partial mortality is predicted by the size of individual colonies (0.02±0.26(S.D.)), colony density (-0.33±0.07(S.D.)), species diversity (-0.03±0.01(S.D.)), and colony morphology. Colony size was positively correlated with partial mortality, whereas colony density and diversity showed slightly negative relationships with partial mortality. Columnar and mounding lobate morphologies exhibited the strongest effects with partial mortality. Understanding the relationship between coral community demographics and coral health can provide useful insight into how various coral populations may respond to increased levels of stress and disturbance. This research provides an example of how long-term monitoring data and hierarchical statistical modeling can provide information to help managers better understand coral health.

Introduction

Coral reefs are ecologically and economically important ecosystems that provide physical habitat structure which supports a high abundance and diversity of marine organisms. Coral reefs support more species per unit area than any other marine ecosystem, (Reaka-Kudla 1997). Despite the intensive research investigating degradation of coral reefs around the globe (Richmond and Wolanski 2015), little research has been conducted to determine how coral reef community structure and demographics directly influence coral health and disease. Studying the relationships among these parameters is needed in order to understand how the structure of a coral assemblage will influence its susceptibility to disturbance and disease. Mortality and natality of individuals are constantly changing and driving community growth (Connell 1961; Caughley 1966 Hughes and Tanner 1966; Bak and Meester 1998). While we possess a wealth of knowledge about community demographics of model organisms such as humans, mammals, birds, and insects, there is little known about sessile colonial organisms, such as corals, which exhibit highly complex and plastic morphologies and exhibit large variability in age and size.

Coral community structure and demographics likely have played a large role in the susceptibility of corals to disturbance and disease, but this has yet to be thoroughly studied among coral reefs throughout the Papahānaumokuākea Marine National Monument (PMNM). The Hawaiian Archipelago consists of the inhabited main Hawaiian Islands and the uninhabited Northwestern Hawaiian Islands (NWHI). The PMNM is the single largest U.S. conservation area. This protected region encompasses 1,508,870 $km^2$ of the Pacific Ocean and includes remote islands, atolls, submerged banks, and reefs. Due to the geographical isolation and federal protection of the monument, islands and atolls located within this monument have coral reefs that are only exposed to global impacts and very few local anthropogenic stressors (Friedlander et al. 2005). Due to the nature of its protection and isolation, the NWHI are considered one of the last pristine coral reef ecosystems on the planet. The health of coral is particularly important for isolated regions like the Hawaiian Islands, which naturally foster low levels of biodiversity and high levels of endemism (Friedlander et al 2005). To thoroughly understand coral health and its relationship with coral community structure and demographics, one must have comprehensive ecological baseline data.

Coral reef throughout the global ocean are affected by stressors such as climate change, disease, acidification, and eutrophication. Habitat degradation is the greatest cause of species extinction, and coral reef ecosystems are exhibiting these losses (Pratchett et al. 2012; Holbrook et al. 2015). A small increase in temperature of 1-2°C above 26°C can cause corals to expel their symbionts and appear bleached (Jokiel and Coles 1974; 1977; Hoegh-Guldberg et al. 2007). While bleached corals have the potential to recover symbiotic relationships, if temperature conditions do not return to a supportive living state, they become more susceptible to mortality thus leading to environmental regime shifts. Coral health is further compromised by eutrophication in which excess nutrient runoff enters reef ecosystems, suffocates corals, and facilitates algal overgrowth (Rogers, 1990). In addition, ocean acidification is another factor that can lead to coral mortality by decreasing levels of calcium carbonate, thereby decreasing overall carbonate ion concentrations and increasing the pH of the oceans. The loss of the carbonate ions, calcite, and aragonite will limit skeleton formation in corals (Hoegh-Guldberg et al. 2007). Chronic degradation of coral reefs and habitat structural complexity has the potential to cause trophic cascades, phase shifts, and declines in fish assemblages (Graham & Nash 2013). In light of the projected increase in global and local stressors, it is critically important to understand how coral community structure and demographics may associated with vulnerability to disturbance and disease.

Corals are sessile animals that possess ecological characteristics resembling those of both plants and animals (Hughes and Connell 1987). Partial mortality of live coral tissue is considered a useful measurement of coral health (Figure 1). The susceptibility of corals to partial mortality is affected by demographics, competition, disease, and both natural and anthropogenic disturbance. Disease emerges from complex interactions between disease host, agent, and environment (Lafferty and Holt 2003, Aeby et al. 2011). Many coral diseases have caused drastic changes within affected coral communities (Aeby 2006; Ruiz-Moreno et al 2012, Maynard et al. 2015). Understanding the relationships between coral community structure, demographics and coral health is critical in the face of increasing anthropogenic stressors, disease, and other natural disturbances. For example, previous studies have found coral assemblages with low values of coral cover and coral size to have high levels of coral disease and mortality (Hughes and Connell, 1987; Meester and Tanner, 2000). These findings provide valuable

information for identifying coral communities that are likely to be highly susceptible to disturbance and disease, and this knowledge can be utilized by managers to develop effective strategies for conserving coral reefs.

Although coral disease outbreaks often occur within relatively small geographic scales, the prevalence, severity, and distribution of diseases have increased globally within the last two decades (Aeby 2006, Ruiz-Moreno et al 2012, Maynard et al. 2015). Global disease outbreaks have wiped out large areas of coral reefs, primarily in the Caribbean but also recently in the Pacific (Richardson 1998). Environmental conditions such as increased temperature and poor water quality have all been linked to increasing coral susceptibility to disease by weakening their immune system and introducing pathogens (Harvell et al. 2007). Climate change is creating unstable environmental conditions that allow diseases to persist. Although the disease prevalence is relatively low in the Hawaiian archipelago compared to other regions, Hawaii has also shown an increase in disease outbreaks in the last two decades (Friedlander et al 2005, Aeby 2006). Diseases have been more common in the Main Hawaiian Islands, where corals face stressors from climate change in addition to direct anthropogenic stressors such as pollution, sedimentation and overfishing (Friedlander et al 2005, Aeby 2006). Black band disease outbreaks were recently documented on coral reefs off Kauai (Aeby et al. 2016, and in the uninhabited NWHI there was an disease outbreak of white syndrome on *Acropora* species (Aeby 2006). The most prevalent disease throughout the NWHI is *Porites* trematodaisis, which results from a digenetic trematode effecting only *Porites* species (Friedlander et al. 2005). Although there have been numerous instances of coral diseases being documented and linked to various environmental stressors, there is still a considerable gap in knowledge regarding how community structure and demographics drive the susceptibility of a given coral reef to conditions of reduced health and disease.

Individual corals within a community are often dissimilar in terms of growth rates, morphologies, reproduction, and mortality (Hughes and Connell, 1987). Corals are also influenced by their environment, and thus exhibit large variation in growth, fusion, and fission (Hughes and Connell 1987, Harvell 2007). Although many researchers have documented disease at global and local scales, it can be assumed that

each coral reef system will exhibit a unique set of responses to a given environmental disturbance (Friedlander et al. 2005; Aeby 2006; Harvell 2007; Hoegh-Guldberg et al. 2007). It is still unclear how community structure and demographics influence these responses to disturbance and disease. To better understand the links between coral ecology and coral health, this study examined colony size, density, diversity, morphology, and depth in relation to coral health, specifically partial mortality. Individually, all of these variables have been shown to influence coral health. Simultaneous examination through statistical modeling will indicate which variables have the greatest effect on coral health and provide useful insight for managers to better assess vulnerability of coral communities to disturbance and disease.

Coral colony size exhibits significant relationships with disturbances and diseases. Ecologists have traditionally analyzed size rather than age when studying coral population demographics of coral (Hughes and Connell, 1987; Bak and Meester, 1998; Meester and Tanner, 2000). This is because coral colony size and age are not always directly correlated (Hughes and Connell, 1987). Mortality of corals has been previously linked to colony size, with smaller colonies accounting for 20% out of 26% overall mortality in a sampled community while larger corals showed a higher prevalence of partial mortality (Hughes and Connell 1987; Bak and Meester 1998). This research suggests a trade-off where larger colonies rarely escape partial mortality but are less vulnerable to complete mortality than smaller colonies (Meesters et al. 1996). Size has also been shown to have a substantial influence on vulnerability to diseases. Larger colonies have been found to be exposed to more physical stressors then smaller coral colonies and have higher levels of severity and prevalence of coral disease (Burns and Takabayashi 2011; Walsh et al. 2013). This could be due to the amount of surface area associated with the larger colonies. This demographic information allows one to predict that larger colonies within communities will experience more signs of disease than smaller colonies.

Species diversity can be expected to significantly affect disease prevalence. Some coral genera are more vulnerable to disturbance and disease than others. For example, *Porites* species are dominant throughout the Hawaiian archipelago and this genus exhibits the highest prevalence, widest distribution and largest number of coral diseases as compared to any other coral taxa in the Hawaiian Archipelago

(Aeby et al. 2011). *Acropora* species are found within the NWHI and are primarily restricted in distribution to one atoll. *Acropora* species dominate certain reef zones surrounding this atoll and are also very vulnerable to reduced coral health in the Hawaiian Archipelago and Indo-Pacific (Vargas-Angel 2009, Aeby et al. 2011). Coral communities comprised of *Porites* or *Acropora*, for example, can be expected to have relatively high levels of disease and susceptibility to disturbances. Diversity can be expected to significantly affect disease prevalence and with site-specific relationships. The intermediate disturbance hypothesis suggests that disturbance within an ecosystem can produce a higher biodiversity, if the frequency is not too rare nor too frequent (Connell 1987). A number of the islands located in the NWHI have seen mass bleaching and disease outbreaks (Kenyan and Brainard, 2006; Couch et al. 2017). These disturbances have significantly influenced corals reefs found at Kure, Midway, Pearl and Hermes, and Lisianski (Kenyan and Brainard, 2006; Couch et al. 2017). As a result of these disturbances, there has been a dramatic loss in dominant coral species and cover coral (Kenyan and Brainard, 2006; Couch et al. 2017). It is important to know the history of these sites to understand the current community structure and demographics at each location to accurately decipher the relationship between coral diversity and disease.

Spatial distribution or coral colonies within a given reef environment will also exert an influence on community density (Caugley 1966). Connell (1961) showed that community densities of the intertidal barnacle, Balanus balanoides, were driven by settlement choice and post-settlement mortality rates. The crowding, smothering, and displacement of smaller barnacles caused increased rates of mortality that indicated these barnacles had reached a carrying capacity (Connell 1961). The influence of available space and mortality likely play similar roles in coral communities. Larger and more dominant coral species have the ability to monopolize available habitat space and have higher success rates of settlement (Polato et al. 2010) and recruitment (Harriott and Banks 1995). Prevalence of coral disease is also influenced by environmental conditions and the density of coral colonies within a community. For example, on the Great Barrier Reef (GBR) in Australia there was an outbreak of white syndrome affecting reef-building corals including, *acroporids*, *pocilloporids*, and *faviids*. (Bruno et al. 2007). This study found that increased temperature influences white syndrome, and interestingly, that this disease was only

prevalent where coral cover was higher than 50% (Bruno et al. 2007). Therefore, the density of the host agent can play a major role in the severity and prevalence of white syndrome disease. Areas of increased coral cover are vulnerable to increased prevalence of natural disturbance and disease. It is essential to characterize the effects of density on coral populations in order to understand reduced coral health and disease.

Depth has also shown to have a substantial influence on coral health. Coral are photosynthetic organisms needing light and available nutrients in order to grow. As depth increases light becomes more sparse and available nutrients are depleted (Kuta and Richardson 2002). Stressors of shallow water communities include natural and anthropogenic disturbances; wave action, runoff, sedimentation and temperature changes all been shown to affect coral health (Kuta and Richardson 2002). In the NWHI there have been several cases of mass bleaching, during the years of 2002, 2004, and 2014-15. Coral reefs found at Kure, Midway, Pearl and Hermes and Lisianski were significantly affected by mass bleaching events (Kenyon and Brainard 2006, Couch et al. 2017). Depth was found to be associated with severity of bleaching amounts. Shallow backreef coral communities exhibited a higher amount of bleaching than the forereef coral communities (Kenyon and Brainard 2006). Another example of depth effects on coral disease is with black band disease. This disease is limited to shallow depths, since black band is dominated by a photosynthetic cyanobacterium (Kuta and Richardson 2002). This cyanobacterium accumulates in surfaces, which causes coral at shallower depths to be affected by black band disease at a higher rate. Shallow water communities are expected to experience more disturbances and disease then deeper water communities.

Coral colony morphologies are influenced by their environment; for example, wave energy and availability of light can impact the morphologies of coral colonies (Muller-Parker et al. 2015). Coral morphology can be highly plastic, and even colonies in the same population can exhibit an array of growth forms (Meester and Tanner 2000, Muller-Parker et al. 2015). Morphological plasticity complicates the ability to decipher how coral community structure and demographics influences coral health. In addition, the circumference to surface area ratio is correlated with partial mortality (Meester et al. 1996;

Mercado-Molina et al. 2018). Corals exhibiting complex morphologies (e.g., branching, plating and corymbose growth forms) are generally more susceptible to disturbance than slow-growing corals that exhibit massive morphologies (Gates & Ainsworth, 2011; Woesik et al., 2011). Considering the relationships found between morphological complexity and coral health, it is important to examine how specific morphologies may influence the susceptibility of a coral community to disturbance and disease.

Corals exhibit highly variable levels of partial mortality, which is a useful indicator of overall coral health, thus it is important to identify correlates of this condition. This study examines long-term monitoring data from the Reef Assessment and Monitoring Program surveys. This is an ideal dataset to establish baseline information about how community structure and demographics influence the partial mortality of corals. The objectives of this study are to 1) quantify community structure and coral demographics for the islands, atolls, reefs, and banks of PMNM and 2) determine the relationships between community structure and coral demographics with partial mortality using mixed-effect hierarchical modeling statistical techniques. Researching the effects of community structure and demographics in relation to degraded coral health can provide useful insights into how different coral reefs will respond to environmental disturbances in the PMNM. This research provides an example of how long-term monitoring data and hierarchical statistical modeling can provide information to help managers better understand coral health and determine how reefs may respond to disturbances in the future.

Hypotheses

$H_1$: An increase in colony size will be correlated with increasing partial mortality in corals.

$H_{2:}$ An increase in density will be correlated with increasing partial mortality in corals.

$H_3$: An increase in diversity will be correlated with decreasing partial mortality in corals.

$H_4$: Coral colony morphology will have an effect on partial mortality.

$H_5$: Partial mortality will vary between sites.

## Methods

### *Study Sites*

The Hawaiian archipelago consists of the inhabited main Hawaiian Islands and the uninhabited Northwestern Hawaiian Islands (NWHI). Papahānaumokuākea Marine National Monument (PNMN) is the single largest U.S. conservation area, established on June 15, 2006 (Figure 3). This protected region encompasses 1,508,870 $km^2$ of the Pacific Ocean and includes remote islands, atolls submerged banks, and reefs. Due to the geographical isolation and federal protection of the monument, islands and atolls located within this monument have coral reefs that are only very minimally exposed to anthropogenic impacts (Friedlander et al 2005). For this study, a total of seven islands, reefs and atolls were examined to determine how demographics are associated with partial mortality of corals: French Frigate Shoals (23.7489° N, 166.1461° W) , Maro Reef (25.4150° N, 170.5900° W), Lisianski (26.0662° N, 173.9665° W), Laysan (25.7679° N, 171.7322° W) , Pearl and Hermes Atoll (27.8333° N, 175.8333° W), Midway Atoll (28.2072° N, 177.3735° W) and Kure Atoll (28.3925° N, 178.2936° W) (Figure 3).

### *Survey Data*

Reef survey data were obtained from NOAA's Rapid Ecological Assessment (REA) surveys. REA surveys are conducted annually throughout the PMNM. All sites are selected using a random stratified sampling design that selects locations on hard bottom habitats within three reef types: fore reef, back reef, and lagoon. Surveys are conducted across three depth categories: shallow (1-6m), mid (6-18m) and deep (18-30m). Overall, corals in this study were generally healthy; roughly 4,000 corals out of 34,000 showed incidence of degraded coral health. The sample proportion used in this study and all subsequent statistical analyses was 4449 coral colonies; which consisted of only corals with presence of partial mortality.

### *Coral Survey Methodology*

Two 18m belt transect surveys are conducted at each site. Adult coral colonies are surveyed within a $10m^2$ area on each transect. Adult coral colonies defined by REA methods are coral colonies greater than 5cm in minimum dimension. Coral colonies that were at least 50% within the $10m^2$ were also

surveyed. All colonies within the 10m$^2$ area were identified down to the lowest possible taxonomic level. Community structure and demographic parameters such as greatest colony length (diameters are measured to nearest cm) and morphology (Table 2) were noted. Partial mortality of each coral colony is measured with a ruler and the diver visually estimated the proportion of colony surface area (%) occupied by dead tissue. Partial mortality is visually estimated "old dead", the portion of the colony that no longer has live tissue and is cover by algae and "recently dead", the portion of the colony that has recently died and there is a stark white skeleton with no live tissue (Figure 1). The cause of partial mortality was also noted down to specific disease, predation, sedimentation, overgrowth and physical damage. In addition to partial mortality, other health conditions of each colony were recorded down to type, severity (ranging from moderate to acute) and extent (percent of colony affected). Data from surveys conducted from 2014-2016 were used for this study (Table 1).

*Statistical Analyses*

All statistical analyses were processed using R statistical software (3.6.0). Analysis of variance with Tukey's Honestly Significant Difference (HSD) groupings were completed for partial mortality and all variables of community structure and demographics to examine differences among the study sites within the PMNM (Tukey 1949). There was a maximum colony size limit of 100cm used for this data analysis. Shannon-Wiener diversity index and density values were calculated for each transect (Spellerberg et al. 2003). A logit transformation was applied to the proportional data for partial coral mortality (eq. 1). The logit transformed partial mortality data were used for all statistical analyses. Only corals that exhibited partial mortality were analyzed.

$$eq.1 \quad Logit\ Transformation = LN\left(\frac{p}{1-p}\right)$$

*Mixed Effect Modeling*

Mixed-effects models were used to determine the relative contribution between fixed and random variables that affect coral partial mortality. A nested or hierarchical structure is used for the RAMP surveys throughout the PMNM. Mixed effect models are designed to deal with this nested data by

incorporating two types of parameters; fixed and random effects. Fixed effects are informative factor levels such as size, density, diversity, species, morphology), while random effects often have uninformative factor levels such as depth and sites. The response variable is the logit transformed average partial mortality of coral colonies and the predictor variables are size, density, depth, diversity, morphology, and site. A top-down approach was used to select the best-fit model for each analysis. There are three different modeling strategies that are used within mixed effect modeling. The first model is a generalized least squares (GLS) model that includes all explanatory variables but no interactions. The results from this GLS model will reflect the results of a normal linear regression model (Zuur et al. 2009). The second is a random intercept model, were the intercept of the linear regression is allowed to change per Island. This model includes a site effect, assuming that the variation around the intercept for each site is normally distributed with a slight variance. This type of modeling defines the amount of variance found between each site. Random intercept allows for a random shift from the intercept resulting in fitted lines parallel to the mean population fitted line. The random intercept models enable the adjustment of the intercept for each site to better represent the relationship of each parameter on our response variable, partial mortality. Since we are able to do this for intercept, it is also possible to use this same characteristic for the slope of the regression line. Therefore, the last type of model is the random intercept and slope model. This model allows both intercept and slope to vary among levels. For this study a comparison of all three types of models was completed to determine the best model for this dataset.

## Results

### *Depth*

A one-way analysis of variance (ANOVA) compared the average survey depth among sites in NWHI. The difference was significant, ($F(6,4442)$= 37.9, $p$ = < 0.01, Figure 4). Tukey HSD indicated there was a significant difference between the sites and showed three different groupings (Figure 4). Pearl and Hermes atoll has the largest range of survey depths from 14 to 90-fsw compared to Midway Atoll. Post hoc comparisons using the Tukey HSD test indicated that Laysan (M= 52.87, SD= 17.65), Lisianski (M= 51.92, SD= 18.11), and Kure (M= 49.91, SD= 17.65) were significantly deeper than other sites. In

addition, French Frigate Shoals (M=43.19, SD= 18.93) and Midway Atoll (M= 38.15, SD= 19.59) were shallower than the other sites (Figure 4).

*Colony Size*

An ANOVA compared the colony sizes among sites in the PMNM and found significant differences in size among the sites ($F(6,4442) = 20.44$, $p < 0.01$, Figure 5). Lisianski the highest mean colony size of 27.83 cm, whereas Pearl and Hermes showed the smallest mean colony size of 19.57cm. Post hoc comparison using the Tukey HSD test indicated that the mean values for colony size Kure, Midway, Pearl and Hermes and Laysan were significantly smaller from other sites.

*Diversity*

An ANOVA found significant differences in diversity among the surveyed sites ($F(6,164) = 2.162$, $p = 0.048$, Figure 6). French Frigate Shoals showed the highest average diversity (mean= 1.49 H). Diversity values showed a decreasing trend with increasing latitude (Figure 6). Post hoc comparisons using the Tukey HSD test indicated that the mean values for diversity at French Frigate Shoals were significantly higher than the other six sites. In addition, Kure Atolls showed the lowest average diversity (mean= 1.12 H) then compared the six other sites.

*Density*

Density was calculated for each transect. An ANOVA compared the density values between sites in PMNM. The results were significant ($F(6,164) = 9.768$, $p < 0.01$). The highest mean was found at Maro Reef (mean = 10.57 $m^2$) and the lowest at Midway (mean = 2.62 $m^2$). Similar to diversity, density decreased with increasing latitude (Figure 7). The high latitude atolls (Pearl and Hermes, Midway, Kure) had the lowest density values (Figure 7). Post hoc comparisons using the Tukey HSD test indicated that the mean values for density at high latitude atolls Kure, Pearl and Hermes, and Midway Atolls were statistically lower than the more central sites.

*Partial Mortality*

An ANOVA found significant differences in the average values of partial mortality among the survey sites in the PMNM ($F(6,4442) = 26.80$, $p = < 0.01$, Figure 8). Midway had the highest average partial mortality 48.60 %. Finally, Layson (mean = 17.18%) showed the lowest partial mortality mean of (Figure 8). Post hoc comparisons using the Tukey HSD test indicated many different significances between the seven sites (Figure 8). High latitude atolls show some of the highest and lowest mean partial mortality values (Figure 8).

*Morphology*

Twelve different morphological distinctions were used in the survey data for this project (Table 2). An ANOVA compared the partial mortality values between coral morphologies (Figure 9). Results showed significant differences in partial mortality of different morphology ($F(11,4437) = 34.35$, $p < 0.01$). Mounding lobate showed the highest partial mortality mean of 49.99%, whereas encrusting columnar showed the lowest mean of 17.60% (Figure 9). Post hoc comparisons using the Tukey HSD test indicated many different significances between the twelve morphologies (Figure 8).

*Mixed Effect Modeling for Partial Mortality*

Partial mortality was influenced by multiple predictors; size, density, diversity and morphology. Size showed a positive effect with partial mortality, with an effect size of 0.02 (Table 3, Figure 10). Diversity and density both had a negative effect on partial mortality, with an effect size of -0.03, 0.-31 (Table 3, Figure 10). Finally, the twelve different morphological types were also found to affect partial mortality in corals. In particular encrusting columnar (EC) morphology showed a strong negative effect on partial mortality, with an effect size of -1.99. In addition, mounding lobate (ML) morphology showed the strongest positive effect with partial mortality (Table 3, Figure 10).

## Discussion

*Effects of Latitudes on Coral Health*

The findings from this study suggest that there are significant latitudinal trends in the examined parameters of coral community structure and demographics in the NWHI. The gradient is likely associated with the unique geomorphology and physiochemical characteristics of the seawater at each island and atoll, which change throughout the island chain. For example, the atolls at higher latitudes have older reef substrate and protected lagoon habitats whereas the island reef habitats at lower latitudes are more exposed to wave action and typically have higher sea surface temperatures (Grigg 1982). Results from the linear mixed-effect models showed colony size, density, diversity and morphology have significant relationships with partial mortality of corals. Larger corals experience higher partial mortality compared to smaller corals. Monotypic communities are more vulnerable to partial mortality then highly diverse communities. Density showed a negative effect with partial mortality, thus sites with high colony density showed lower partial mortality values. Furthermore, morphologies also varied in partial mortality. Complex morphologies such as mounding lobate showed strong positive relationships with partial mortality. These findings suggest community structure and demographics are significantly associated with partial mortality of corals. Size, density, diversity and morphology all have different effects on partial mortality at the seven islands, atolls and reefs in NWHI. Mixed effects modeling in this study identifies the unique relationships each site has with partial mortality. This study provides comprehensive and novel insight on how hierarchical statistical modeling can be used to predict areas of vulnerability to coral disease using long-term monitoring data.

*Effects of Colony Size on Coral Health*

Levels of coral partial mortality are positively associated with coral colony size. Sites at higher latitudes (Kure, Midway and Pearl and Hermes atolls) had lower mean values in colony size, diversity and density than other sites (Figure 5, 6, 7). Lisianski Island and Maro Reef showed the highest mean values of colony size (Figure 5) and coral communities at French Frigate Shoals were predominantly occupied by large coral colonies. This was expected as the three sites previously mentioned are located centrally in the NWHI and are believed to have reached a climax state, thus exhibiting maximum values of demographics such as colony size, diversity, and density (Maragos et al. 2004, Aeby et al. 2011). The

results of this study support previous research that has shown colony size, species richness, and diversity decrease with increasing latitude within the NWHI (Maragos et al. 2004; Aeby et al. 2011). Colony size was strongly associated with partial mortality of corals (Figure 10). Larger coral colonies experienced higher levels of partial mortality, and this pattern persisted across sites, except for the Island of Lisianski where smaller corals showed higher partial mortality (Figure 11).

Small coral colonies dominated most of the communities surveyed in this study. Previous studies have shown that smaller colonies could be more severely affected by disease than larger coral colonies due to their circumference to surface area ratio (Meesters et al. 1996). This is due to the regeneration capabilities and life history processes of coral after partial mortality occurs. Larger lesions will take much more regeneration capabilities then smaller lesions. The amount of coral tissue that can be regenerated is determined by the lesion perimeter length and subsequently, the shape of a lesion (Meesters et al. 1997). Within the same time period, smaller coral colonies are more vulnerable to full mortality than partial mortality because of the lesion perimeter length compared to live tissue area (Meesters et al. 1997). This could explain why the smaller colonies observed in this study were observed to exhibit full colony mortality compared to partial mortality (Figure 11). The colony size frequencies of these coral communities can be an important factor in determining the overall health of each coral community. For future research, size frequency distributions of communities should be considered when studying coral health metrics.

*Effects of Diversity on Coral Health*

Partial mortality was also affected by coral species diversity in PMNM. Species diversity of coral communities were found to have a negative relationship with partial mortality in corals, with monotypic reefs exhibiting the highest values of partial mortality (Table 3, Figure 12). For most sites, the levels of partial mortality decreased as coral diversity increased (Figure 12). Layan was the only site that did not exhibit this trend, which could be due to the limited amount of surveys collected at this site compared to the other islands and atolls. This negative relationship between coral diversity and partial mortality could be due to the Dilution Effect of biodiversity on disease risk (Keesing et al. 2006). A previous study found that disease risk in the plant named Chiltepin increased with the reduction of plant species diversity due

to an increase of host plant species (Pagan et al. 2012). These associations between diversity and disease in other organisms could explain the negative trend we observed between diversity and partial mortality of corals in the NWHI.

The Hawaiian Archipelago spans about ten degrees of latitude and straddles the Tropic of Cancer. Thus, the northern half of the archipelago is technically out of the tropics. High latitude coral reefs are known for being isolated and having high levels of endemism (Friedlander et al. 2005; Aeby et al. 2011). Species diversity in the NWHI is lower in the high latitude atolls (Pearl and Hermes, Midway and Kure (Figure 6). It can be expected that partial mortality would be high at these sites (Figure 8). This could be due to environmental condition and the physiochemical characteristics of seawater at the higher latitudes. The cooler temperature causes slower growth rates that may be unable to keep pace with the subsidence in some taxa (Griggs 1982; Aeby et al. 2011). This could also be related to past mass bleaching disturbances that occurred at the high latitudes in 2002 and 2004 (Kenyon and Brainard 2006). Kure, Midway and Pearl and Hermes were strongly affected by bleaching and a large number of dominant coral species were obliterated (Kenyon and Brainard 2006). Subsequently some of these sites went through phase shifts from coral dominated to algae dominated (Kenyon and Brainard 2006). These communities could be experiencing low diversity and coral size due to the coral assemblage shifts after these disturbances. The frequency of disturbances these coral communities experienced could also explain the low amounts of diversity observed at the high latitudes.

In addition, the dominant species found at these sites may be determining the overall health of the communities. Certain coral species exhibit more of a tolerance to diseases than other species (Aeby 2004; Aeby et al. 2011, Keesing et al. 2010). For example, *Porites* species are dominant throughout the Hawaiian archipelago. Porites has shown the largest prevalence, widest distribution and highest number of coral diseases as compared to any other coral taxa in the Hawaiian Archipelago. Determining the dominant species and levels of coral diversity that are found in communities can help identify areas or regions that may be disproportionately vulnerable to future disturbances and diseases.

*Effects of Population Density on Coral Health*

The relationship between coral population density and partial mortality varied between sites throughout the PMNM (Table 3, Figure 10). Other factors such as size or diversity exhibited stronger associations with partial mortality than density. This was an interesting result because a positive relationship with density and prevalence of diseases, especially transmissible ones, has been demonstrated in many monotypic and diverse populations of corals (Bruno et al. 2007; Myers and Raymundo 2009). Disease emerges from complex interactions between disease host, agent, and environment (Lafferty and Holt 2003, Aeby et al. 2011). The density of the host agent has a major role in the severity and prevalence of coral diseases (Lafferty and Holt 2003). Areas of high coral cover are vulnerable to increasing prevalence of natural disturbance and disease. Coral species can also influence the amount of coral disease present. For example, studies investigating coral disease in Guam have shown host density to be associated with infectious disease prevalence, which resulted in *Acropora* and *Porites* species being more affected by disease than other species (Myers and Raymundo 2009). Species composition can heavily influence the relationship between coral density and disease, which could explain why sites throughout the NWHI are showing varied relationships between coral density and partial mortality.

This study documented a general trend of coral density decreasing northward along the NWHI archipelago, which was expected (Figure 7). High latitude sites such as Kure, Midway and Pearl and Hermes Atoll had the lowest mean values of coral density. The frequency of disturbances in the past, and unfavorable environmental conditions such as lower seawater temperature seen in the high latitudes, could be contributing to the low observed values of coral density (Kenyon and Brainard 2006). Coral species all have different growth rates and experiencing environmental stress, such as decreased temperature and island subsidence, growth rates can be even more reduced (Griggs 1982). All these factors may be synergistically exacerbating one another and may explain the low values in colony size, diversity and density at these high latitude sites.

Interesting results were found at Midway, where a strong negative relationship between partial mortality and density was observed(Figure 13). Midway had the lowest overall colony density values and smaller-sized coral colonies, yet the corals found at Midway showed very high percentages of partial mortality (Figure 11 and 13). Partial mortality decreased with an increase in coral density at sites

throughout this atoll (Figure 13). This could be due to the dominant coral species found at Midway, *Montipora* and *Porites* (Aeby 2006). These species are very vulnerable to diseases and disturbances (Aeby 2006). In order to have a better grasp on how density is associated with partial mortality, further research and additional surveys should be added to the mixed effect model. High density sites are vulnerable during coral disease outbreaks and it is important to be able to identify areas of vulnerability to predict how coral communities in the Monument may respond to future disturbances.

*Effects of Morphology on Coral Health*

There was a significant difference found in partial mortality between morphologies, with complex morphologies exhibiting the highest partial mortality values (Table 2, Figure 9). Branching, mounding lobate, and columnar morphologies showed high partial mortality values (Figure 9), whereas plating and encrusting morphologies showed the lowest partial mortality values. Our findings are in-line with previous research that has shown complex coral morphologies to be more susceptible to disturbance and disease than slow-growing corals that exhibit massive morphologies (Gates & Ainsworth, 2011; Woesik et al., 2011). Previous research has also examined the effects of coral morphologies with vertical and horizontal orientation on growth anomalies. This research found that growth anomalies was higher in colonies with horizontal orientation then compared to vertical orientation, this could be due to the coral's exposure to light, sedimentation and water flow (Burns et al. 2011). Morphologies similar to branching and columnar are commonly found in deeper depths or areas with low wave energy (Dollar 1982). Water flow is essential to the overall health of a coral colony by providing mixing of nutrients, gas and removal of sedimentation (Lesser et al. 2007; Burns et al. 2011). This allows corals to increase their photosynthesis and respiration. A decrease in water flow and increase environmental stressors can reduce coral immune system function, leading to increases in disease (Lesser et al. 2007; Burns et al. 2011). The twelve different morphologies all exhibited varying association with partial mortality. (Table 3, Figure 10). Knowing the morphotypes or morphologies that are only found within certain species can be to advantage when depicting areas of vulnerability. This study shows specific morphotypes are more susceptible to coral disease than other morphotypes. Coral genera like *Porites* or *Acropora* are known to be susceptible to multiple diseases and have specific morphotypes (Meesters et al. 2006; Aeby et al. 2011). Collating

our understanding of coral community structure with this knowledge of morphology driven disease susceptibility can further the ability of scientists and managers to pin-point areas of high vulnerability to disease and disturbance using reef monitoring data. This study also shows the utility of comprehensive coral community characterization and supports the need for detailed monitoring data to assess how reef systems may respond to future climate conditions.

## Conclusion

This study demonstrates how community structure and demographics affect partial mortality in corals in the NWHI. Studying the coral reef communities in the PMNM provides valuable insight into reef ecology from areas not exposed to direct human stressors. This system is ideal for examining how coral reefs communities naturally cope with disease and disturbances. Larger corals experienced high amounts of partial mortality lesions. Monotypic communities are more susceptible to partial mortality then diverse communities. Density was associated with partial mortality in corals, yet the relationships varied at each site. Lastly, morphology of corals had varying associations with partial mortality. Complex morphologies showed the highest partial mortality values. It's important to acknowledge each one of these parameters of coral community structure has a different magnitude of effect on partial mortality. The frequency of past disturbances and environmental conditions at the high latitude sites have led to a reduced fitness in the coral colonies on these reef systems. Knowing the history of these sites can help us understand how these communities have been shaped over the years. Therefore, the findings in this research can help direct management in future areas of vulnerability to degraded coral health for PMNM. This research provides an example of how long-term monitoring data can be used in important ecological hypotheses. Finally, this type of hierarchical statistical modeling can be use with any set of monitoring data to provide information toward helping managers better understand coral health in their communities.

List of Tables

**Table 1. Survey summary data. Total number of colonies with partial mortality presence for each site within NWHI and the years surveyed. Only coral colonies with partial mortality were used for statistical analyses.**

| Site | Total Number of Colonies | Year |
|---|---|---|
| French Frigate Shoals | 1667 | 2014-2016 |
| Maro Reef | 362 | 2015-2016 |
| Laysan Island | 33 | 2015-2016 |
| Lisianski Island | 1003 | 2014-2016 |
| Pearl and Hermes Atoll | 766 | 2015-2016 |
| Midway Atoll | 120 | 2014-2016 |
| Kure Atoll | 498 | 2015-2016 |

**Table 2. List of coral morphologies surveyed between years of 2014-2016 in NWHI.**

| Coral Morphology | Code | Complexity Rating |
|---|---|---|
| Branching | BR | 1 |
| Columnar | CO | 2 |
| Knobby | KN | 3 |
| Mounding Lobate | ML | 4 |
| Mounding | MD | 5 |
| Tabulate | TB | 6 |
| Plating | PL | 7 |
| Laminar | LM | 8 |
| Foliose | FO | 9 |
| Encrusting Mounding | EM | 10 |
| Encrusting Flat | EF | 11 |
| Encrusting Columnar | EC | 12 |

**Table 3. Summary results for best fit model the effects of demographics on Partial Mortality in NWHI. Fixed effects are shown in this table and all variables were standardized. P < 0.05 = **, P <0.001= **.**

| Fixed Effects | Estimate Value | Std. Error | DF | t-value | p-value |
|---|---|---|---|---|---|
| (Intercept) | -0.13 | 0.50 | 4427 | -0.24 | 0.80 |
| Size | 0.02 | 0.00 | 4427 | 12.81 | 0.00 ** |
| Diversity | -0.33 | 0.07 | 4427 | -4.54 | 0.00 ** |
| Density | -0.03 | 0.01 | 4427 | -4.55 | 0.00 ** |
| Depth | 0.00 | 0.00 | 4427 | 0.15 | 0.87 |
| *Morphology (Reference is Branching)* | - | - | - | - | - |
| Columnar | -0.56 | 0.18 | 4427 | -3.11 | 0.00 ** |
| Encrusting Columnar | -1.99 | 0.30 | 4427 | -6.60 | 0.00 ** |
| Encrusting Flat | -1.27 | 0.13 | 4427 | -9.28 | 0.00 ** |
| Encrusting Mounding | -1.08 | 0.07 | 4427 | -15.22 | 0.00 ** |
| Foliose | -1.66 | 0.22 | 4427 | -7.61 | 0.00 ** |
| Knobby | -1.05 | 0.13 | 4427 | -8.36 | 0.00 ** |
| Laminar | -1.36 | 0.16 | 4427 | -8.39 | 0.00 ** |
| Mounding | -0.83 | 0.09 | 4427 | -9.47 | 0.00 ** |
| Mounding Lobate | 0.24 | 0.15 | 4427 | 1.64 | 0.10 * |
| Plating | -1.54 | 0.19 | 4427 | -8.19 | 0.00 ** |
| Tabulate | -1.66 | 0.31 | 4427 | -5.44 | 0.00 ** |

**Table 4. Summary results for best fit model the effects of demographics on Partial Mortality in NWHI. Random effects are shown in this table and all variables were standardized.**

| Random Effects | Std. Dev. | Corr. |
|---|---|---|
| Formula: ~1 + Depth \| fISLANDCODE | - | - |
| (Intercept) | 1.25 | - |
| Depth | 0.02 | -0.86 |
| Residuals | 1.69 | - |

List of Figures

**Figure 1. Example of partial mortality found on *Porites lobata* colony. The area contained within the solid black line is old mortality, and the area between the dashed black line is recent mortality.**

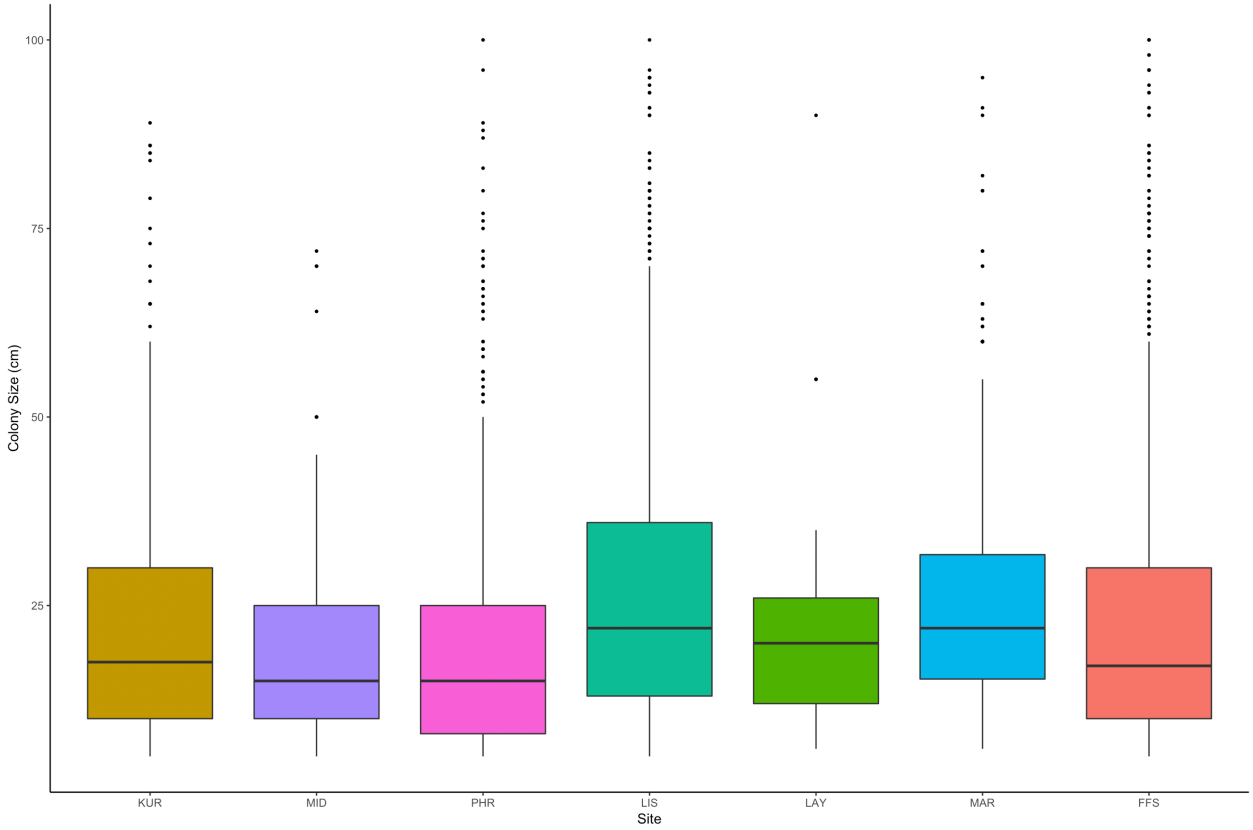


**Figure 2. Average partial mortality among the seven sites surveyed for the Rapid Assessment and Monitoring Program within the PMNM during 2014-2016.**

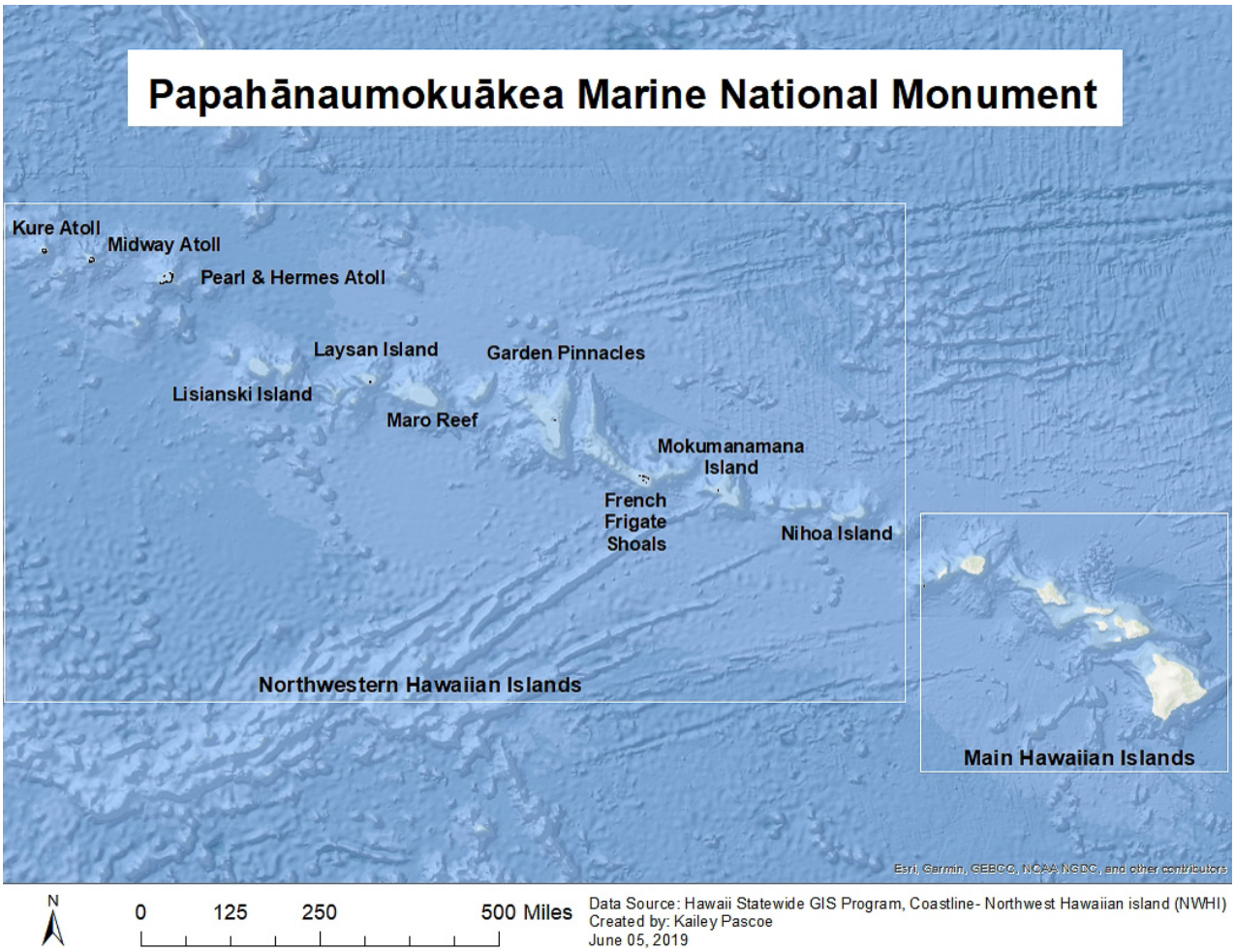


**Figure 3. Map of the Papahānaumokuākea Marine National Monument. The Monument encompasses 10 islands, atolls, reefs and banks. This project analyzed data from French Frigate Shoals, Maro Reef, Laysan Island, Lisianski Island, Pearl and Hermes Atoll, Midway Atoll and Kure Atoll.**

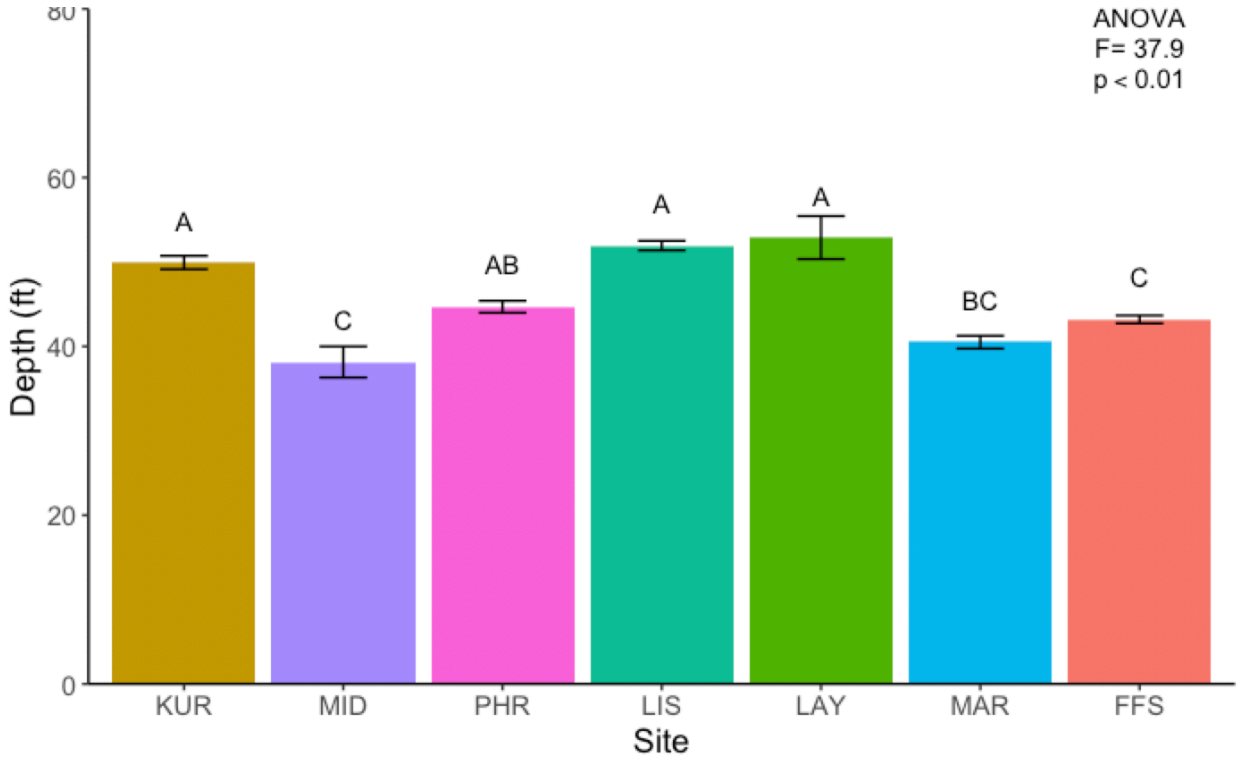


**Figure 4. Average survey depths (ft) among the sites used for this study. A, B, and C denote groupings that were identified by statistical significance using Tukey HSD pairwise comparisons ($p<0.05$). Error bars represent the standard deviation.**

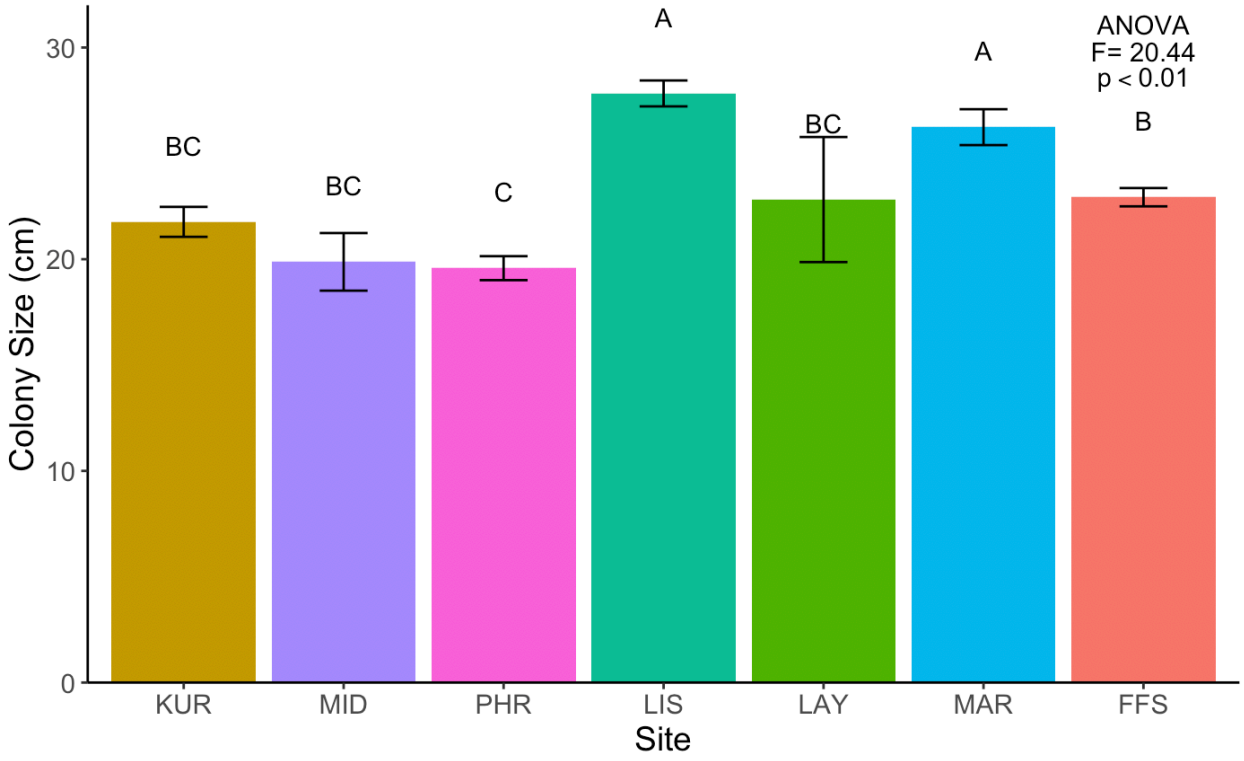


**Figure 5. Average values of coral colony size (cm) among the sites used in this study. A, B, and C denoted groupings identified by statistical significance using Tukey HSD pairwise comparisons ($p<0.05$). Error bars represent the standard deviations.**

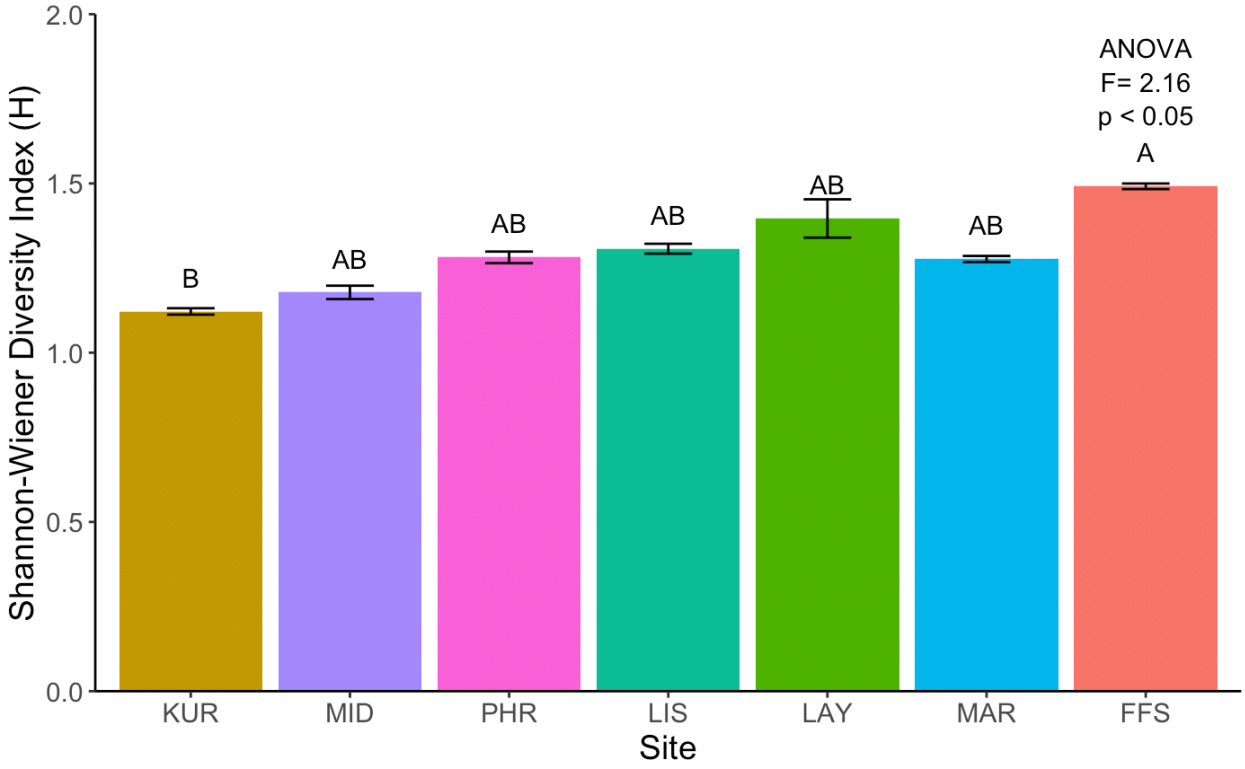


**Figure 6. Comparison of Shannon-Weiner diversity index using species richness and abundance of each species to calculate how evenly distributed species are at each study site. Denoted groupings were identified by statistical significance in Tukey HSD ($p<0.05$). Error bars represent the standard deviations.**

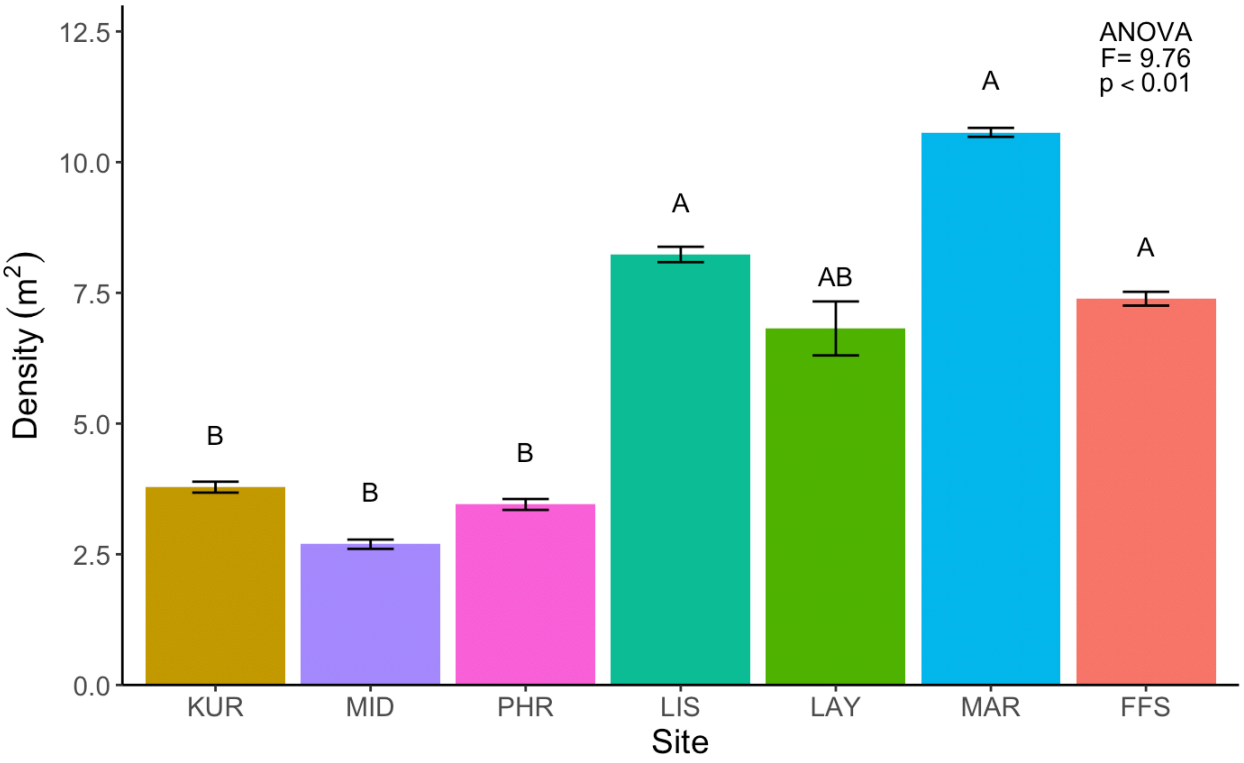


**Figure 7. Comparison of density ($m^2$) averages among sites. Denoted groupings were identified by statistical significance in Tukey HSD ($p<0.05$). Error bars represent the standard deviations.**

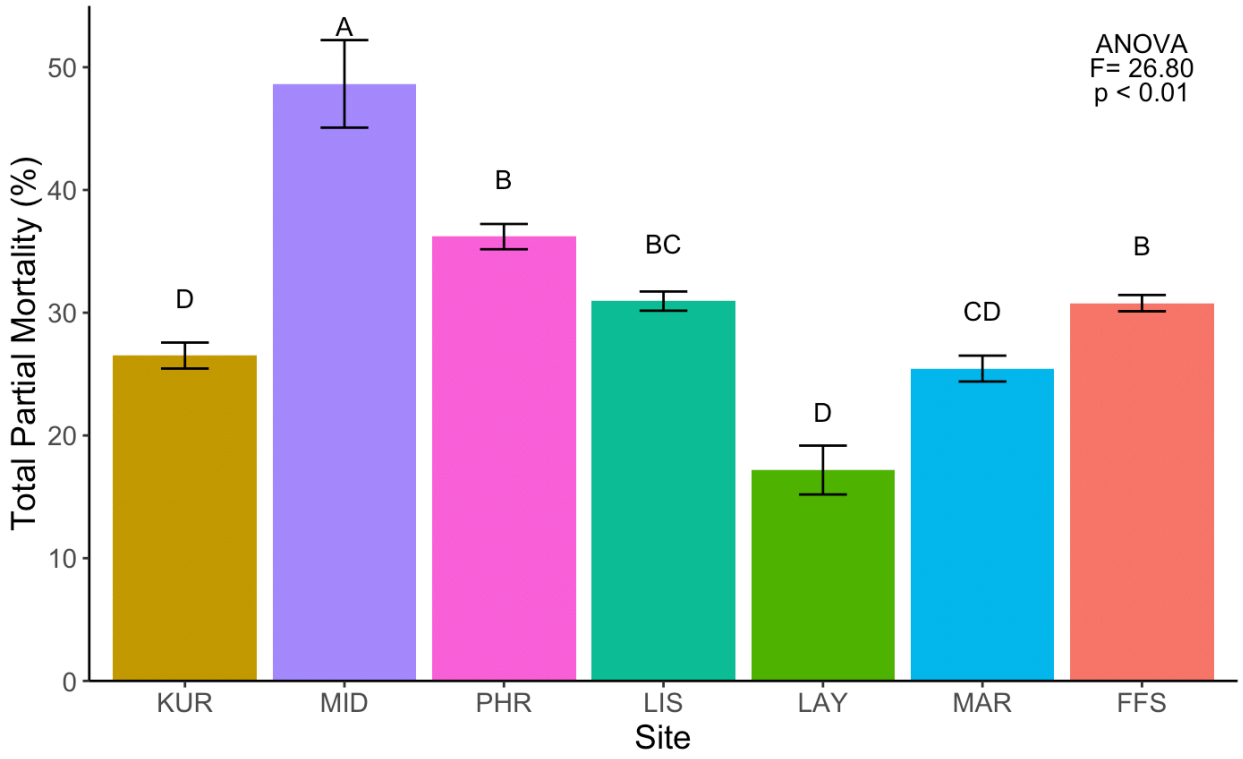


**Figure 8. Comparison of mean partial mortality of corals among sites. Denoted groupings were identified by statistical significance in Tukey HSD ($p<0.05$). Error bars represent the standard deviations.**

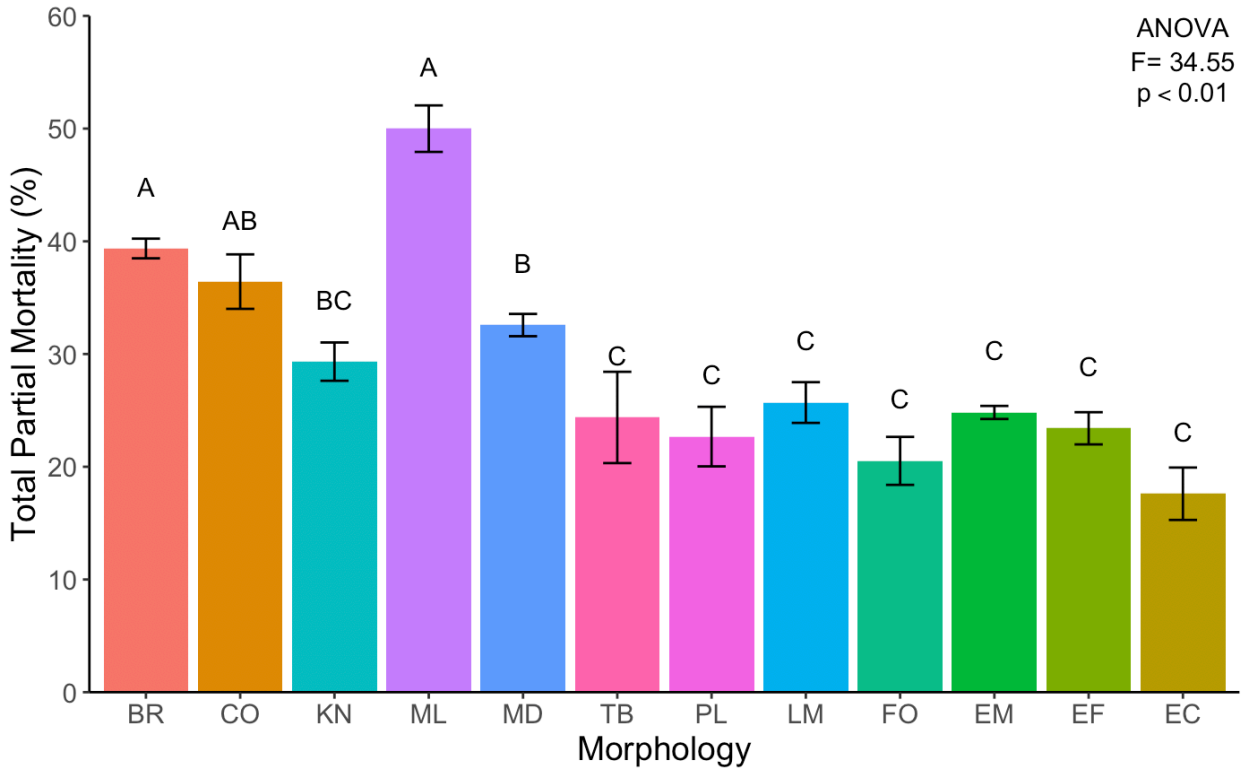


**Figure 9. Comparison of average partial mortality among coral morphologies. Denoted groupings were identified by statistical significance in Tukey HSD ($p<0.05$).**

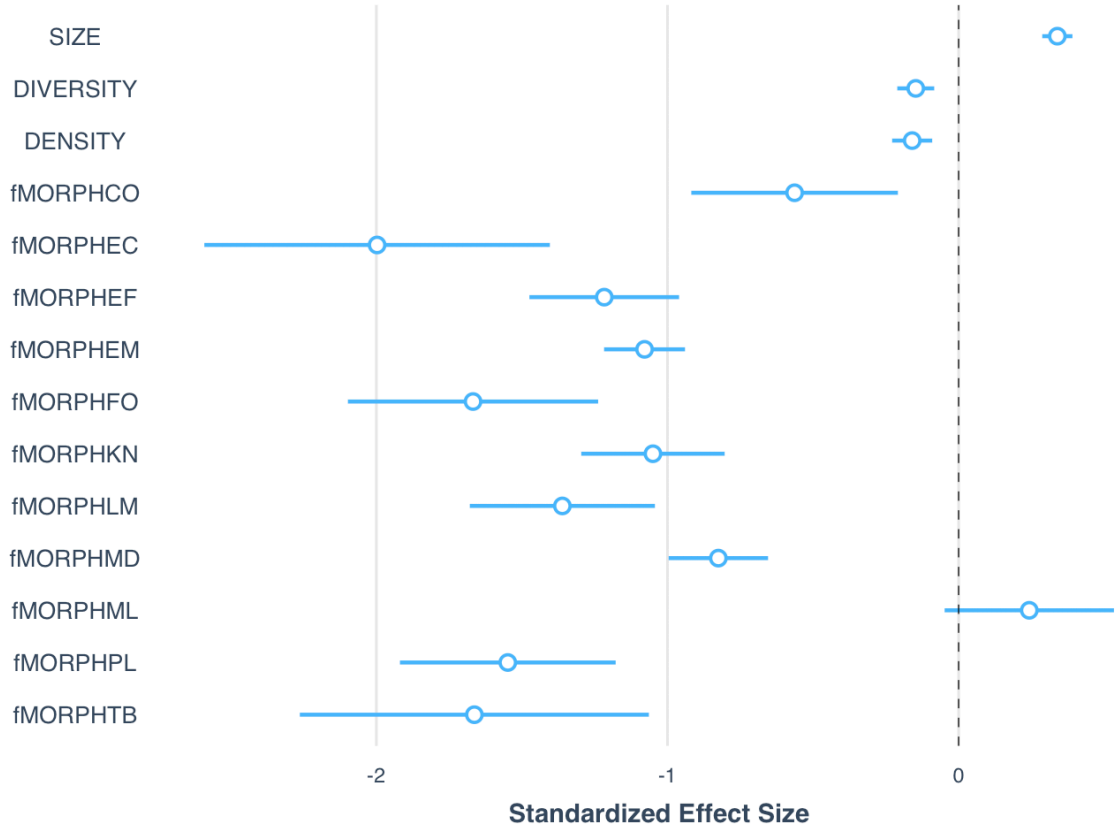


**Figure 10. Relative effect of demographics parameters on partial mortality of corals. Standardized effect sizes for partial mortality (Table. 5). Predictor variables are colony size, coral diversity, coral density, and morphologies found within dataset. Values are effect sizes ± 95% Confidence interval.**

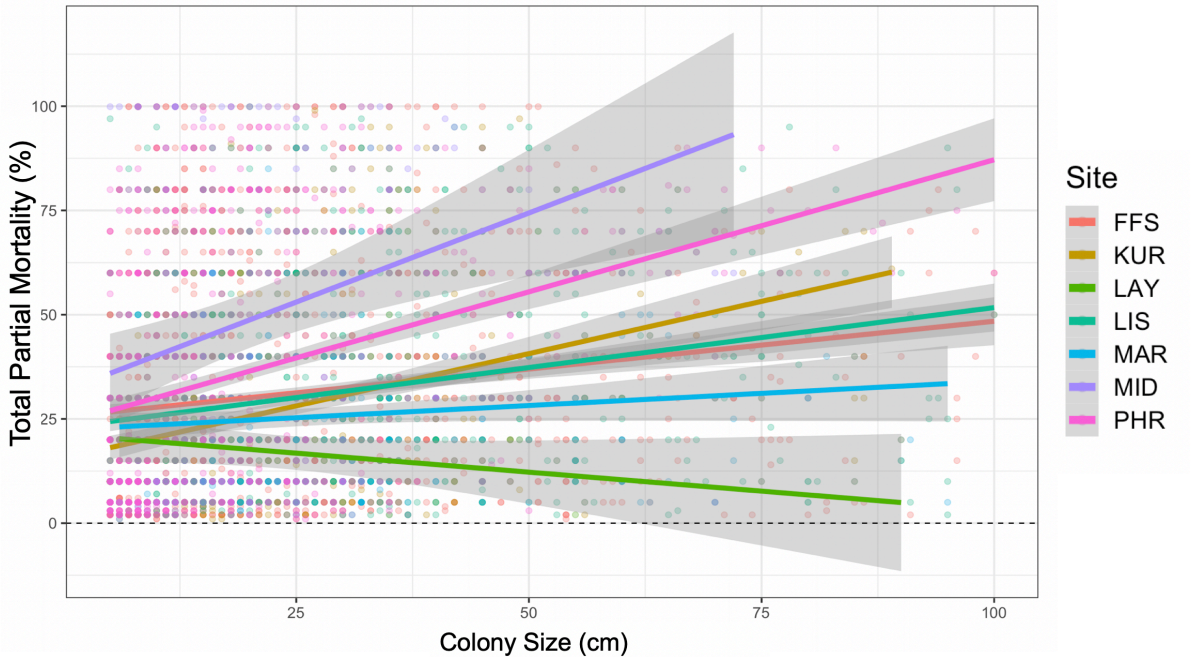


**Figure 11. Relationships between size and average partial mortality (logit transformation) among all sites in the NWHI. This figure shows the different linear relationships between sites. All data points are plotted along with best-fit lines for each site and shaded 95% confidence intervals.**

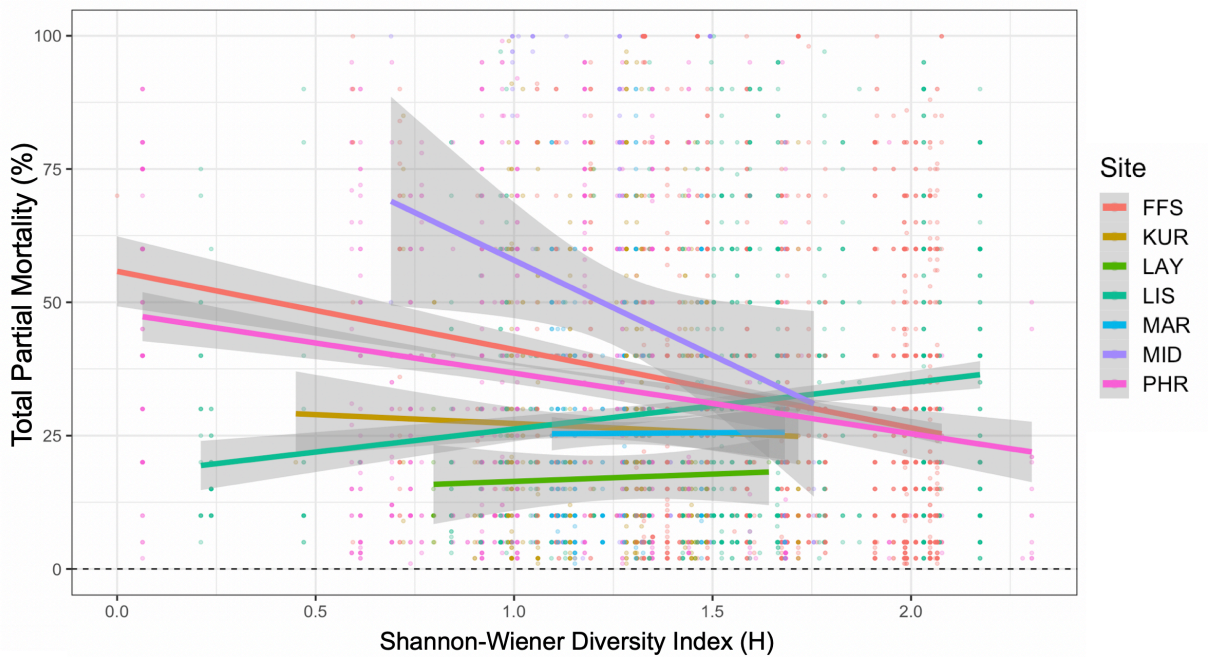


**Figure 12. Relationships between diversity and average partial mortality (logit transformation) among all sites in the NWHI. This figure shows the different linear relationships between sites. All data points are plotted along with best-fit lines for each site and shaded 95% confidence intervals.**

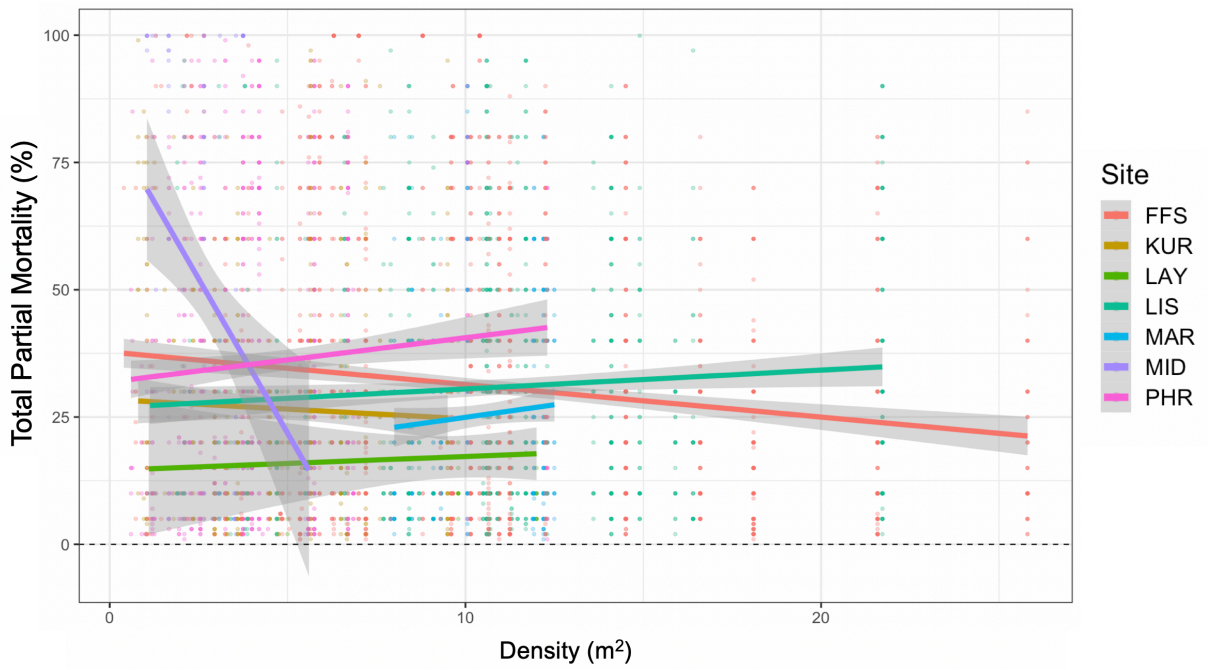


**Figure 13. Relationships between density and average partial mortality (logit transformation) among all sites in the NWHI. This figure shows the different linear relationships between sites. All data points are plotted along with best-fit lines for each site and shaded 95% confidence intervals.**

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Appendix A

**Table 1. Coral species that were surveyed between 2014-2016 and used in statistical analyses.**

| Coral Species | |
|---|---|
| *Acropora spp.* | *Pocillopora damicornis* |
| *Acropora cytherea* | *Pocillopora eydouxi* |
| *Acropora humilis* | *Pocillopora ligulata* |
| *Acropora paniculata* | *Pollicopora meandrina* |
| *Cyphastrea ocellina* | *Porites annae* |
| *Leptastrea bewickensis* | *Porites bernardi* |
| *Leptoseris spp.* | *Porites brighami* |
| *Leptastrea pupurea* | *Porites compressa* |
| *Montipora capitata* | *Porites evermani* |
| *Montipora flabellata* | *Porites lichen* |
| *Montipora incrasata* | *Porites lobata* |
| *Montipora patula* | *Porites lutea* |
| *Montipora turgescens* | *Porites duerdeni* |
| *Pavona duerdeni* | *Porites spp.* |
| *Pavona maldivensis* | *Porites solida* |
| *Pavona varians* | *Psammocora haimeana* |
| *Pocillopora capitata* | *Psammocora stellata* |
| *Pocillopora spp.* | |

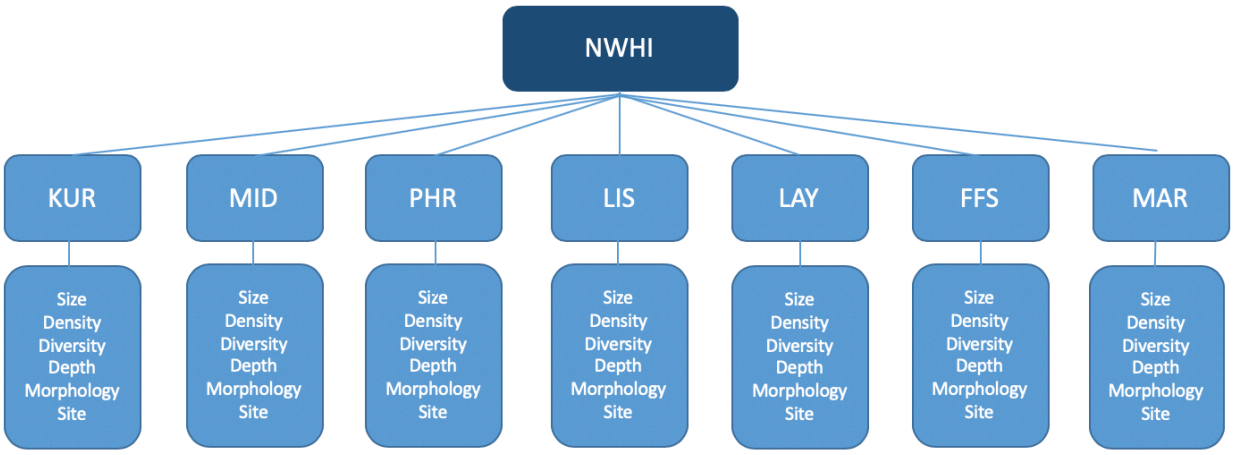



**Figure 1. Nested structure of the RAMP data collected from the Northwestern Hawaiian Islands (NWHI). Mixed effect models incorporate two types of parameters, fixed and random variables. Fixed variables are unknown constants to be estimated from the data. Random effects govern the variance-covariance structure of the response variable (% partial mortality). Fixed effects are informative factor levels (size, density, diversity, species, morphology), while random effects often have uninformative factor levels (site).**

Appendix B

**Top-Down Model Selection in R software using *nlme* package**

**Step 1: This type of strategy indicates to start with as many explanatory variables are possible in the fixed component. For this model, started with depth, size, density, diversity and morphologies. This will be completed in the three different methods, gls, random intercept model, and random slope and intercept model. The first three models will be completed with the Restricted Maximum likelihood (REML). Looking at the summary values in Table 1., The random slope and intercept model is therefore thee preferred option due to the low AIC values.**

**Table 1. Top-Down Model Selection used with *nlme* package on R Software. Shown is the comparison between Restricted Maximum Likelihood (REML) and Maximum Likelihood estimates between models (ML). The last modeled listed showed the lowest AIC and BIC scores and the method used for the model was random intercept and slope model. * showing the lowest AIC and BIC values**

| Method | Top-Down Model Selection | AIC | BIC | logLik |
|---|---|---|---|---|
| REML | gls(LN_TPM~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH) | 13216.51 | 13402.64 | -6579.25 |
| REML | lme(LN_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data = Part_Mort_NWHI, random = ~1 \| fISLANDCODE | 13174.12 | 13366.67 | -6557.06 |
| **REML** | **lme(LN_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data= Part_Mort_NWHI, random = ~1 + DEPTH \| fISLANDCODE** | **13150.12*** | **13355.51*** | **-6543.061** |
| ML | gls(LN_TPM~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH | 12972.17 | 13158.49 | -6457.085 |
| ML | lme(LN_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data = Part_Mort_NWHI, random = ~1 \| fISLANDCODE | 12934.11 | 13126.85 | -6437.055 |
| ML | lme(LN_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data = Part_Mort_NWHI, random = ~1 + DEPTH \| fISLANDCODE | 12913.28* | 13118.86* | -6424.638* |

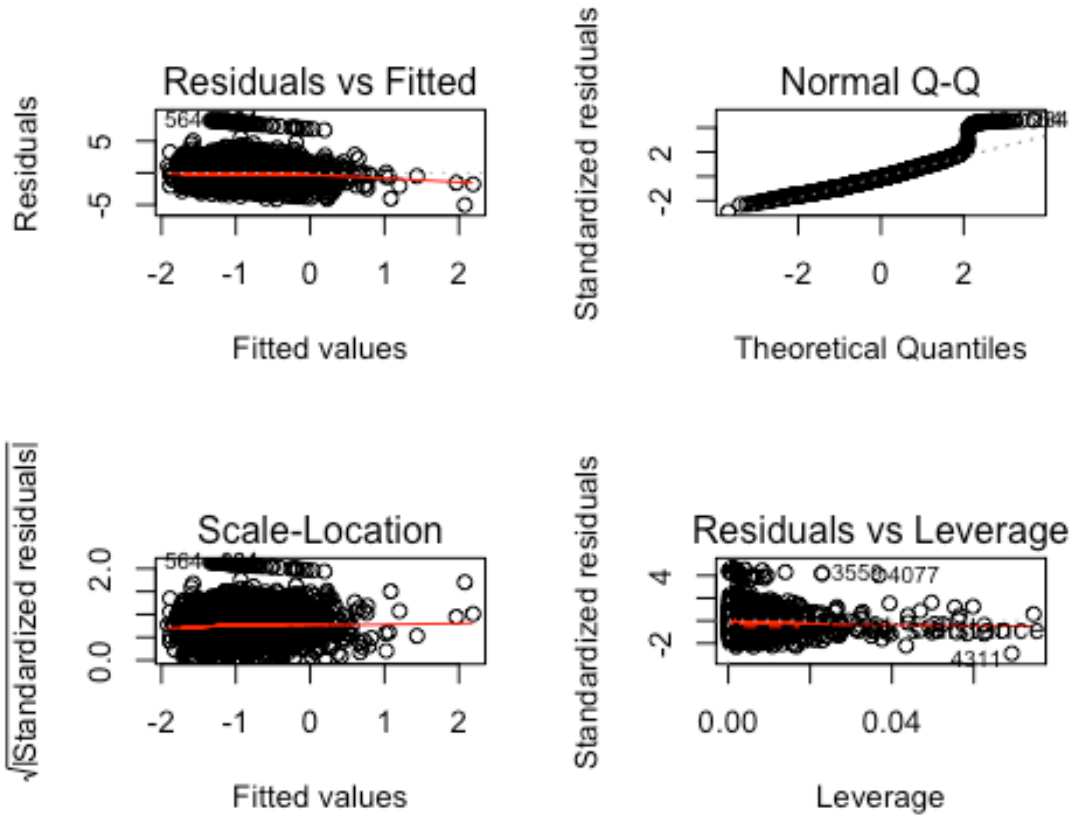
```
ME1 <- gls(Logit_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY * + fMORPH, method = "REML",
data = Part_Mort_NWHI)

ME2 <- lme(Logit_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data = Part_Mort_N
WHI, random = ~1 | fISLANDCODE, method = "REML")

ME3 <- lme(Logit_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data= Part_Mort_N
WHI, random = ~1 + DEPTH | fISLANDCODE, method = "REML")

summary(ME1)  # AIC = 17744.86



summary(ME2)  # AIC = 17575.64



summary(ME3)  # AIC = 17534.39**
```

**Step 2: Compare restricted maximum likelihood estimation (REML) to maximum liklihood (ML)**

```
ME4 <- gls(Logit_TPM~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, method = "ML", data
= Part_Mort_NWHI)

ME5 <- lme(Logit_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data = Part_Mort_N
WHI, random = ~1 | fISLANDCODE, method = "ML")

ME6 <- lme(Logit_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data = Part_Mort_N
WHI, random = ~1 + DEPTH | fISLANDCODE, method = "ML")

summary(ME4)   # AIC = 17535.28

summary(ME5)   # AIC = 17371.14

summary(ME6)   # AIC = 17333.29
```

**Step 3: Create linear regression model to compare to mixed effects REML model**

```
M.lm <- lm(Logit_TPM ~ DEPTH * SIZE * DENSITY * DIVERSITY, data = Part_Mort_NWHI)

par(mfrow=c(2,2))

plot(M.lm)
```



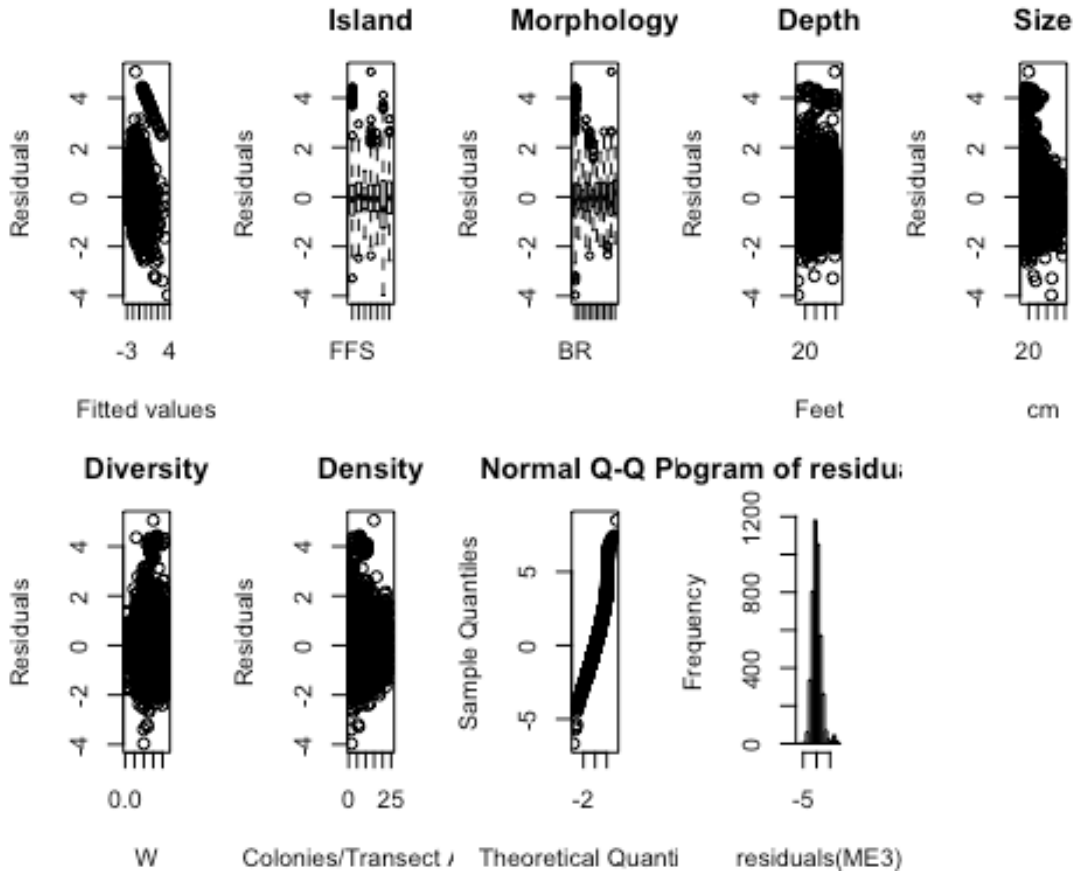

**Step 4:** Fit the Model with GLS to compare to linear regression model

```
Form <- formula(Logit_TPM ~ DEPTH * SIZE * DENSITY * DIVERSITY, data= Part_Mort_NWHI)

M.gls <- gls(Form, data=Part_Mort_NWHI)

# Compare two compare GLS with full REML model to assess need of random intercept

anova(M.gls, ME3)

## Warning in nlme::anova.lme(object = M.gls, ME3): fitted objects with
## different fixed effects. REML comparisons are not meaningful.

##       Model df      AIC      BIC    logLik   Test  L.Ratio p-value
## M.gls     1 17 18045.32 18154.07 -9005.662
## ME3       2 31 17534.38 17732.61 -8736.193 1 vs 2 538.9382  <.0001
```

**Step 5:** Check residuals of full REML mixed-effects model

```
op <- par(mfrow = c(2,5), mar = c (4, 4, 3, 2))
E1 <- resid(ME3, type = "normalized")
F1 <- fitted(ME3)
MyYlab <- "Residuals"
```

```
plot(x = F1, y = E1, xlab = "Fitted values", ylab = MyYlab)
boxplot(E1 ~ fISLANDCODE, data = Part_Mort_NWHI, main = "Island", ylab = MyYlab)
boxplot(E1 ~ MORPH, data = Part_Mort_NWHI, main = "Morphology", ylab = MyYlab)
plot(x = Part_Mort_NWHI$DEPTH, y = E1, ylab = MyYlab, main = "Depth", xlab = "Feet")
plot(x = Part_Mort_NWHI$SIZE, y = E1, ylab = MyYlab, main = "Size", xlab = "cm")
plot(x = Part_Mort_NWHI$DIVERSITY, y = E1, ylab = MyYlab, main = "Diversity", xlab = "W")
plot(x = Part_Mort_NWHI$DENSITY, y = E1, ylab = MyYlab, main = "Density", xlab = "Colonies/Transect Area")
qqnorm(residuals(ME3))
hist(residuals(ME3))
```

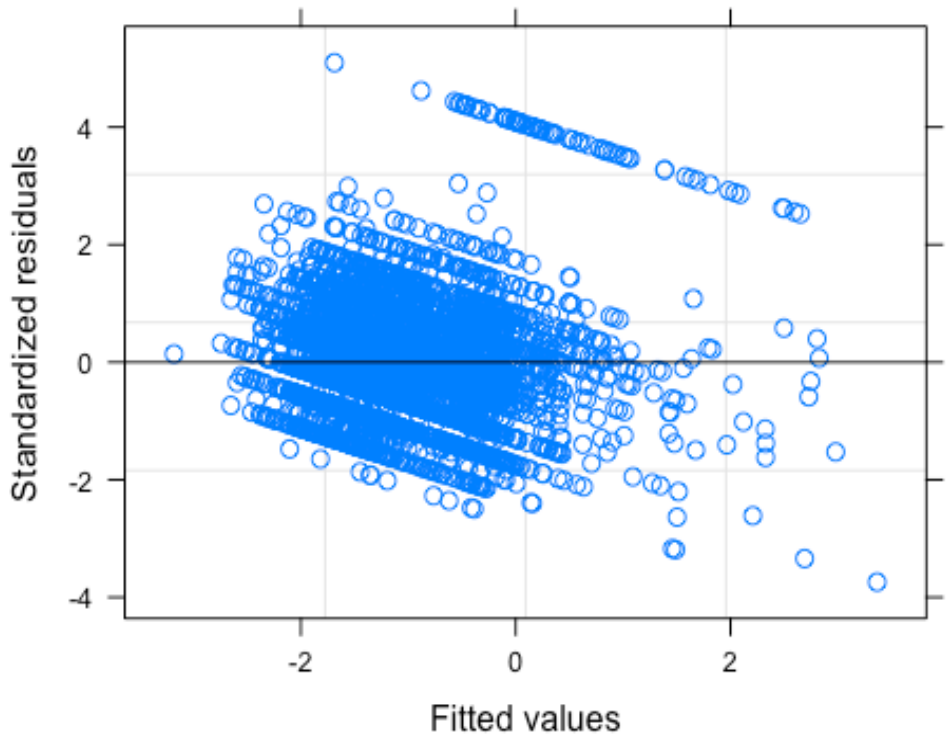



**Step 6:** Explore best model according to AIC and p-values between each model (Maximum Liklihood with Random Intercept Model)

```
ME7 <- lme(Logit_TPM ~ 1 + DEPTH * SIZE * DENSITY * DIVERSITY + fMORPH, data = Part_Mort_NWHI, random = ~1 + DEPTH | fISLANDCODE, method = "ML") #BEST ML model M6

Form1 <- formula(Logit_TPM ~ DEPTH * SIZE * DENSITY *  DIVERSITY + fMORPH)

M7.full <- lme(Form1, random = ~1 + DEPTH | fISLANDCODE, method = "ML", data = Part_Mort_NWHI)

summary(M7.full)
```

```
M7.A <- update(M7.full, .~. -DEPTH:SIZE, -DEPTH:DIVERSITY, -DEPTH:DENSITY, -SIZE:DENSITY, -D
IVERSITY:DENSITY, -DEPTH:SIZE:DIVERSITY, -DEPTH:SIZE:DENSITY, -DEPTH:DIVERSITY:DENSIT
Y, -SIZE:DIVERSITY:DENSITY, -DEPTH:SIZE:DIVERSITY:DENSITY)

anova(M7.full, M7.A)  # Drop interactions terms as they are not significant

##        Model df      AIC      BIC    logLik   Test   L.Ratio p-value
## M7.full     1 31 17333.29 17531.70 -8635.645
## M7.A        2 30 17331.42 17523.43 -8635.708 1 vs 2 0.1250449  0.7236

Form2 <- formula(Logit_TPM ~ DEPTH + SIZE + DENSITY + DIVERSITY + fMORPH)

M7.full2 <- lme(Form2, random = ~1 + DEPTH | fISLANDCODE, method = "ML", data = Part_Mort_N
WHI)

M7.2A <- update(M7.full2, .~. - DENSITY)

M7.2B <- update(M7.full2, .~. - DIVERSITY)

anova(M7.full2, M7.2A) # Drop Density as it is not significant p= <0.0001

##        Model df      AIC      BIC    logLik   Test  L.Ratio p-value
## M7.full2     1 20 17344.94 17472.95 -8652.469
## M7.2A        2 19 17363.30 17484.91 -8662.651 1 vs 2 20.36436  <.0001

anova(M7.full2, M7.2B) # Keep Diversity as it is significant p= <0.0001

##        Model df      AIC      BIC    logLik   Test  L.Ratio p-value
## M7.full2     1 20 17344.94 17472.95 -8652.469
## M7.2B        2 19 17363.51 17485.12 -8662.757 1 vs 2 20.57521  <.0001

Form3 <- formula(Logit_TPM ~ DEPTH + SIZE + DIVERSITY + DENSITY + fMORPH)

M7.full3 <- lme(Form3, random = ~1 + DEPTH | fISLANDCODE, method = "ML", data = Part_Mort_N
WHI)

M7.3A <- update(M7.full3, .~. - DEPTH)

M7.3B <- update(M7.full3, .~. - SIZE)

M7.3C <- update(M7.full3, .~. - fMORPH)

anova(M7.full3, M7.3A) # Depth as it is not significant p= 0.8544, but need to keep because random
factor.

##        Model df      AIC      BIC    logLik   Test    L.Ratio p-value
## M7.full3     1 20 17344.94 17472.95 -8652.469
## M7.3A        2 19 17342.97 17464.58 -8652.486 1 vs 2 0.03365383  0.8544

anova(M7.full3, M7.3B) # Keep Size as it is significant p= <0.0001

##        Model df      AIC      BIC    logLik   Test  L.Ratio p-value
## M7.full3     1 20 17344.94 17472.95 -8652.469
## M7.3B        2 19 17504.62 17626.23 -8733.312 1 vs 2 161.6862  <.0001

anova(M7.full3, M7.3C) # Keep Morphology as it is significant p= <0.0001
```

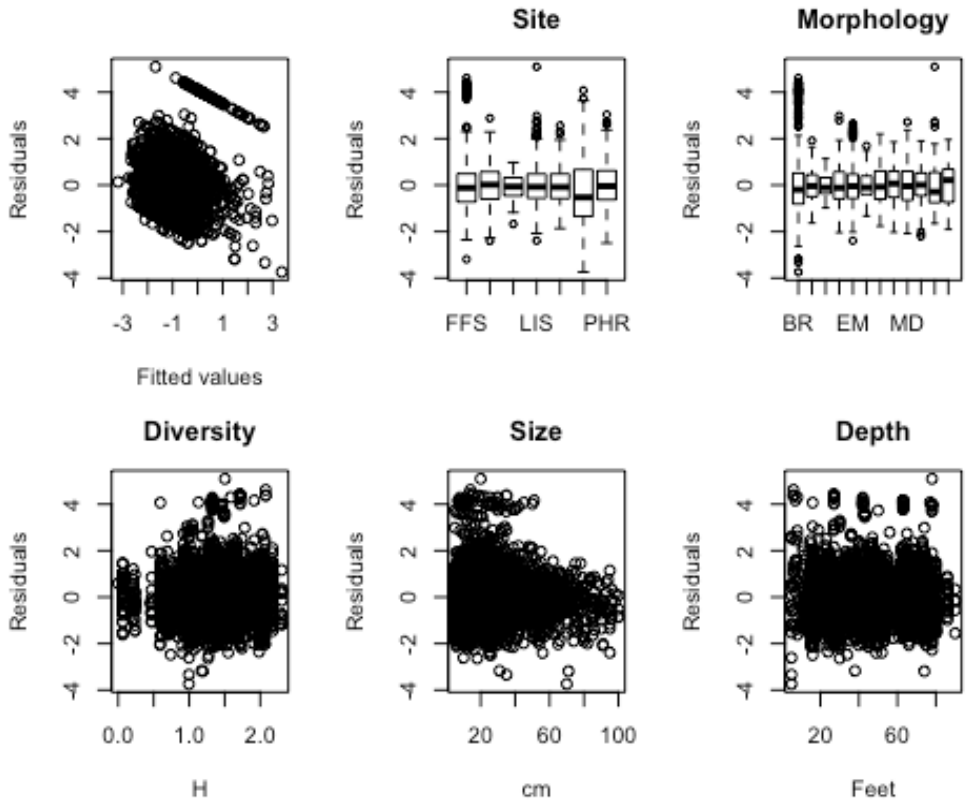
```
##         Model df      AIC      BIC    logLik   Test  L.Ratio p-value
## M7.full3     1 20 17344.94 17472.95 -8652.469
## M7.3C        2  9 17704.22 17761.82 -8843.108 1 vs 2 381.2784  <.0001

# Refit the model with REML (because mixed model, don't want random factors to affect ML)

ME7 <- lme(Logit_TPM ~ 1 + DEPTH +  SIZE + DIVERSITY + DENSITY + fMORPH, data = Part_Mort_
NWHI, random = ~1 + DEPTH | fISLANDCODE, method = "REML")

summary(ME7)

plot(ME7)
```




**Step 8: Plot the residuals of the best-fit model**

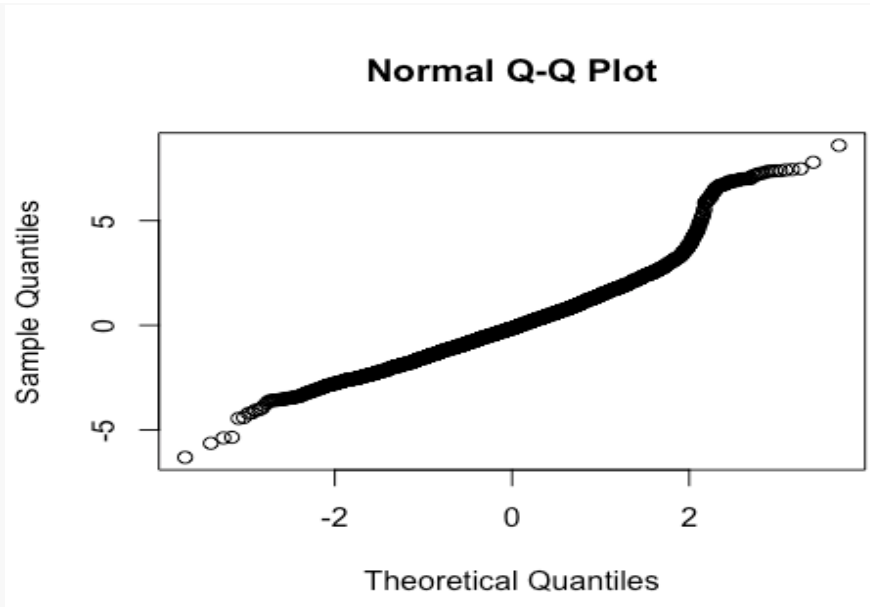
```
par(op)

E1 <- resid(ME7, type = "normalized")
F1 <- fitted(ME7)
op <- par(mfrow = c(2,3), mar = c (4, 4, 3, 2))
MyYlab <- "Residuals"
plot(x = F1, y = E1, xlab = "Fitted values", ylab = MyYlab)
boxplot(E1 ~ fISLANDCODE, data = Part_Mort_NWHI, main = "Site", ylab = MyYlab)
boxplot(E1 ~ MORPH, data = Part_Mort_NWHI, main = "Morphology", ylab = MyYlab)
plot(x = Part_Mort_NWHI$DIVERSITY, y = E1, ylab = MyYlab, main = "Diversity", xlab = "H")
```

```
plot(x = Part_Mort_NWHI$SIZE, y = E1, ylab = MyYlab, main = "Size", xlab = "cm")
plot(x = Part_Mort_NWHI$DEPTH, y = E1, ylab = MyYlab, main = "Depth", xlab = "Feet")
```




**Step 9: Plot normality of residuals with line and histogram**

```
qqnorm(residuals(ME7))
```



```
hist(residuals(ME7))
```