AN ABSTRACT OF THE THESIS OF David Ben Lacapa Benavente for the Master of Science in Biology presented April 17, 2014.

Title: TEMPORAL AND SPATIAL CHARACTERIZATION OF LAOLAO BAY CORAL-REEF FISH ASSEMBLAGES: STATUS AND FUNCTION

Approved: _____
               Peter C. Houk, Chairman, Thesis Committee

Laolao Bay represents a culturally and economically important natural resource on Saipan, Commonwealth of the Northern Mariana Islands (CNMI). This study used a unique historical baseline to examine how coral reef assemblages have shifted across the bay over the past two decades. Subsequently, the study also examined the plausible drivers of change. Initial analyses found a significant decrease in functional, food fish densities for all sites across the bay. This decline mainly consisted of reductions in the majority of large-bodied herbivores as well as secondary consumers. The declines in larger-bodied fish groups were accompanied by a shift in dominance to smaller-bodied counterparts; mainly opportunistic parrotfishes and surgeonfishes that rapidly respond to disturbances and altered environments, yet have limited functional roles due to their smaller adult body sizes. When grouping sites across the bay, these generalized trends were due to a reduction in the density of several species (*Monotaxis grandoculus*, *Naso unicornis*, *Naso lituratus*, *Chlorurus sordidus*, *Scarus rubroviolaceus*, and other mixed acanthurids), and the spatially-inconsistent increase in density in some species of

rabbitfish (*Siganus* spp.), a small-bodied grouper (*Cephalopholis urodeta),* and mixed small-bodied parrotfishes besides *Chlorurus sordidus*). Unexpectedly, depth (15m as compared to 5m) did not offer refuge for food fish populations. Coral assemblages also declined markedly across Laolao Bay over the past 20 years. Most sites had a significant reduction in mean colony sizes, and a shift in species assemblages to tolerant assemblages dominated by smaller colonies offering less reef architecture. Interestingly, the decline in both coral and fish assemblages was not spatially consistent across Laolao, with gradients in wave exposure, watershed geology, and water quality representing influential correlates of change. Analyses indicated that both water quality and wave exposure had associations with the fishes, corals, and benthic substrates that suggested similar plausible pathways for explaining change since 1992, and the spatial gradients in 2012. Diminished water quality across space and through time had a similar, positive association with small-bodied species, and negative association with larger-bodied, mixed species assemblages. Given that no evidence existed to link the gradient in water quality with coral assemblages or benthic substrates, which were expected intermediary drivers of habitat loss and larger-bodied fish declines, the major driver of bay-wide coral declines were attributed more towards compromised fish assemblages (i.e., herbivory loss) rather than water quality. In support, the gradient in benthic substrate condition was best predicted by wave exposure (historical analyses) in combination with herbivore assemblages (2012 spatial gradients). Wave exposure was also associated with more heterogeneous fish assemblages (i.e., a diversity of large-and-small bodied species), attributed to enhanced flushing and reduced fisher access with exposure. However, significant declines in water quality were inferred through time for two sites, representing

site-specific instances where water quality impacts were greatest. Together, both bottom-up and top-down processes appeared to be influential to temporal and spatial dynamics in coral-reef assemblages across Laolao, yet stronger evidence existed for herbivory-mediated change when considering the reef slopes habitats across the bay as a single entity. Collection of fishery-dependent data are recommended to better understand how fishing pressure influences change at Laolao Bay. The present datasets depicted plausible pathways for negative changes in coral reef resources across an economically and culturally significant habitat in CNMI, providing resource managers with foundational knowledge to improve the conservation of Laolao Bay.

TO THE OFFICE OF GRADUATE STUDIES

The members of the committee approve the thesis of David Ben Lacapa Benavente presented May 2, 2014.

_____
Peter C. Houk, Chairman

_____
Alexander Kerr, Member

_____
Ryan Okano, Member

_____   _____
John A. Peterson, Ph.D.   **Date**
Assistant Vice President, Acting
Of Graduate Studies,
Sponsored Programs And Research

TEMPORAL AND SPATIAL CHARACTERIZATION OF LAOLAO BAY CORAL-REEF FISH ASSEMBLAGES: STATUS AND FUNCTION

BY

David Ben Lacapa Benavente

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

IN

BIOLOGY

UNIVERSITY OF GUAM
MAY 2014

Table of Contents

List of Tables

List of Figures

Introduction:

Coral-reef fisheries provide essential food resources and ecological functions for island societies required for their sustainable livelihoods and economies (Johannes 1981, McGoodwin 2001, Pauly 2008). However, a deeper understanding of how coral-reef fisheries contribute to healthy ecosystems remains hampered by complex trophic interactions (Hughes, Rodrigues et al. 2007) and intricate life histories (Choat and Robertson 2002) that govern diverse reef fish assemblages, coupled with an inadequate history of exploitation and resource status (Pauly 1995, Greenstein, Curran et al. 1998, Knowlton and Jackson 2008). As a result, there is much difficulty in setting harvesting thresholds for reef fish because they can be determined in accordance with multiple attributes of the coral-reef fishery (i.e., sustainability of piscivore-dominated assemblages, herbivore-dominated assemblages, specific trophic levels, age based data for exploited reef fish) that are dependent upon unknown histories (Jennings and Polunin 1996, Jennings, Reynolds et al. 1999, Dulvy, Polunin et al. 2004, Cinner, Daw et al. 2009). In contrast, ecological thresholds are more uniform because they are founded in the maintenance of measurable functional roles. Thresholds in herbivore biomass have been established based upon their functional role of grazing and maintaining low macroalgal cover required for coral recruitment and coral-dominated reefs (Mumby and Harborne 2010). Yet, the collective evidence to date suggests that coral-reef fisheries have been assessed more from a harvesting perspective than from an ecological perspective (Zeller, Booth et al. 2007, Houk, Rhodes et al. 2012), perhaps due to the economic considerations associated with reef fish as a food resource. This is concerning because for many island nations reef fisheries actually provide disproportional benefits to

the local economy through the recreational and tourism industries as compared with their monetary value as a harvested resource (Brander and Scott Taylor 1998, Cesar, Burke et al. 2003, van Beukering, Haider et al. 2006). Therefore, improving our understanding of the functional roles and thresholds that coral-reef fish stocks play in maintaining coral-dominated reefs remains a priority.

The Commonwealth of the Northern Mariana Islands (CNMI) comprises a series of islands within the Marianas Archipelago, Western Pacific Ocean, where coral-reef resources are heavily relied upon for sustenance, culture, and economic prosperity (Gilmour, Smith et al. 2013). Like many island nations, management of their near shore marine resources is complicated by competing interests from resource users that stem from the tourism, recreational, and fisheries sectors. One of the most notable coral-reef resources that exist within the CNMI is Laolao Bay, located on the capital island of Saipan. The reef habitats in Laolao Bay have long been used by indigenous Chamorro people as a food and cultural resource (Russel 1998). In recent times Laolao Bay has become one of CNMI's most frequented tourist destinations for diving, with reefs valued at over 10 million USD per square kilometer to the tourism industry (van Beukering, Haider et al. 2006). Despite the obvious importance of Laolao Bay to the people and economy of CNMI, very little research has been conducted to describe the status and trends of its coral-reef resources, highlighting the need for further study. The lack of baseline information from the past increases the difficulty in evaluating the nature and magnitude of ecological change over time in the CNMI.

Shifting Baselines:

This situation is not unique to the CNMI, and has been characterized as the shifting baseline syndrome (Pauly 1995). Shifting baselines are defined by major changes in the abundances of natural resources that have occurred in the past due to harvesting, other human influences, or major disturbance regimes, however, these changes are not well perceived by the new generations of resource users who consider modern resource conditions to be 'natural' or 'normal'. Shifting baselines in fisheries often result from over-exploitation of target species and can lead to establishing inappropriate harvesting policies that are tied with the compromised resource abundances evident today. One of the main causes of shifting baselines is the lack of information pertaining to the abundance of resources in the past. Despite the limited availability and resolution often associated with historical datasets, when present, they are invaluable in assisting scientists and fishery managers with capturing a better understanding of how coral-reef ecosystems function naturally.

Studies have employed a variety of techniques in an attempt to help understand how past abundances of resources have shifted through time, ranging from examinations of fossil records to estimating fishery catches from photographs over the years. Pandolfi and Jackson (2006) analyzed coral species abundance data from well-preserved, raised Pleistocene reef terraces in Barbados to examine how species diversity and community composition shifted over geological time scales with inference to anthropogenic stress. Multivariate analyses of the coral assemblage data showed a stark contrast between Pleistocene and modern reefs due to a lack of *Acropora palmata* and *A. cervicornis* on modern reefs that were instead dominated by more opportunistic and tolerant corals

(*Porites asteroids, P. porites, Siderastrea radians, and Agaricia agaricites*). From a fisheries perspective, McClenachan (2009) estimated the lengths of trophy fish from photographs taken by a charter company in the Florida Keys, over a period of ~30 years (1956-1985), and compared these with photographs from the same charter companies in 2007. The results suggested a decrease in average size and weight when all trophy fish were grouped for analyses, and depicted a shift in catch composition to species with shorter average lengths. In the CNMI, Zeller et al. (2006) assessed the history of fisheries landings by integrating historical accounts of fish consumption and fishing effort shortly after World War II, and using the reported data as an anchor point to put modern fishery landings into perspective. Results revealed a 77% decline in total landings over the fifty year re-estimation period, yet methodological concerns associated with officially reported catch data limited the ability to accurately depict the gradient of change over each decade, and may limit the overall trends that were depicted.

Shifting baselines are important because they highlight how coral reefs are not static ecosystems, and can change over time due to both acute and chronic disturbances. Acute disturbances are known to cause major ecological changes within a short time period, and despite their impacts, recovery typically becomes evident within 10 years (Bellwood, Hughes et al. 2004, Golbuu, Victor et al. 2007). Thus, acute disturbances are often considered to be beneficial for the ecosystem because they provide a natural opportunity for species turnover within coral and fish assemblages that helps to maintain diversity and function (Talbot and Anderson 1978, Hubbell 1997, Aronson 2002). In the absence of chronic stress, reef systems should readily regenerate following most acute disturbance events (Connell 1997, Bellwood, Hughes et al. 2004). However, chronic

exposure to anthropogenic stress (e.g. overfishing and reduced water quality) inhibits coral reef recovery through a variety of mechanisms (Connell 1997, Dulvy, Polunin et al. 2004, Fabricius, De'ath et al. 2005, Houk, Musburger et al. 2010, De'ath, Fabricius et al. 2012), ultimately compromised ecological states can emerge and persist (Brodie, Fabricius et al. 2005, Gardner, Côté et al. 2005, Chollett, Mumby et al. 2012).

Compromised Fisheries and Water Quality as Localized Stressors to Coral Reefs:

Studies support that impaired water quality negatively impacts coral-reef ecosystems through many vectors (Fabricius, De'ath et al. 2005, De'ath and Fabricius 2010). Chronic exposure to increased levels of nutrients, sedimentation, and turbidity was shown to impede coral growth (Salinas-de-León, Dryden et al. 2013) and reproduction (Loya, Sakai et al. 2001). Specifically, increased sedimentation has resulted in reduced photosynthetic rates of zooxanthellae (Anthony and Hoegh-Guldberg 2003), decreased symbiont density (Nugues and Roberts 2003), and decreased coral growth (Marubini and Davies 1996). Likewise, increased nutrient levels have been shown to adversely affect coral growth by reducing coral polyp density (Bruno, Petes et al. 2003, Bruno and Selig 2007) and increasing exposure to infectious pathogens (Brown and Bythell 2005). At the ecosystem level, poor water quality promotes algal blooms that, if left unmaintained, can overgrow and compete with coral communities. Through all of these combined mechanisms, pollution serves to homogenize coral-reef architecture, leaving less habitat complexity for fish (Halford 1996, Friedlander, Brown et al. 2003, Wilson, Fisher et al. 2010). Despite the obvious importance of water quality to local reefs, eutrophication of coastal areas has continued to increase (Brodie, Devlin et al. 2011).

Similar to good water quality, healthy fish populations contribute greatly to ecosystem function by maintaining a suitable environment for coral recruitment and growth (McClanahan 1995, Almany, Hamilton et al. 2010, Mumby and Harborne 2010). Over-exploitation of coral-reef fisheries typically begins with the removal of large predators (Hutchinson and Rhodes 2010), followed by the subsequent shift in catch composition towards smaller-sized species in the same trophic group (Jennings, Reynolds et al. 1999) or species groups of lower trophic levels (Jackson, Kirby et al. 2001, Friedlander and DeMartini 2002, Myers and Worm 2003, Pauly, Watson et al. 2005, Essington, Beaudreau et al. 2006). Although mechanisms remain poorly understood, the loss of predators has been correlated with increased *Acanthaster plancii* densities (McCook, Ayling et al. 2010, Wilson, Fisher et al. 2010, Sweatman, Delean et al. 2011, Houk, Benavente et al. 2012) and reductions in coral cover (Bell 1992, Dulvy, Freckleton et al. 2004, De'ath, Fabricius et al. 2012). Herbivorous fish populations contribute to ecosystem functions by maintaining low macroalgal cover on reef habitats (Bellwood, Hoey et al. 2012). Because exploitation progressively removes larger herbivore species with longer life spans, the functional role of herbivorous grazers is transferred to smaller herbivore populations (i.e., the replacement of herbivore assemblages with species that no longer attain large adult sizes). This is problematic in that herbivore size is exponentially related to grazing function, whereby a doubling in fish size can equate to a $16 - 32$ times increase in grazing (Lokrantz, Nyström et al. 2008, Bellwood and Choat 2011). While studies have found evidence for an increase in the population density of smaller herbivorous fish species along gradients of fishing pressure (Grigg, Polovina et al. 1984, Rhodes and Tupper 2007), the noted increases are not sufficient to offset the

disproportional roles of larger fish, and net grazing potential is significantly decreased (Bellwood 2003, Bonaldo and Bellwood 2008).

In the end, the combined influences of poor water quality and reduced functionality of fish populations can push reef systems towards the verge of ecological collapse (McClanahan, Graham et al. 2011), meaning that key functional roles of grazing and calcification are compromised, and directional shifts in ecological assemblages through time are eminent, or already taking place. However, few studies have attempted to partition the roles of individual stressors, and quantified their relative contribution for reef function (Houk, Musburger et al. 2010, Graham, Nash et al. 2011).

Laolao Bay, Commonwealth of the Northern Mariana Islands:

General evidence of declining ecosystem health in Laolao Bay has been documented previously by the CNMI's Marine Monitoring Team (MMT). Over the past twelve years, this multi-agency program has collected standardized ecological data across 30 fore-reef sites around the CNMI (Starmer and Houk 2008). Between 2004 to 2006 high populations of predator crown-of-thorns starfish (COTS) were evident and caused widespread declines in coral cover throughout the CNMI. In the years since COTS disturbances, many of CNMI's reefs have shown signs of recovery, yet Laolao Bay reefs have exhibited minimal recovery in terms of coral coverage, species composition, and overall abundances of calcifying benthic substrates. Ongoing CNMI-wide examinations attribute the lack of recovery at Laolao and other sites around Saipan, to compromised herbivore assemblages and water quality (Houk, Benavente et al. 2013). Nevertheless, herbivore assemblages have explained a disproportional amount of the variance in recovery rates to date. The perceived decline of coral reef resources in Laolao Bay is

cause for concern because of their value to the CNMI's tourism economy, local fishermen, and culture. A recently completed technical report associated with the Laolao Bay revegetation and revitalization project was the first to provide quantitative insight into the coral reefs and associated fisheries over longer periods of time, and helped to improve upon the shifting baseline syndrome (Houk, Benavente et al. 2012). Study results suggested that negative changes to the coral and fish assemblages have become evident in comparison to a 1992 anchor point, along with a decline in water quality. However, negative changes were perceived to be spatially consistent across Laolao Bay, and degradation patterns were predicted by proxies to two localized stressors, pollution and herbivory, as well as one natural environmental regime, wave exposure. Specific changes to the fish assemblages included reduced densities of many large-bodied fishes (i.e., species that have estimated reproductive maturity sizes greater than 30 cm) and reduced sizes of entire coral assemblages. Ultimately, the 2010 study purported a direct correlation between both herbivory and water quality represented chronic stressors and negative change in Laolao Bay, yet the study called for an improved understanding of fish assemblages through generating species-level datasets to better depict the nature and consequences of change. In an effort to build upon current knowledge and better describe the ecological details and consequences behind fish assemblage changes, this study has attempted to integrate novel datasets with improved taxonomic resolution and depth coverage to better evaluate the status and function of coral-reef fish populations in Laolao Bay.

This thesis project first re-examined the dynamics of coral-reef assemblages across Laolao Bay over the past 20 years using improved datasets that help define the functional

roles of reef-associated fisheries. Historical datasets originated from a study by the University of Guam Marine Laboratory as part of an environmental impact statement prepared for the development of the Laolao Bay golf course in the early 1990s (Company 1992). Historical data was first compared with contemporary data to contextualize the change in marine resources across Laolao Bay. While these datasets represent two snapshots in time of Laolao Bay's coral-reef resources separated by 20 years, both datasets are spatially extensive, encompassing six independent sites across Laolao Bay, and had high site-level replication. Briefly, historical datasets described ~400 individual fish counts/measurements per site and ~300 coral colony measurements per site. Given their spatial extent and level of replication, historical datasets offer a unique ability to assess major changes that have occurred in Laolao Bay over the past 20 years, offering insight into the nature, but not rate, of change. Given that the only historical data available were obtained from shallow-reef crests (~5 m depth) and the fact that depth refuges are expected to exist for exploited coral-reef fish stocks (Tyler, Speight et al. 2009), this thesis project also integrated new datasets collected from deeper reefs (~15 m) into the present analyses in order to address the extent which depth refuges might contribute to current fish stocks. Building upon the improved perspective of change since the early 1990's, this thesis project next described spatial gradients in the coral and fish assemblages across Laolao Bay and built plausible association models to assess the role of watershed pollution, herbivore grazing, and wave exposure in predicting ecological change. One set of association models focused upon benthic substrate as a dependent variable (in response to grazing, water quality, and wave exposure), while the other set

focused upon the fish assemblages as dependent variables (in response to a loss of coral architecture). Sequentially, the following hypotheses were tested:

$H0_1$: There were no detectable differences in food-fish assemblages of Laolao Bay based upon comparisons between historical (1992) and contemporary datasets, in terms of: 1) species composition, 2) numeric density of functional groups defined by trophic status, and 3) spatial gradients that extend across LaoLao Bay.

$H0_1$ will be falsified if significant differences are detected when comparing temporal datasets across Laolao Bay considered as an individual entity, or when examining change in a spatially-dependent manner across six study locations within Laolao Bay. Because $H0_1$ was falsified, $H0_2$, $H0_3$, and $H0_4$ were used to further investigate the causes and characteristics of ecological change. Respectively these hypotheses were:

$H0_2$: Depth did not act as a refuge for exploited fish populations. There were no detectable differences in contemporary food-fish populations at varying depths based upon: 1) species composition, 2) numeric density, and 3) relative abundance (i.e., biomass) of function groups defined by body-size and trophic status.

Two final null hypotheses were also examined to approach the cause and effects of changes to Laolao Bay.

$H0_3$: Univariate metrics associated with fish population measures were not predicted by influential environmental regimes such as wave exposure and/or water quality, with ensuing consequences to the coral and benthic assemblages. $H0_3$ would be falsified if evidence suggests fish populations have contributed to shifting coral and

benthic assemblages through time, and/or across space themselves, or interactively with water quality and/or wave exposure.

H04: Univariate metrics associated with coral and benthic assemblages were not predicted by environmental regimes such as wave exposure and/or water quality, with ensuing consequences to the fish populations. H04 would be falsified if evidence suggests metrics of coral assemblage architecture or benthic composition may have contributed to shifting fish populations through time, and/or across space themselves, or interactively with water quality and/or wave exposure.

Methods:

Site Background:

Laolao Bay represents a unique geological feature on the east coast of Saipan, CNMI, where coral reef environments thrive due to their protection from prevailing northeast trade wind-generated swells and the presence of large volcanic watersheds that have created gentle bathymetric slopes conducive for extensive reef growth and development. In 2010, Houk et al. examined coral reef assemblages and water quality within six sub-drainages across Laolao Bay, following sample designs that were established in 1992. Historical ecological assessments were conducted as part of permitting requirements for the construction of the Laolao Bay golf course (Figure 1). During the 2010 study, ecological data was collected from two key habitats where historical datasets were available: 1) the outer reef flat, and 2) the reef slope at 3–5 m depth. The present thesis project has expanded upon previous studies by conducting detailed, species-level food-fish assessments at the six reef slope sites (3-5 m depth), and establishing six new sites parallel to these at a depth of 15m (Figure 2). Because the

Figure 1. Map of historical sites surveyed in 1992, as required by the CNMI government,

prior to construction of the Laolao Bay Golf Course.
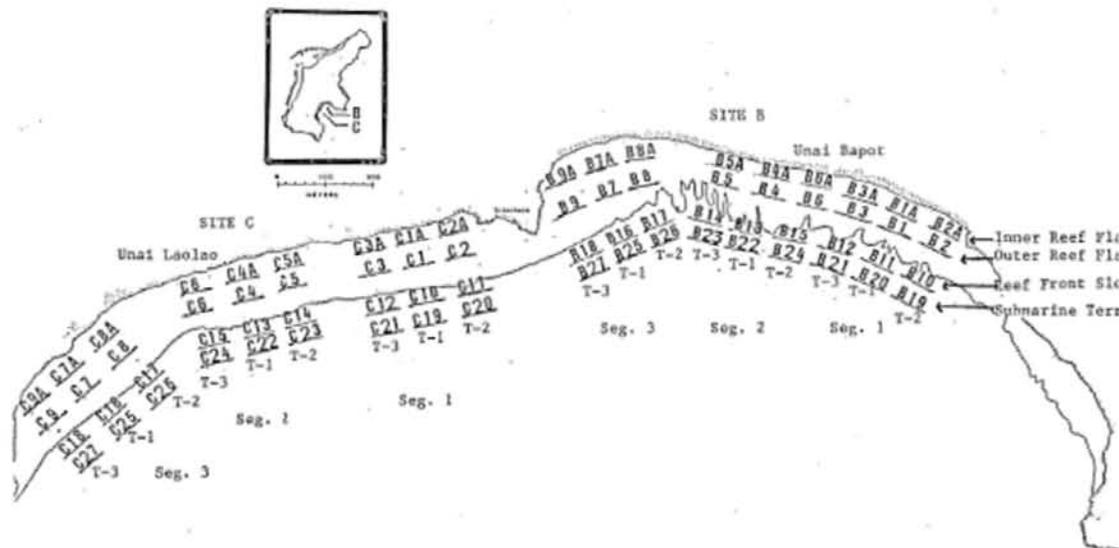
Figure 3. Study sites B and C showing the location of reef segments, transect areas, and numbered transects.

present thesis is focused upon food-fish assemblages, their dynamics, and their relationship with other ecosystem components, reef slope and deeper reef habitats were of primary interest, as reef flats held disproportionally lower food-fish biomass in comparison. For each site, novel fish data were collected and integrated with existing benthic substrate and coral assemblage data to address the outlined hypotheses.

Ecological Data Collection:

To understand if significant changes in fish assemblages were detected between historic and modern surveys, as well as the relationships between the dynamics of fish, coral, and benthic assemblages, standardized data collection protocols were utilized across Laolao Bay. First, the present study generated formal databases for all of the benthic substrate and coral assemblage data that were collected in 1992 and 2010. In 1992, benthic substrate abundances were estimated along each transect by haphazardly tossing five, 1 x 1 m quadrats at ten-meter intervals. Benthic substrates were recorded under each of the 16 intersecting cross-lines, within the quadrat, using the highest taxonomic resolution possible. Data were typically recorded at the genus or species level. Turf and crustose coralline algae were separated, while rubble and sand were combined into a single category. These methods yielded a total of 80 data points per transect and three transects to generate statistical estimates at the station level. In 2010, Houk et al. used the same number of transects and transect placement, but increased the level of replication to improve statistical confidence. Fifty, 0.5 x 0.5 m quadrats were placed at 1 m intervals. On the reef slopes, a digital photograph was taken at each 1m interval and

Figure 2. Map of survey sites for the present project depict the sub-watersheds of Laolao Bay and the associated land practices for the areas throughout. Survey sites were also established parallel to the current sites but at a depth of 15m.
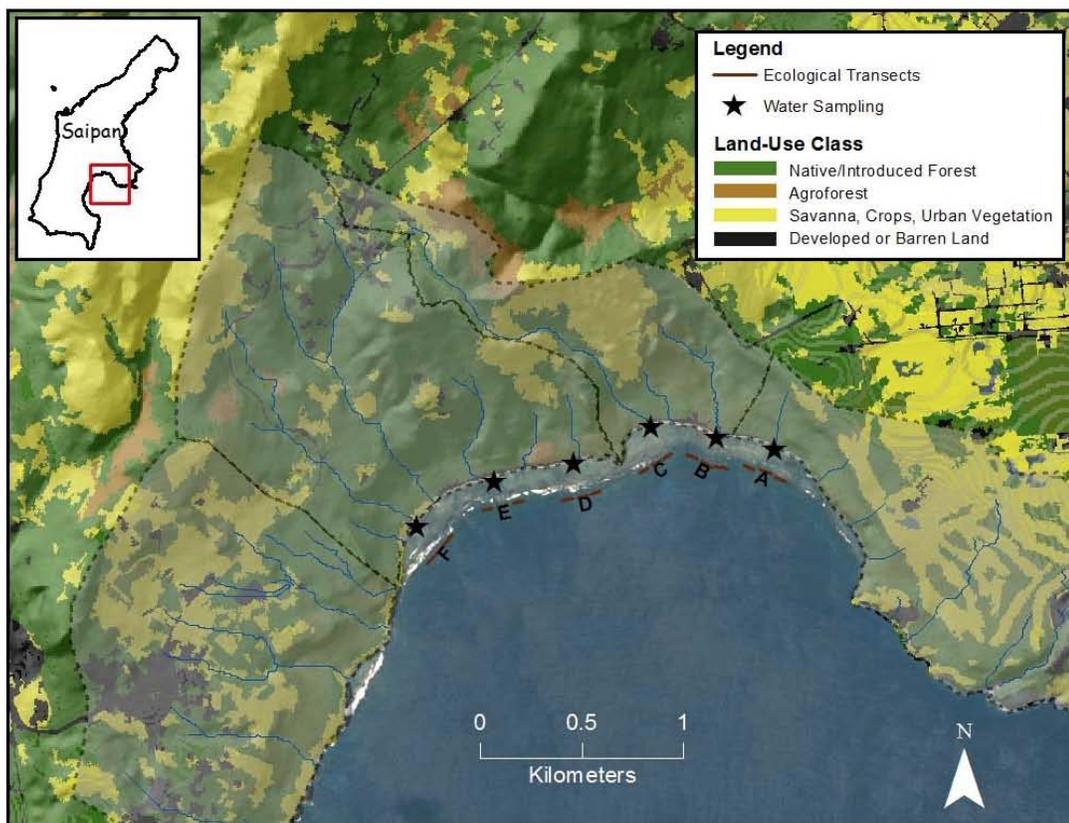
the benthos under each of five random points were assigned a pre-defined category using the computer software, Coral Point Count (Kohler and Gill 2006). These methods yielded a total of 250 data points per transect, and three transects to generate sound statistical estimates at the station level (Houk and Van Woesik 2006). The benthic categories for analysis were corals (to genus level), turf algae (less than 2 cm), macroalgae (greater than 2cm, to genus level if abundant), fleshy coralline algae known to overgrow coral (*Peyssonnelia, Pneophyllum*) (Keats, Chamberlain et al. 1997, Antonius 1999, Antonius 2001) crustose coralline algae, sand, and other invertebrates (genus level if abundant). Means, standard deviations, and standard errors were calculated based on the three 50m replicates, with n = 300 individual points per transect and n = 250 points per transect. Within the present study, benthic data were used to create a standardized univariate metric of the ratio between calcifying to non-calcifying substrates, also known as the benthic substrate ratio or BSR. This metric was defined by the percent cover of corals and heavily-calcified coralline algae, divided by turf, fleshy-coralline, and macroalgae.

Coral assemblages were evaluated using similar protocols in 1992 and 2010. For both survey periods coral population data were collected in a similar manner. In each instance, replicate 1 x 1 m quadrats were tossed at equal intervals along the transect lines. In 1992, fifteen replicate quadrats were sampled, while the 2010 survey used ten following an initial inspection of the data showing sufficient statistical power to meet survey demands, as well as species saturation considerations. Within each quadrat, all corals were identified to the species level, and the maximum diameter and the diameter perpendicular to the maximum were recorded. Surface area of colonies were calculated

by taking the geometric diameter and assuming coral colonies were circular in nature, common for both study periods.

The present study collected food-fish abundance data using similar protocols employed in past studies. At each of the twelve stations where data were collected, 12 stationary point counts (SPC's) were performed at equal intervals along three, 50 m transect lines (Bohnsack and Bannerot 1986). During each SPC, the species name and size of all food-fish within a 5 m radius were recorded for 3-minutes. In 1992, similar SPC surveys of 5 m radius for 3-minutes were performed, however only numeric densities (and not size) were recorded. Thus, comparisons with past fish datasets were based upon numeric densities, while spatial analyses across Laolao using 2010 data included size estimates (*detailed in data analyses section below*). Size estimates were used to calculate biomass based upon length-to-biomass coefficients available from fishbase (www.fishbase.org). In all instances, fish size estimates were binned into 5 cm categories prior to calculating biomass to reduce any variation caused by observer bias. In addition, recruit data, fish less than 5 cm, as well as sharks (n=1 seen during entire surveys) were excluded from analyses to account for biases associated with variable recruitment or species with disproportionally large range sizes. Target food-fish for both time frames included acanthurids, scarids, serranids, carangids, labrids, lethrinids, lutjanids, balistids, kyphosids, mullids, and holocentrids that are known to be harvested. For some analyses, species were grouped by trophic category (i.e., herbivores/detritivores grouped as one category) based upon their reported diet (www.fishbase.org), and/or family. Finally, modern fish surveys were conducted during the same season (fall/winter) as historical surveys in 1992.

Environmental Data collection:

During the 2010 survey, spatial water quality profiles augmented ecological data collection to understand the relative contribution of surface discharge during rain events and groundwater discharge during the lunar extremes (i.e., full and new moon periods). Spatial profiles were conducted on a quarterly basis during 2010 to characterize discharge patterns for the near-shore reef slopes adjacent to each study region (1-3 m depth, outer reef) using a YSI 6600 EDS that was attached to a slow moving boat (n = 6 total events). In each instance, an auxiliary bilge pump system was used to generate a continuous flow of near-shore marine waters (~1ft. in depth) through the YSI sensor casing system, and the boat was driven along the reef line following a pre-defined track that was confirmed with GPS locational data collected at 10 second intervals. High resolution data (±0.01 in all cases) were collected for salinity (ppt), conductivity (S/m), turbidity (NTU), chlorophyll-a (mg/L), pH, and temperature (degree C). Based upon unpublished insight from CNMI Marine Monitoring Team, two types of freshwater discharge events were focused upon: 1) groundwater discharge during the lunar maximum and minimum when tidal exchanges were largest, and 2) surface water discharge following major storm events. Sample-based water quality data were collected during both the 1992 and the 2010 studies. Monthly samples were collected at six, permanent reef flat monitoring stations that were established during the 1992 study, adjacent to the reef slope sites investigated (Figure 2). Reef flat sampling was conducted at monthly intervals over the course of a year for all stations during mid-to-high tides in the morning hours (9 to 11 AM). During each event, sampling consisted of taking YSI measurements (same parameters noted above) as well as grab samples from the top 0.5 m of water that were

later processed for total suspended sediments (CNMI Division of Environmental Quality Laboratory) and nutrients (University of Guam Water and Energy Research Institute Laboratory). All samples for nutrient analyses (nitrate, nitrite, total nitrogen) were filtered immediately, stored on ice or frozen, and processed within 48 hours. Nutrient and turbidity data from monthly reef flat water sampling were available from both the historical and present data collection effort. Because of shifting analytical techniques used to process the samples and technological improvements to nutrient sampling in general, no direct temporal comparisons were appropriate. In lieu, relative comparisons across the sampling stations were made for each time period. Data were compared using ANOSIM testing on rank-transformed data, and visualized using principle components ordinations (Anderson et al. 2008; described in detail below.

Wave energy was derived from long-term wind datasets and estimates of fetch (described in Ekebom et al. (2003) and applied to the Mariana Islands by Houk et al. (2013) *in review*). For each site, fetch (i.e., distance of unobstructed open water) was first calculated for 16 radiating lines equally distributed between 20 to 360 degrees. Fully develop sea conditions were considered if unobstructed exposure existed for 20 km or greater. Ten-year windspeed averages were calculated from Saipan airport data (http://www7.ncdc.noaa.gov/), and used as inputs to calculate wave height following Ekebom et al. (2003). Mean height was calculated by:

$$Hm = 0.019 \ U^{1.1} \ F^{.45} \tag{1}$$

Where Hm is the wave height (m) for each quadrant, U is the windspeed at an elevation of 10 m, and F is the fetch (km). Windspeed corrections for varying elevations were

made following Ekebom et al. (2003). Last, wave height was converted to energy following:

$$E = (1/8)\rho g H^2 \tag{2}$$

Where ρ is the water density (kg/m^3), g is the acceleration due to gravity (9.81 m/s^2), and H is the wave height (m).

Data Analysis:

Historical data from the 1992 ecological assessment of Laolao Bay were available only as appendices to the printed submitted report. Combined efforts transcribed these data for analytical purposes.

To analyze temporal differences in coral and food-fish assemblages across Laolao Bay (H0$_1$), multivariate analyses techniques were used to understand how entire assemblages may have shifted across the entire bay (i.e., all sites aggregated for temporal comparisons of Laolao bay as a single entity) and across individual sites (i.e., site-based temporal comparisons) (Figure 3a-b). Multivariate procedures described below followed standard protocols (Anderson, Gorley et al. 2008). Fish assemblage data were aggregated at the SPC-level, log-transformed, and Bray-Curtis similarity matrices were generated to define the ecological distances between each pair of SPC's (Anderson et al. 2008). Distance-based similarity matrices (i.e. Bray-Curtis dissimilarity matrix) were created using numeric density data for temporal analyses. Prior to any comparisons, tests of multivariate homogeneity were conducted to determine if Bray-Curtis similarity measures (i.e., dependent variables) were evenly distributed across timeframes. Given non-homogeneous variances, multivariate comparisons were made using rank-transformed abundance data (ANOSIM tests), while homogeneous data were examined

Figure 3A-C. Designs for multivariate analysis of temporal, spatial and depth data associated with metrics of fish assemblages. For temporal analysis (A), sites are compared by survey years. For the spatial analysis (B), gradients of change are assessed and then compared with one another. For analysis of fish assemblages at varying depths (C), sites were compared in a manner identical to temporal analysis, just analyzed by depth rather than survey date.
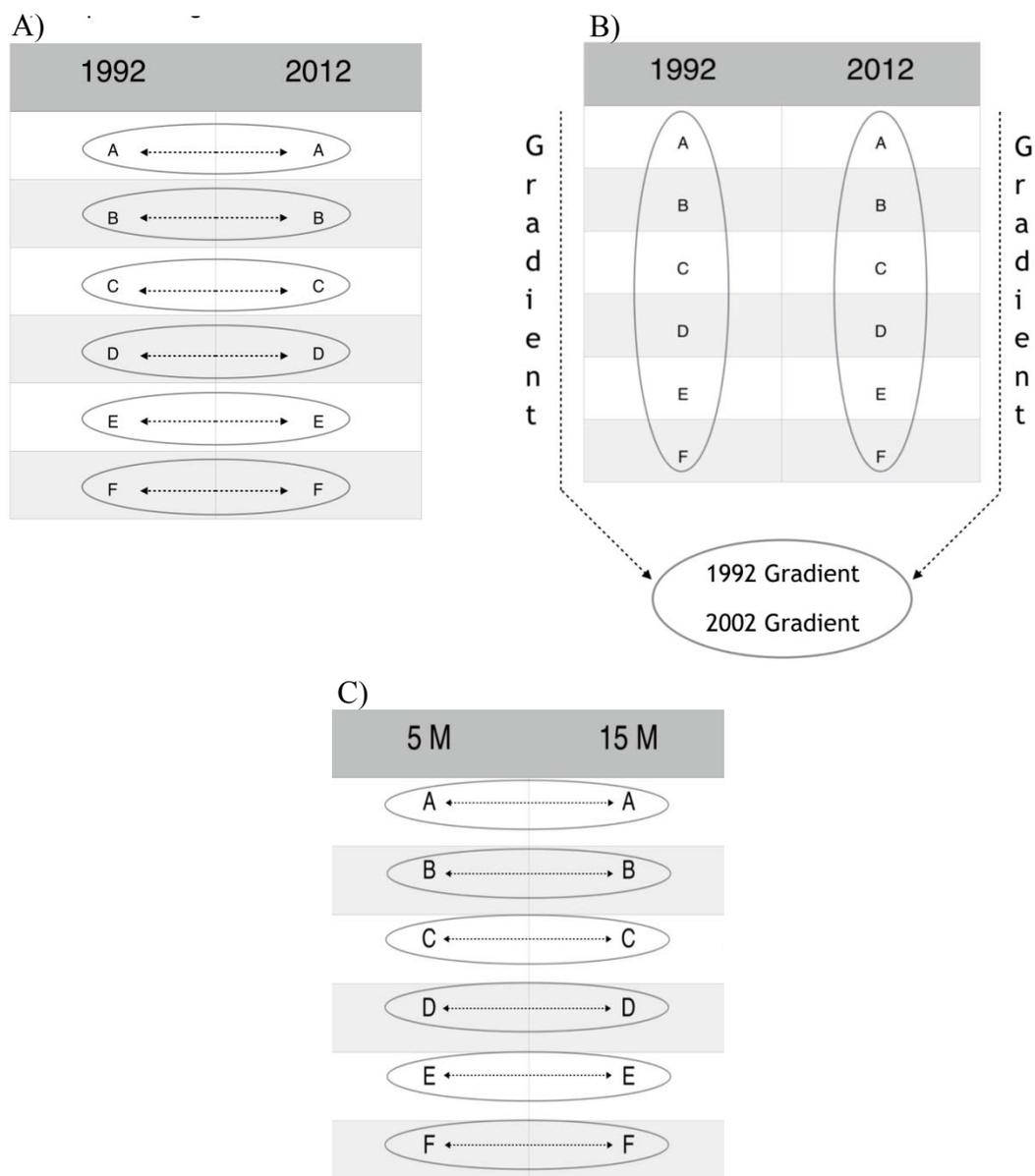
using analogs to ANOVA testing (PERMANOVA). Bray-Curtis similarities across timeframes were homogeneous, so a crossed PERMANOVA procedure was used to test for differences between the fixed factors of time across each individual site. PERMANOVA tests are evaluated based upon a pseudo F-statistics (analogs to ANOVA F-statistics), and t-statistics for post-hoc comparisons. Finally, a principal coordinate ordination (PCO) was performed on the similarity matrices to depict the PERMANOVA results in two-dimensional space. Given that PCO is a standard ordination procedure, each axis has an 'eigenvalue' associated with it, that describes the amount of variation in the multivariate assemblages being explained. Vector overlays, based on Spearman's rank correlation coefficients with the PCO axes, were added to PCO plots to identify species that have contributed most to the underlying change being depicted.

The present study also analyzed patterns in fish assemblages moving across Laolao Bay to examine if spatial gradients in fish species abundances existed in 1992 and 2012, and if so, were these spatial gradients similar (Figure 3c). Initial PERMDISP tests showed non-homogenous variances when looking at gradients across Laolao Bay in both 1992 and 2012. Thus, ANOSIM tests with subsequent graphic interpretations using non-metric multidimensional scaling (n-MDS) plots were conducted. MDS-plots were based upon ranked abundance data and do not have 'eigenvalues' associated with individual axis scores. Instead, stress values are calculated for the MDS plots based upon comparisons between depicted distances between sites and actual Bray-Curtis similarity values. Stress values <0.25 indicated low stress, and that rank-based data visualized in MDS plots accurately depicted Bray-Curtis distances. $H0_2$ was tested in a manner similarly described above. Crossed multivariate designs examined whether fish

assemblages were significantly different across the two depth strata, both for all sites pooled together, and for comparing differences at individual sites. PCO plots were used to depict depth-based differences and vector overlays indicated which species contributed most to the noted trends. Depth comparisons were based upon 2010 data only, and thus species biomass data were available and used for these multivariate examinations.

Coral assemblage data were assimilated from a recent study across Laolao Bay that helped to guide the present thesis (Houk et al. 2010). Coral data were assessed in multivariate space based upon site-level summary statistics. Bray-Curtis similarity distances were calculated between each pair of sites, for both timeframes, and resultant relationships were visualized in non-metric, multi-dimensional scaling plots (n-MDS). Vector overlays were used to depict species which have contributed the most towards both spatial gradients during each timeframe, as well as temporal differences. In addition to multivariate tests of significance, temporal comparisons of colony-size distributions were performed using Kolmogorov-Smirnov (KS) tests that depicted differences based upon distances between cumulative frequency curves.

Finally, regression models and correlation examinations were employed to contextualize cause-and-effect relationships among water quality, wave exposure, and biological assemblages across space and time ($H0_3$ and $H0_4$, Figure 4, Table 1). The rationale behind these examinations was to assess the associations between each factor, and assess the extent to which the combined set of associations might infer directional causation based upon known relationships. For $H0_3$, relationships of interest were associated with two notable trends in fish assemblages through time and across space that became evident: 1) declines in fish densities through time, with strongest declines

Figure 4. Regression Analysis design for $H0_3$ and $H0_4$, respectively. For $H0_3$ fish assemblage metrics are the central focus while measures of water quality, wave exposure and coral population assemblages are used to understand the drivers of change. In contrast for $H0_4$ coral population metrics are the central focus, all other associated variables remain the same
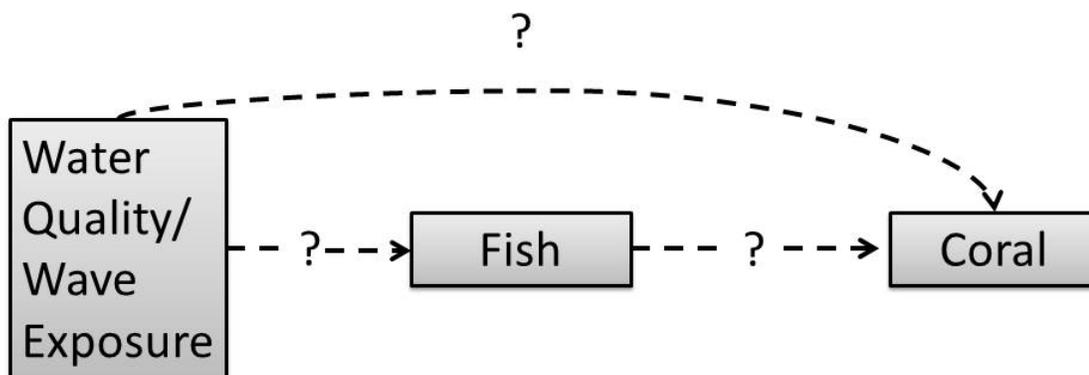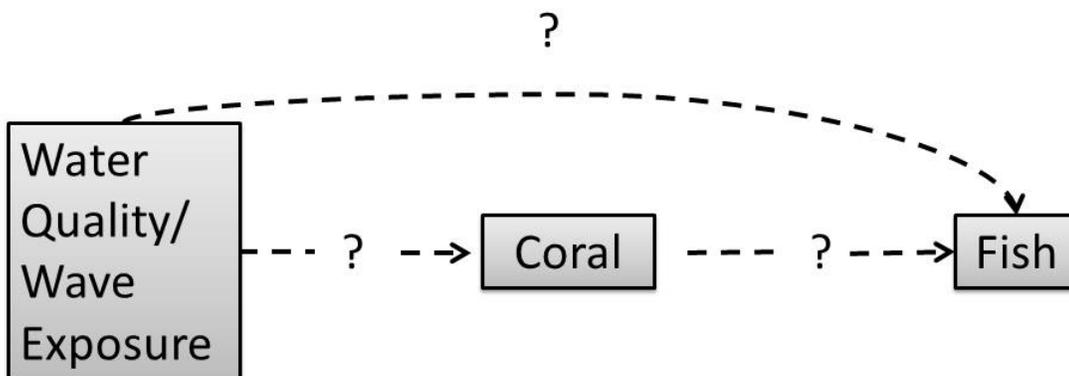
Table 1. List of fish, coral, and environmental variables which were used for historical and present-day regression and correlation analysis. Historical variables of fish and coral include measures of temporal change (i.e., PCO Change), distanced based metrics derived from assemblage differences in multivariate space.

Historical			2012		
Fish	Coral	Environment	Fish	Coral	Environment
Large herbivore population density change	Percent coral cover change	Wave exposure	Mean herbivore/ detritivore biomass	Population Density	Salinity
Small herbivore population density change	Species-richness change	Water quality change	Assemblage heterogeneity	Benthic Substrate Ratio	Land use
Large bodied fish population density change	Skew change		Mean herbivore/ detritivore size	Skew change	Watershed size
PCO change	PCO change				Water quality PCO
	Kurtosis change				Wave exposure
	Population density change				

observed in the larger-bodied species with greater functional roles, and 2) linkages between declining water quality and/or larger fish removal that both may serve to increase small-bodied herbivore/detritivore assemblages that have fast response times to altered trophic dynamics (Connell 1997, Dulvy, Polunin et al. 2004, Fabricius, De'ath et al. 2005, Houk, Musburger et al. 2010, De'ath, Fabricius et al. 2012, Houk and Musburger 2013). $H0_3$ examined the extent to which fish may have been the central component of ecological change to the benthic and coral assemblages independently, or in concert with environmental regimes. In contrast, relationships of interest for $H0_4$ were associated with the decline in coral architecture that has been noted in LaoLao Bay over time (Houk, Okano et al. 2010), and whether this decline might have predicted declining larger-fish densities. In this sense, HO_4 examined whether declining coral architecture, as measured by declining size-class distributions, may have been the central component of ecological change to the fish assemblages, independently or in concert with environmental regimes.

Prior to regression and correlation analyses, all variables were standardized to provide for equal weighting, and constant values were added to make all variables positive. Historical examinations used biological and environmental variables that represented change over time (2012 minus 1992), with the exception of wave exposure which was derived from 10-year averages and assumed to be consistent through time. Thus, for historical examinations, increases in values should be interpreted as a negative change to site health (i.e., increased decline in water quality, fish densities, and coral population measures). Similar examinations were performed for modern data (2012 data only) to see if trends through time resonated with modern spatial trends. For modern

comparisons, increased values represent improved water quality and biological measures. Single variable regression models were used to test for significance in the expected relationships described above, while correlations were generally examined across all variables to help interpret the overall linkages between ecosystem components. Regression models were all inspected for independence and normality of residuals, and log-transformations were used to reduce skewness in some instances. Model fit was indicated by Akaike Information Criterion (AIC) scores that are based upon R^2 values, but also penalized based upon residual normality and adding multiple explanatory factors. In summary, obtaining a better understanding of the interactions between ecosystem components (i.e., coral structure and fish functional roles), through time and across space were the desired outcomes of this analysis.

Results:

Environmental Data:

Environmental data were first summarized to provide a context for understanding the results of biological surveys. Water quality data collected during a 2010 survey by Houk et al. (2010) are summarized to provide a basis for interpreting the present results. Water quality profiling surveys depicted that a natural gradient existed for salinity throughout the bay due to its geomorphological characteristics. Profiling conducted during full and new moon periods with no rainfall found comparatively lower salinity levels in the eastern portion of the bay where karst bedrock exists in the watershed (Figure 5 and 6). Thus, it appeared the natural gradient in salinity may be an artifact of greater connectivity with the island aquifer due to groundwater seepage during large,

Figure 5a-b. Satellite image of Laolao bay with water quality and ecological monitoring stations shown, as well as the results of water quality profiling to understand natural characteristics of Laolao discharge patterns. Characteristic salinity profile shows a greater influence of freshwater (i.e., lower salinity) in the eastern portion of the bay (A), a probable consequence of limestone bedrock in the watershed promoting enhanced connectivity with the aquifer during full moon, maximal tidal exchange periods. During minimal tidal exchange periods and high rainfall, the opposite pattern was found (B), as freshwater delivery was more proportional to watershed size where volcanic bedrock and soils exist.

A)
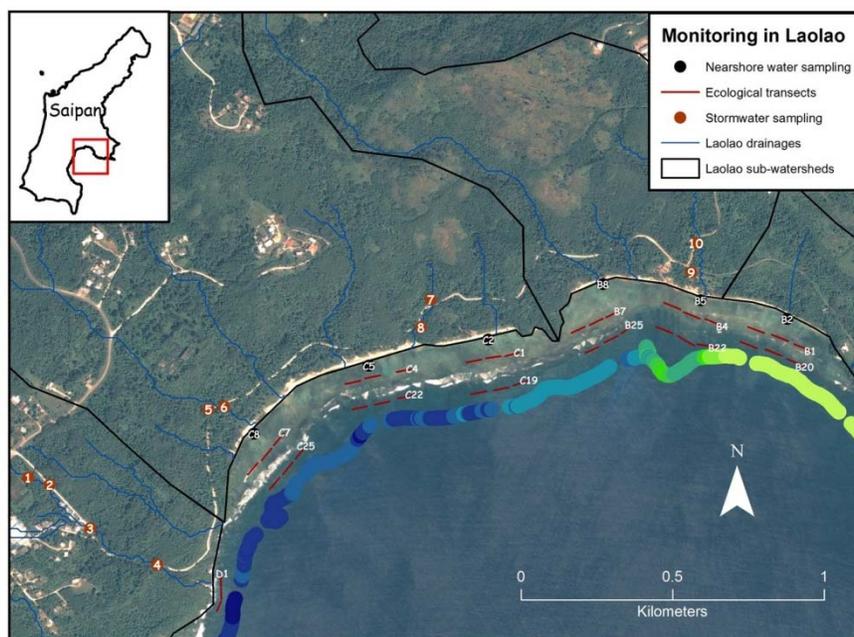
B)
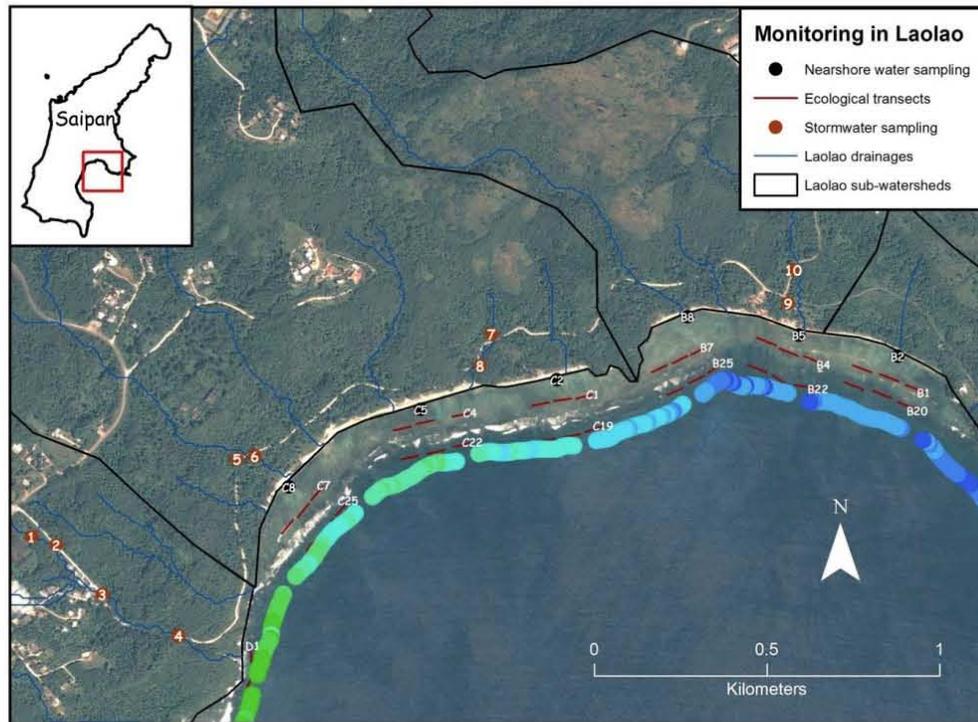
Figure 6. Boxplots summarizing freshwater discharge patterns associated with two characteristics freshwater discharge regimes that existed in Laolao Bay (black lines represents the median, the boxes indicates the 25th (lower) and 75th (upper) percentiles, and the error bars indicate the 5th (lower) and 95th (upper) percentiles). Groundwater discharge associated with lunar extremes (full and new moons and the associated negative low tides) created an east-to-west gradient (A) of freshwater delivery to Laolao Bay. In contrast, significant rain events created a west-to-east gradient (B) of freshwater delivery.
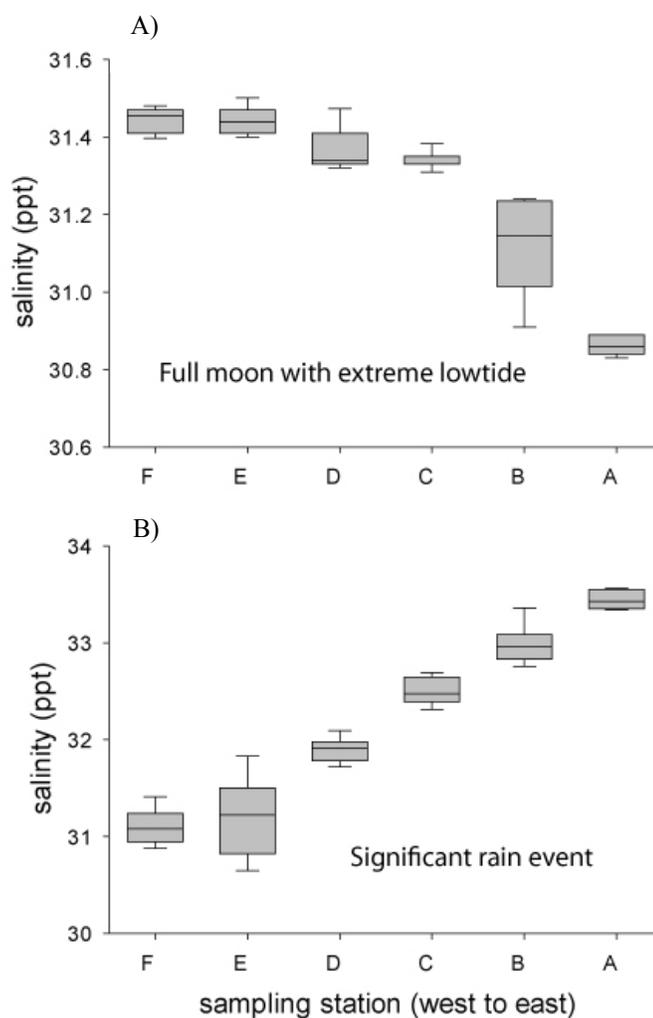
lower salinity levels during rain events. Wave exposure followed an expected trend of being highest with greatest exposure to prevailing northeastern trade winds (i.e., in the western portion of the bay), and lowest where exposure to trade winds was minimal (i.e., the eastern portion of the bay).

Principle components analysis found that between 40 to 56% of the variance in nutrient and turbidity data could be explained by a single PCO-axis for both 1992 and present water quality data (Figure 7). This suggested that the first PCO-axis provided a useful indicator of pollution loading (Table 2). The overall trends in water quality were similar for both time periods, whereby highest nutrient loading was found in the Eastern portion of Laolao Bay, especially during low tides, where profiling depicted high connectivity with groundwater discharge (site A, Figure 5, Table 2). Besides this site, stations B and E were distinguished from others by having relatively lower water quality, while remaining sites were not distinguishable from each other. Despite similar spatial trends for both past and present water quality data, the magnitude of spatial differences between sites became more profound in 2010, suggesting that relative to other sites, some got worse (Figure 7). Based upon these findings, this thesis used PCO scores as metrics of water quality when examining associations with biological assemblages below.

Biological Data:

Two other datasets were also incorporated from Houk et al. (2010), and further analyzed: 1) benthic substrate abundances (2010 timeframe only), and 2) coral species abundances (both timeframes). Benthic datasets collected during 2010 highlighted lower coral coverage in the eastern portion of Laolao, where turf algae dominated the substrate (pairwise t-test for coral and turf algae abundances at site A and B compared with others,

Figure 7. Principle components analysis and ordination of water quality (nutrient and turbidity) data from monthly samples at six monitoring locations across Laolao Bay (see Figure 1). Constituents used for historical water quality data analysis (A) included NO3-+N,PO4-P, and turbidity. Constituents used for the present dataset (B) were NO3-N, NH4, total N, and turbidity.

Legend:
- A
- B
- C
- D
- E
- F

PCO2 (17.4% of total variation)

PCO1 (56.4% of total variation)

B)

turbidity

total nitrogen

nitrate+nitrite

ammonia
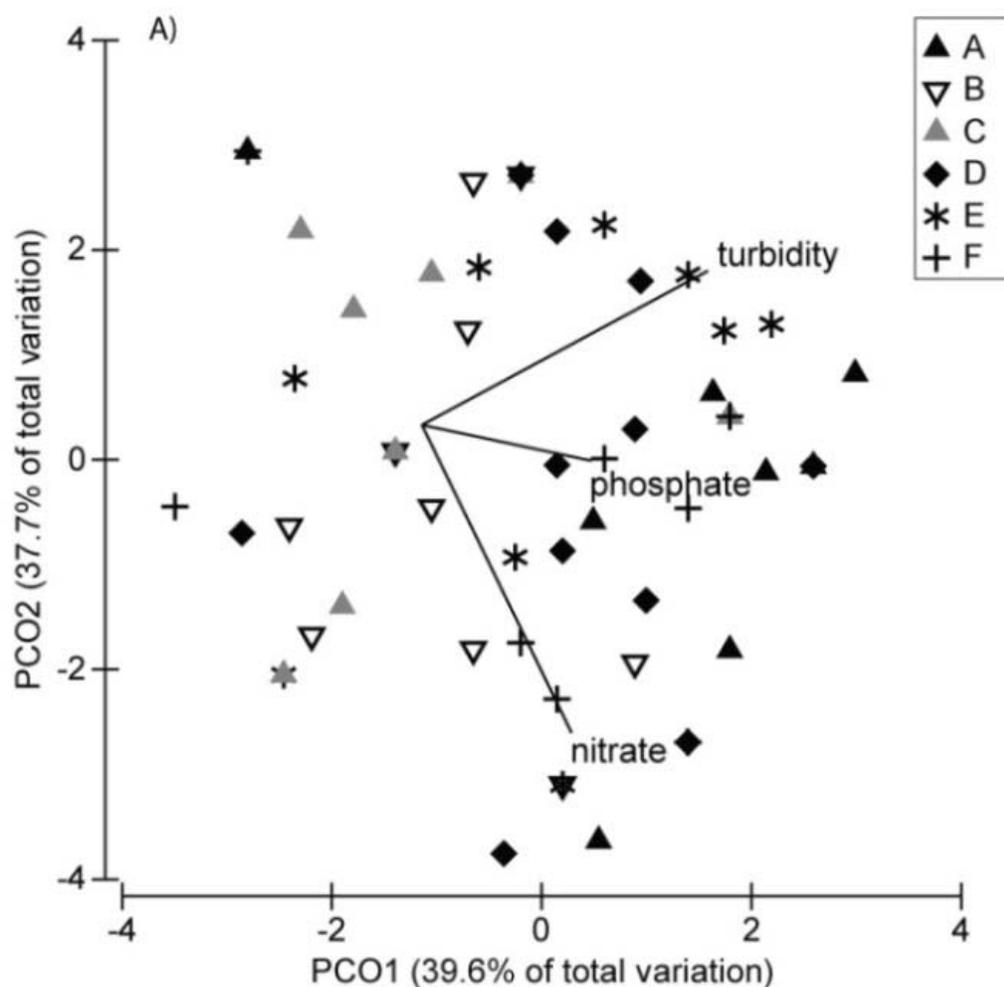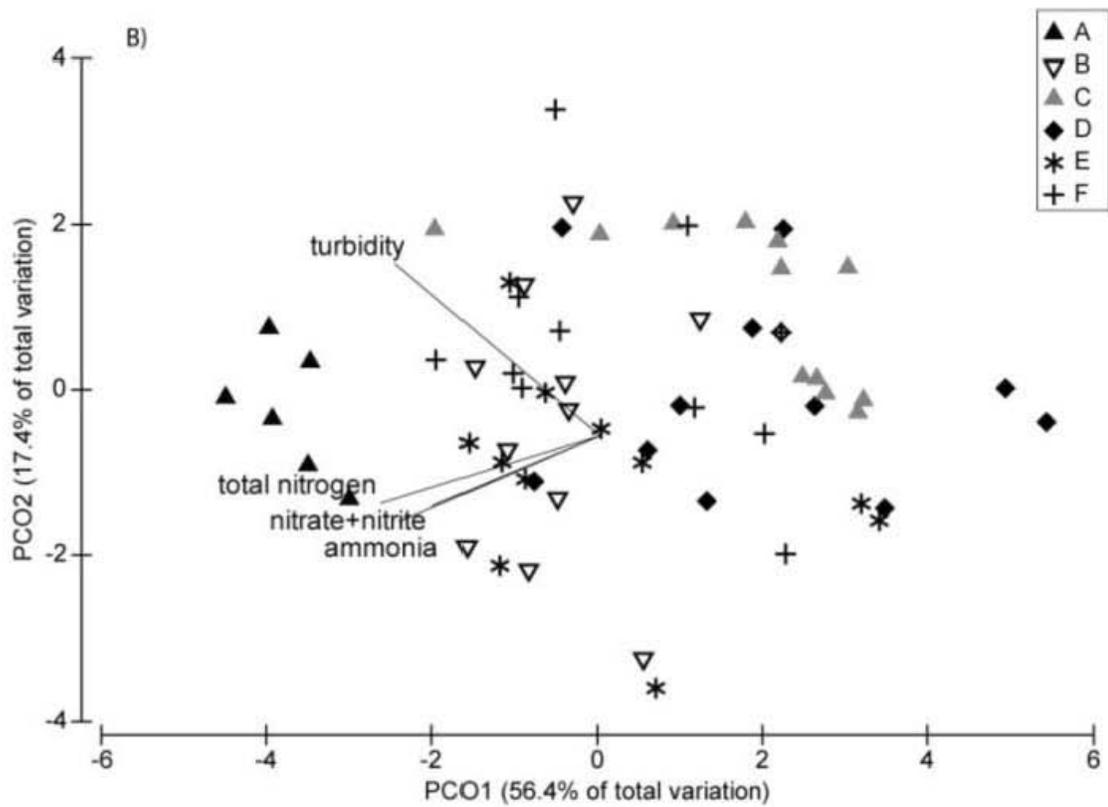
Table 2. ANOSIM results highlighting spatial trends in water quality data from 2011-12 sampling event. High ranks and low PCO-scores indicated poor water quality. Significant groups highlight results from pairwise testing between sampling stations (overall ANOSIM Global R-Statistic = 0.45, P<0.001; significant groups defined by pairwise R-Statistics > 0.45, P<0.05). Refer to Figure 7 for visual representation of results.

Site	Rank	PCO axis-1	Significant groups
A	6	-3.9	A
B	5	-0.5	B
C	1	1.9	c, d
D	2	2.0	b, c, d
E	4	0.1	B
F	3	0.2	b, c, d

P<0.05 in both instances, Figure 8 and 9). In contrast, remaining sites were less differentiated from each other in terms of overall coral cover, with sites C and F showing the highest values. Benthic substrate ratio's (BSR) followed a similar pattern being lowest in the eastern portion of the bay and greatest in west Laolao, however a spatial gradient became more apparent with respect to wave exposure when considering BSR instead of just coral cover. BSR was used as an indicator of favorable substrate for reef accretion that was applied to regression and correlation analyses below.

Beyond cover, coral species abundance data depicted significantly different assemblages between the two sides of the bay, and through time as well (PERMANOVA, F-Statistic >3.5, P<0.05, for both comparisons, Figure 10). Differences were due to a decreased presence of larger colonies and an increase in smaller colonies (KS tests showed a reduction in colony size and increase in skewness most pronounced for sites A, B, D, and E, Figure 11). Results indicated that the strongest changes through time occurred where groundwater influences were high (F-Statistic = 4.29, P<0.01, Figure 10), specifically in the eastern portion of Laolao Bay where reefs were comprised mostly of *Porites, Leptoria, Favia,* and *Galaxea*, all of whose growth forms facilitate limited three dimensional reef growth. Overall, a decrease in the quality and structure of coral assemblages were observed across Laolao, but changes were most pronounced in the eastern part of the bay. This study used coral assemblage skewness when examining regression and correlation analyses below, and assumed skewness was a useful metric of habitat structure provided by corals based upon these results.

Figure 8. Percent cover of dominant benthic substrates on Laolao Bay reef slopes. Clear differences can be seen between survey stations associated with enhanced groundwater connectivity (A and B) compare with others. These conditions are less favorable for coral growth and more favorable for turf algae persistence.
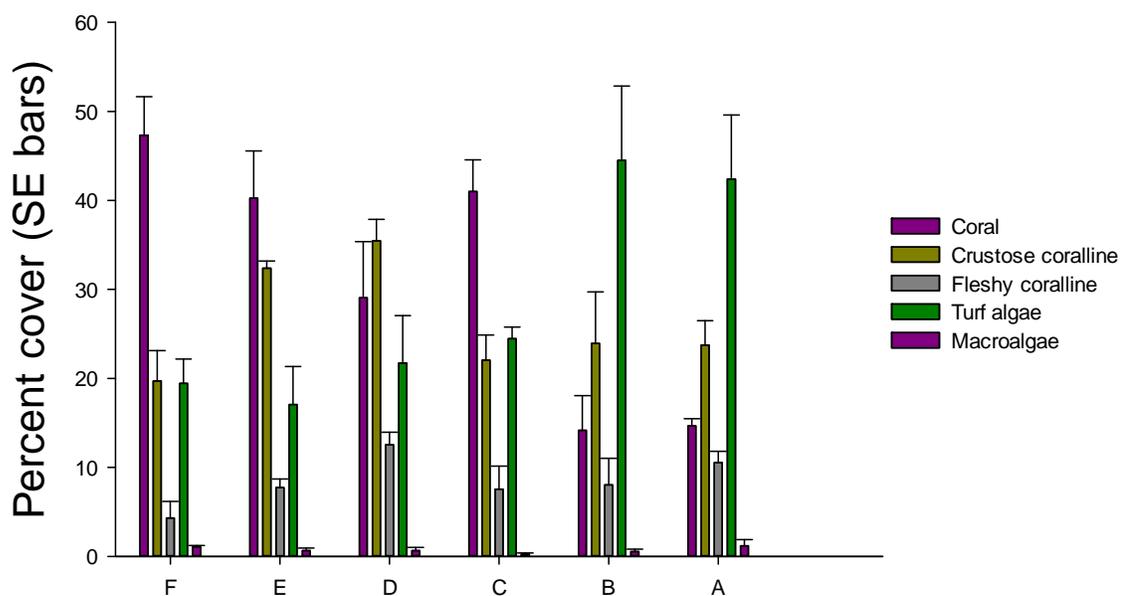
Figure 9. Change in percent coral cover and colony density per m^2 since 1992. Significant increases in population density were noted throughout Laolao (P<0.05, pairwise t-test), however changes in coral coverage were spatially inconsistent. Similar to other ecological data collected on the reef slope, inherent difference can be seen between sites associated with enhanced groundwater delivery (A and B) and others.
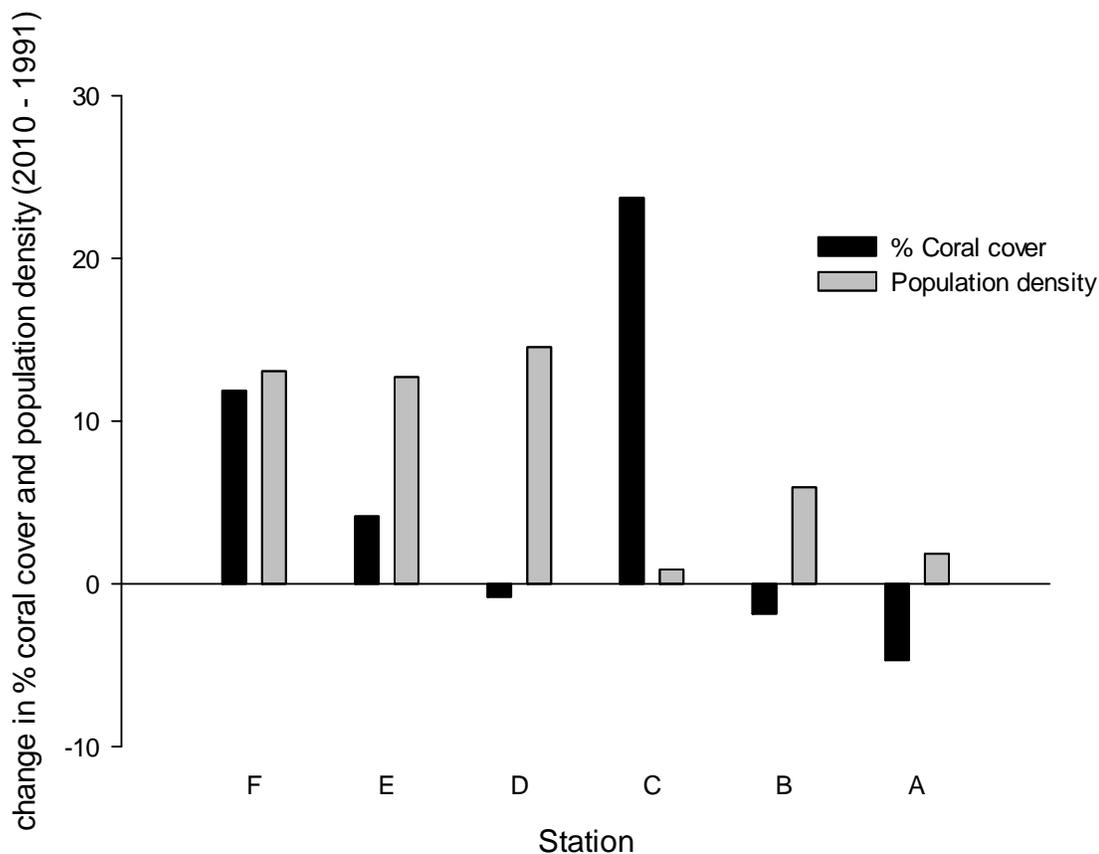
Figure 10. Multi-dimensional scaling plot highlighting spatial and temporal trends in Laolao Bay coral assemblages. Significant differences were attributed to both groundwater influence (low vs. high) and change through time (2010 vs. 1992) (PERMANOVA, F-Statistic >3.5, P<0.05, for both comparisons). Additionally, there was a significant interactive effect (F-Statistic = 4.29, P<0.05) highlighting that greater changes occurred through time where high groundwater influence was evident. Vectors display corals that were significant drivers of these trends (spearman correlation coefficients >0.5)
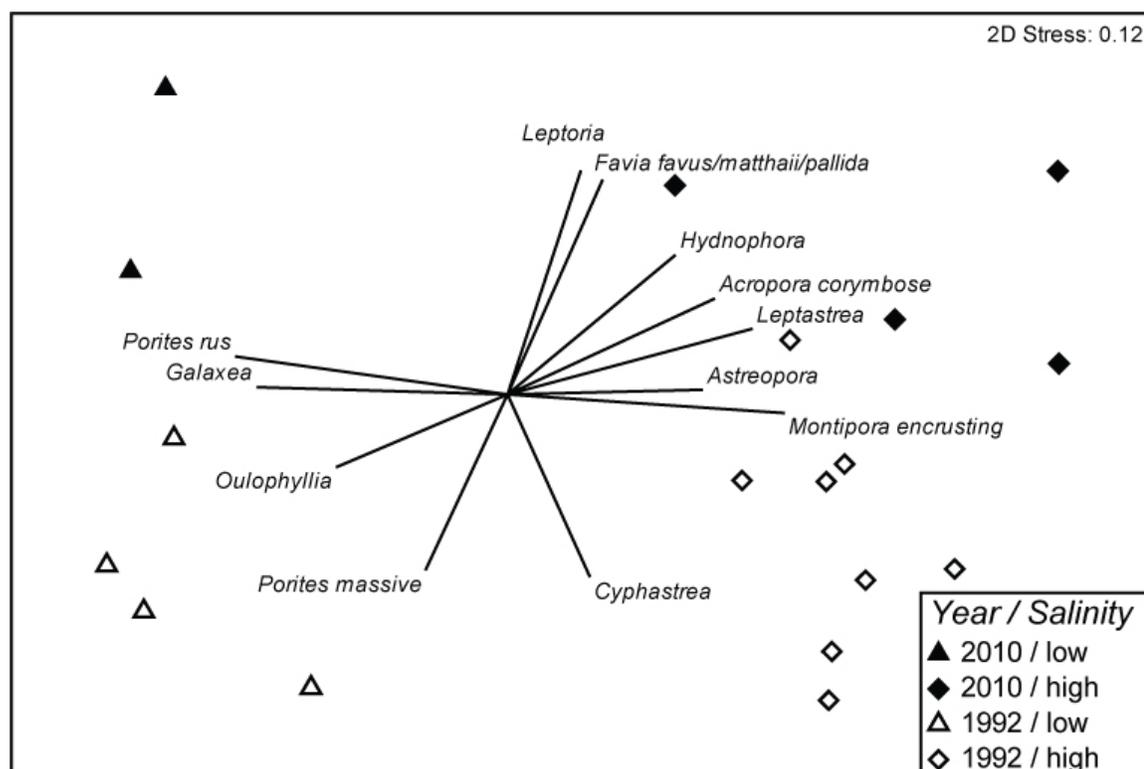
Figure 11A-F. Trends in coral population demography since 1992 (*see methods*). Each graph shows comparative colony-size distributions. Survey stations A, B, D, E, pairwise Kolmogorov-Smirnov tests showed a significant reduction in mean colony size, and a larger proportion of juvenile corals, through time.

H0₁:
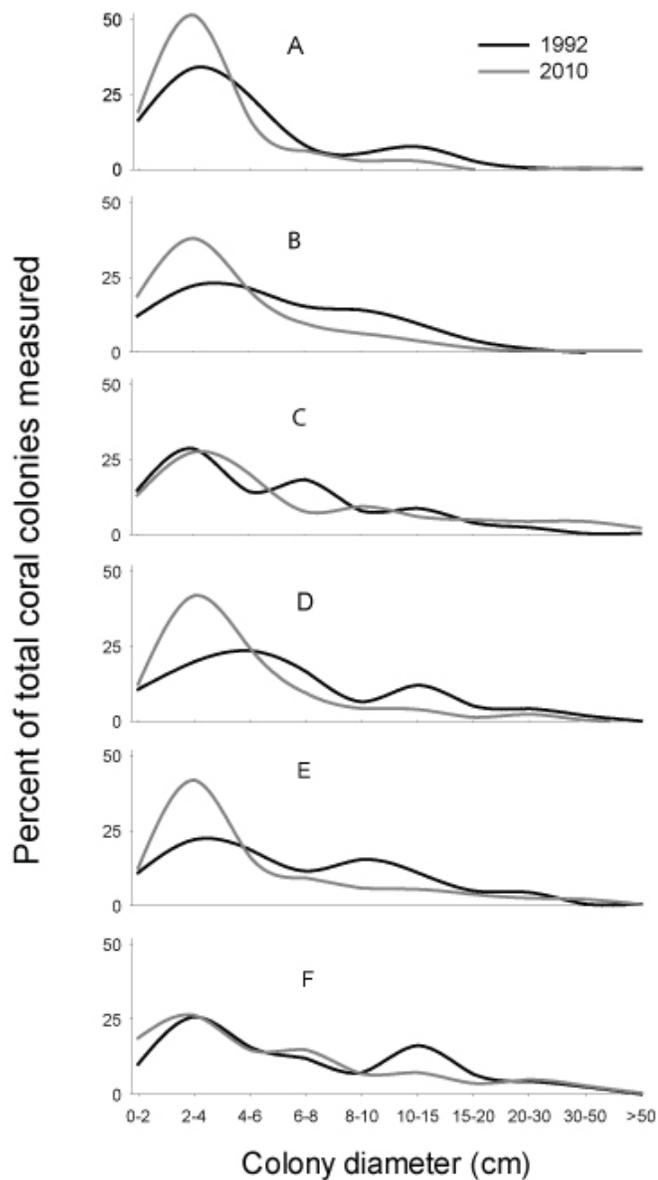
Temporal Analysis:

   Comparative analyses of fish assemblages between 1992 and 2012 depicted significant differences in the numeric density across major functional fish groups (t-statistic =7.4, p <0.001, PERMANOVA). When grouping sites across the bay, these generalized trends were due to a reduction in the density of most food fish species (especially *Monotaxis grandoculus*, *Naso unicornis*, *Naso lituratus*, *Chlorurus sordidus*, *Scarus rubroviolaceus*, and other mixed acanthurids all showed reductions in numeric density), and the spatially-inconsistent increase in density in some species of rabbitfish (Siganus spp.), a small-bodied grouper (*Cephalopholis urodeta)*, and mixed small-bodied parrotfishes besides *Chlorurus sordidus*; Figure 12). Similar trends were observed when focusing analyses at the site-level, whereby pairwise comparisons found consistent reductions in numeric density for the majority of food-fish across all sites, and increases in only a few, small-bodied species (Table 3, Figure. 13, & Figure. 14, t-values = 4.3, 3.9, 3.3, 3.18, 3.05, and 3.03, respectively P-values <0.006 for all, PERMANOVA and pairwise testing). In general, species that consistently contributed greatest to the site-level changes between 1992 and 2012 were small-bodied acanthurids, wrasses, *C. sordidus, A. triostegus, M. grandoculus*, small-bodied parrotfish, *N. lituratus,* and *S. rubroviolaceus* (Table 3, species contribution up to ~70%, SIMPER analyses). Given the nature of change since 1992 (i.e., a reduction in many larger-bodied species and an increase in fewer smaller-bodied species), multivariate heterogeneity has also declined in many instances, as replicate SPC surveys were typically more similar to each other in 2012 compared with 1992. However, site-based changes had several unique

Figure 12. Change in the population density of dominant fish in Laolao since 1992. A significant reduction in fish density, evenness, and functional group abundances was evident, as 2012 fish assemblages have been reduced to populations dominated by small acanthurids.
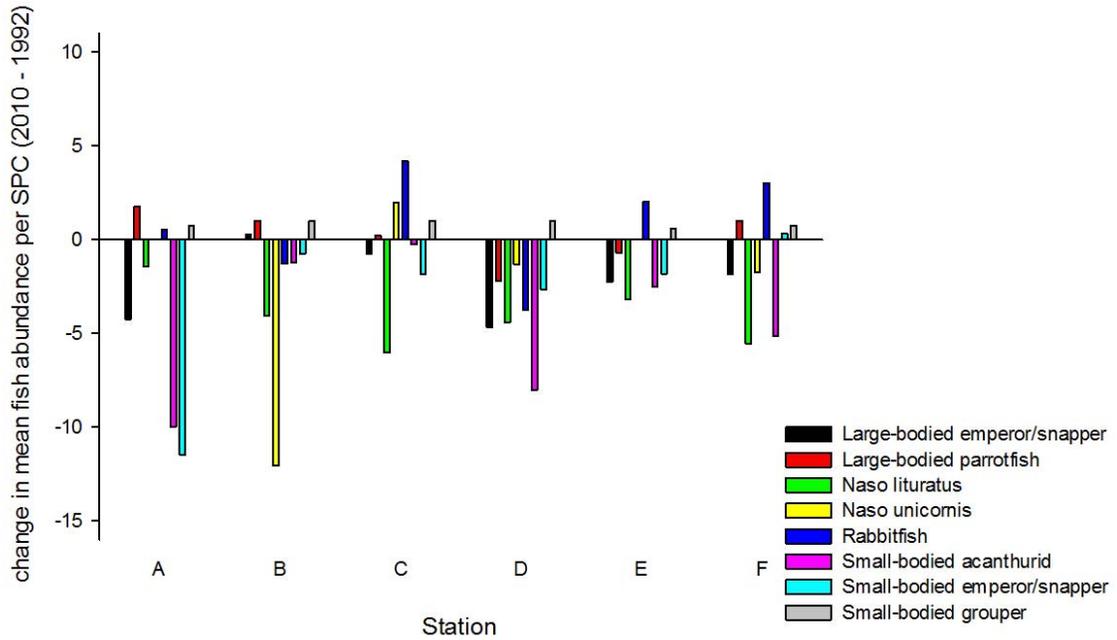
Table 3. Describes results of PERMANOVA, tests of significance, and their associated p-values. SIMPER results describe percentages of key fish groups that have experienced change through time. Numeric density was also calculated to understand differences in densities of key fish groups through the two time periods.

Site	Fish group	Numeric density 1992 (SE)	Numeric density 2012 (SE)	SIMPER Results % Contribution	Cumulative %	Test Statistics PERMANOVA and Pairwise (P-Value)
D						4.33 (0.001)
	Wrasse	10.7 (1.7)	0.08 (.08)	22.22	22.22	
	Small-bodied acanthurid	17.6 (2.4)	1.25 (0.7)	16.4	38.62	
	Naso lituratus	5.4 (1.3)	0.16 (0.1)	12.01	50.63	
	Small-bodied parrotfish	0.0 (0.0)	2.4 (0.7)	10.49	61.12	
	Chlorurus sordidus	11.1 (2.1)	1.4 (.04	5.8	66.92	
	Goatfish	.04 (0.2)	0.16 (.01)	4.53	71.45	
	Scarus rubroviolaceus	2.0 (0.9)	0.3 (0.2)	4.03	75.49	
	Cephalopholis urodeta	0.0 (0.0)	0.83 (0.83)	3.87	79.36	
	Monotaxis grandoculus	3.8 (1.04)	0.0 (0.0)	3.53	82.9	
	Lutjanus kasmira	.25 (.25)	0.0 (0.0)	3.19	86.08	
A						3.9 (0.001)
	Small-bodied acanthurid	21.0 (2.3)	4.3 (0.7)	26.95	26.95	
	Wrasse	2.75 (0.5)	0.0 (0.0)	17.3	44.26	
	Naso lituratus	2.41 (.63)	.25 (.18)	12.54	56.8	
	Chlorurus sordidus	0.0 (0.0)	1.08 (0.2)	8.8	65.6	
	Small-bodied parrotfish	0.4 (0.4)	1.08 (0.3)	8.58	74.18	
	Gnathodentex aureolineatus	4.08 (2.7)	0.08 (0.08)	6.01	80.2	
	Goatfish	0.16 (0.1)	0.3 (0.1)	3.86	84.06	
	Rabbitfish	0.16 (0.1)	0.25 (0.1)	3.3	87.36	
	Cephalopholis urodeta	0.08 (0.08)	0.25 (0.1)	2.87	90.23	
F						3.3 (0.001)
	Wrasse	13.4 (1.8)	0.08 (0.08)	25.39	25.39	
	Small-bodied acanthurid	17.1 (5.1)	2.2 (0.5)	16.99	42.38	
	Naso lituratus	7.16 (2.2)	1.75 (0.3	11.51	53.89	
	Small-bodied parrotfish	0.08 (0.08)	1.8 (0.6)	6.89	60.66	

Chlorurus sordidus	*2.9 (1.5)*	*0.5 (0.3)*	6.22	66.88	
Goatfish	*0.8 (0.5)*	*0.8 (0.3)*	4.88	71.75	
Cephalopholis urodeta	*0.08 (0.08)*	*0.75 (0.2)*	4.59	76.34	
Acanthurus lineatus	*0.4 (0.19)*	*0.3 (0.18)*	3.67	80.02	
Macolor niger	*0.8 (0.6)*	*0.3 (0.2)*	3.24	83.26	
Aphareus furca	*0.6 (0.3)*	*0.08 (0.08)*	2.93	86.19	
Naso unicornis	*1.1 (0.6)*	*0.0 (0.0)*	2.88	89.07	
Naso hexacanthus	*2.0 (1.4)*	*0.0 (0.0)*	2.64	91.72	
E					3.18 (0.001)
Wrasse	*7.9 (1.4)*	*0.08 (0.08)*	22.22	22.22	
Small-bodied acanthurid	*8.25 (1.4)*	*2.5 (0.8)*	16.4	38.62	
Naso lituratus	*4.16 (1.1)*	*0.5 (0.2)*	12.01	50.63	
Small-bodied parrotfish	*0.5 (0.3)*	*3.7 (1.2)*	10.49	61.12	
Chlorurus sordidus	*1.3 (0.6)*	*0.5 (0.3)*	5.8	66.92	
Goatfish	*0.4 (0.2)*	*0.4 (0.1)*	4.53	71.45	
Scarus rubroviolaceus	*1.1 (1.1)*	*0.5 (0.2)*	4.03	75.49	
Cephalopholis urodeta	*0.4 (0.1)*	*0.08 (0.08)*	3.87	79.36	
Monotaxis grandoculus	*0.6 (0.4)*	*0.0 (0.0)*	3.53	82.9	
Lutjanus kasmira	*1.5 (1.5)*	*0.0 (0.0)*	3.19	86.08	
Acanthurus olivaceus	*0.08 (0.08)*	*0.6 (0.4)*	2.5	88.58	
Hipposcarus longiceps	*0.4 (0.3)*	*0.0 (0.0)*	2.21	90.79	
C					3.05 (0.001)
Wrasse	*6.5 (0.6)*	*0.08 (0.08)*	21.31	21.31	
Naso lituratus	*9.1 (2.5)*	*2.08 (0.9)*	12.06	33.37	
Rabbitfish	*5.8 (3.6)*	*1.6 (1.6)*	8.84	42.2	
Naso unicornis	*0.4 (0.4)*	*3.5 (1.8)*	8.59	50.79	
Small-bodied acanthurid	*10.5 (1.6)*	*5.0 (0.4)*	8.32	59.11	
Chlorurus sordidus	*1.7 (0.7)*	*0.25 (0.1)*	6.06	65.18	
Scarus rubroviolaceus	*0.9 (0.3)*	*0.08 (0.08)*	4.92	70.1	
Aphareus furca	*1.4 (0.6)*	*0.0 (0.0)*	4.53	74.63	
Acanthurus xanthopterus	*1.1 (0.6)*	*0.0 (0.0)*	3.44	78.07	
Goatfish	*0.1 (0.1)*	*1.2 (1.0)*	3.2	81.26	
Acanthurus olivaceus	*0.5 (0.2)*	*0.0 (0.0)*	3.16	84.43	
Small-bodied parrotfish	*0.25 (0.25)*	*0.25 (0.17)*	2.34	86.77	
Hipposcarus longiceps	*0.5 (0.3)*	*0.1 (0.1)*	2.31	89.07	
Monotaxis grandoculus	*0.3 (0.1)*	*0.0 (0.0)*	1.98	91.05	
B					3.03 (0.001)
Wrasse	*2.9 (0.7)*	*0.08 (0.08)*	15.87	15.87	

Naso lituratus	*3.41 (1.6)*	*1.08 (.31*	13.3	29.18
Small-bodied acanthurid	*10.2 (1.9)*	*7.6 (0.9)*	12.84	42.02
Rabbitfish	*2.0 (1.6)*	*1.4 (0.4)*	12.83	54.85
Chlorurus sordidus	*0.5 (0.3)*	*1.3 (0.4)*	10.79	65.64
Naso unicornis	*4.5 (4.5)*	*0.4 (0.2)*	6.19	71.83
Small-bodied parrotfish	*0.4 (0.4)*	*0.5 (0.2)*	5.93	77.75
Hemigymnus Spp.	*0.0 (0.0)*	*0.4 (0.1)*	4.3	82.05
Goatfish	*0.4 (0.2)*	*0.4 (0.4)*	3.37	85.42
Lethrinus harak	*0.3 (0.2)*	*0.0 (0.0)*	3.29	88.71
Scarus rubroviolaceus	*0.0 (0.0)*	*0.2 (0.13)*	2.87	91.59

Figure 13. PCO Plot depicting differences in multivariate space between fish assemblages of 1992 and those of the 2012. Vector overlays illustrate species that explain the variation associated with these data in multivariate space. Other fish groups such as small-bodied parrotfish and *Cephalopholis urodeta,* a small-bodied grouper increased in density over time.
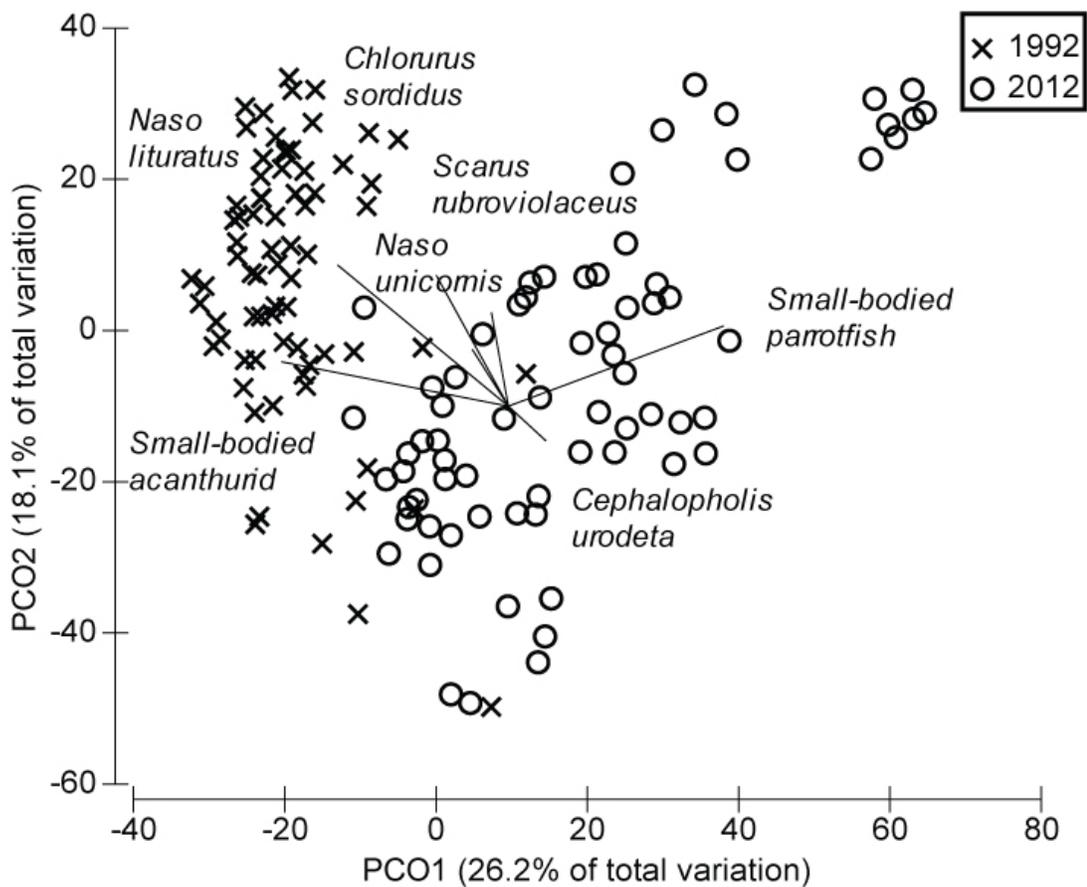
Figure 14A-F. PCO plots illustrating fish assemblage similarities among study years (1992 and 2012). Vector overlays were included to showcase how fish groups have changed through time.
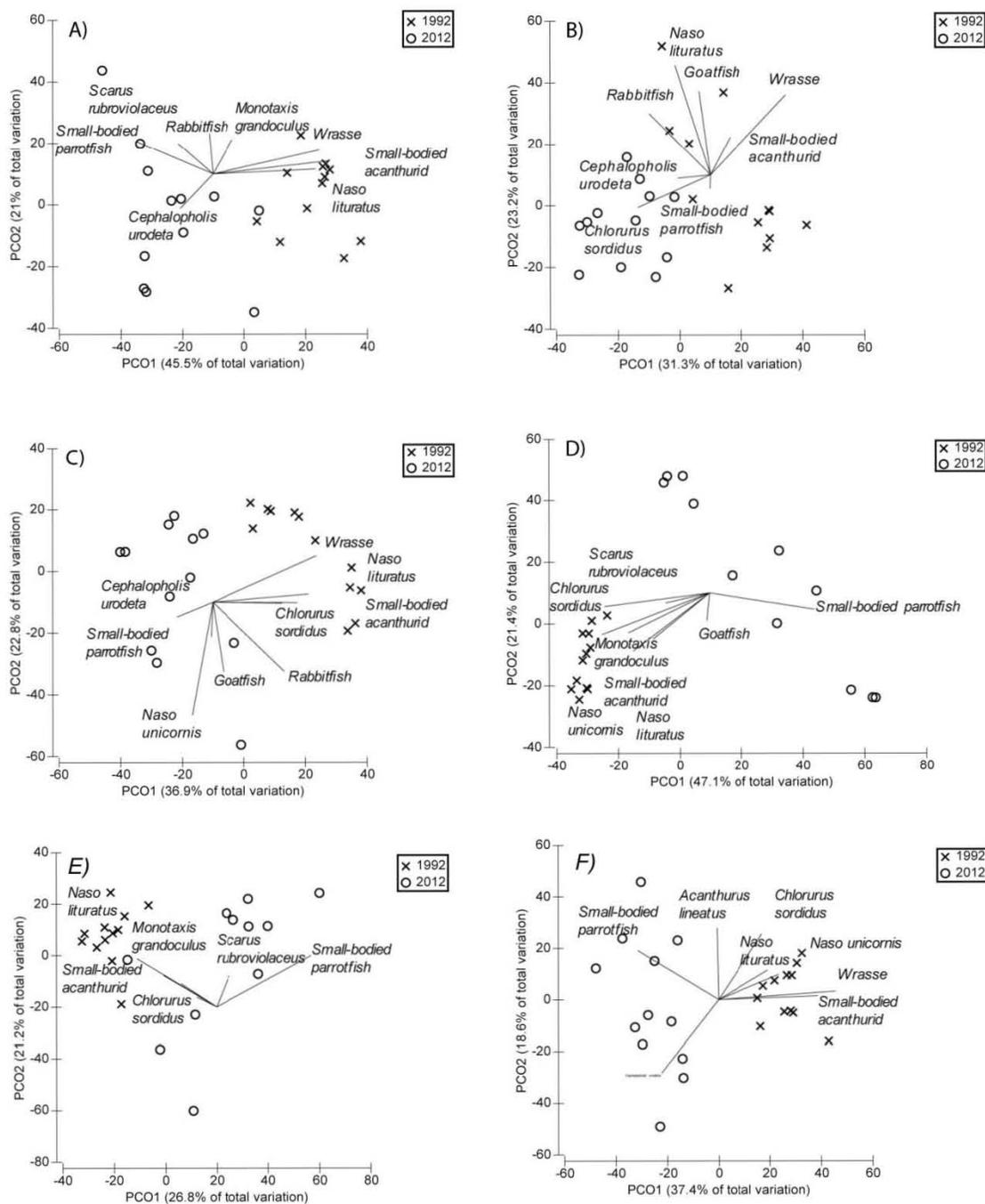
attributes. Site D experienced the greatest negative change (Table 3, t = 4.3, p value = >.001, Figure 14-D) both in terms of reduced heterogeneity and numeric density. Interestingly, reductions were most pronounced for sites in the western part of the study area (D to F), where the greatest wave exposure existed (Figure 2). For parts of Laolao Bay that experience the lowest wave exposure (A to C), the changes in heterogeneity were still significant and consistent in nature with others, but less pronounced. In sum, declines in numeric density across the majority of food-fish were ubiquitous. Another unique attribute of change was found for site C, whereby the popular food fish *Naso unicornis* showed an increase in density. However, this individual species increase was offset by the decrease in net density of a suite of other larger food fish. A second site in the eastern part of the bay also showed a mixed response in terms of numeric density for one large parrotfish, *Scarus rubroviolaceus*, which was also offset by a decrease in overall density across a suite of other species (Site B, Table 3, Figure 14-B).

Spatial Analysis:

Data indicated that heterogeneous fish assemblages existed across several sites, due to less variation among replicate SPC surveys existed in the eastern portion of the bay (Sites A and B, PERMDISPERSE Tests, F = 3.1 and 4.19, p-value = 0.04 and 0.006, respectively for 1992 and 2012). Because of this, spatial gradients during each timeframe were conducted using rank-based ANOSIM comparisons. The main source of spatial variation in 1992 was due to unique fish assemblages occurring at sites A, B, and D (R-statistic > 0.31, P<0.05, ANOSIM for all pairwise comparison with other sites, Table 4, Figure 15). Mixed small-bodied parrotfishes were found in highest density at site B, while mixed small-bodied acanthurids and two larger-bodied foodfish, *Monotaxis*

Figure 15A-B. MDS plots of fish assemblages across Laolao Bay for 1992 (A) and 2012 (B) with vector overlays to indicate species responsible for assemblage orientation in multivariate space.
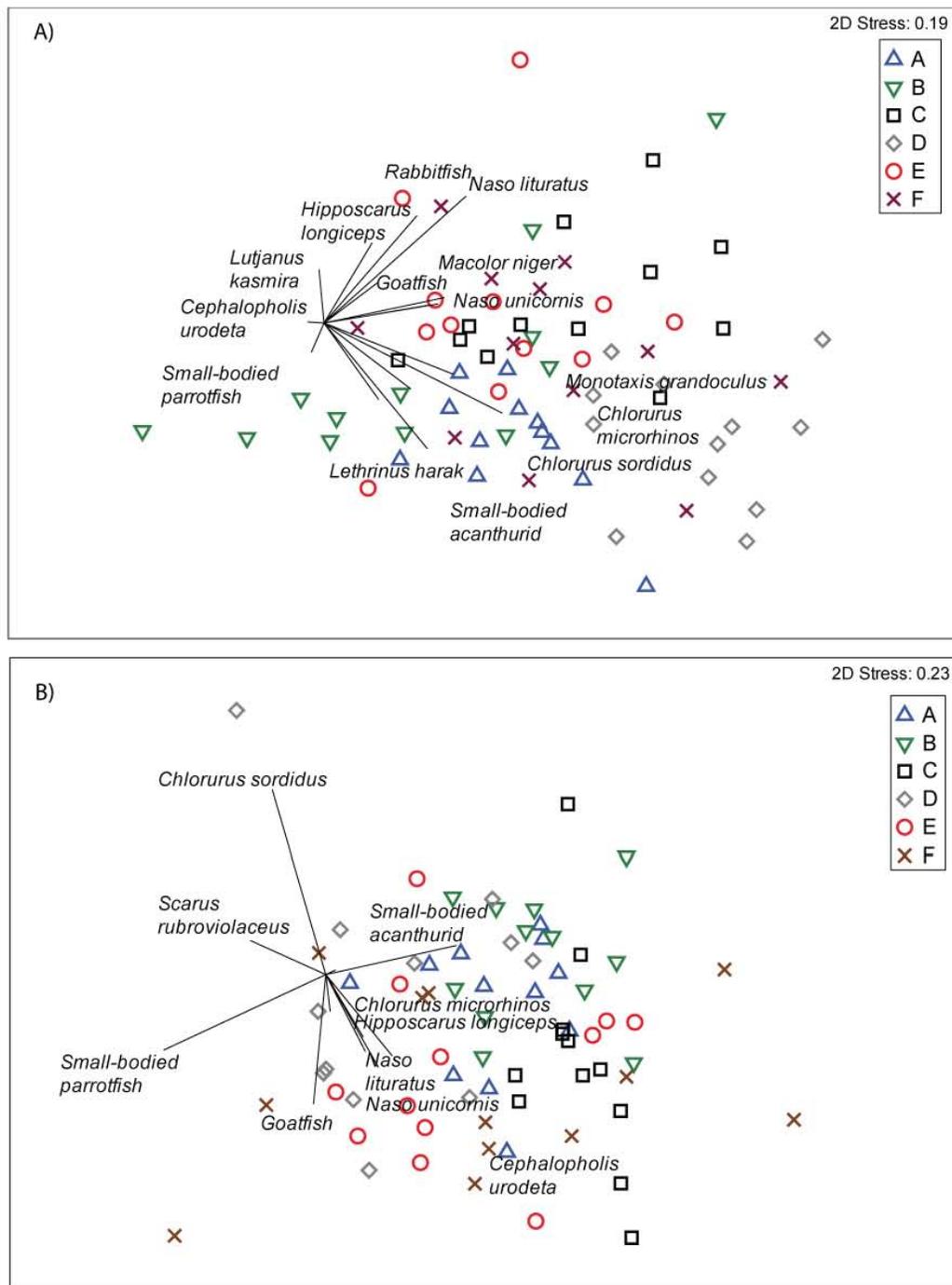
grandoculus and *Chlorurus microrhinos* were found at sites A and D. The subtle difference between the latter two sites was the shift in dominance from small-bodied acanthurids in the wave sheltered portion of the bay (site A), to a dominance of the small-bodied parrotfish *Chlorurus sordidus* (site D). In sum, moving from the sheltered portion of the bay to the more exposed side, small-bodied acanthurids had a notable decrease in density. Fish composition was similar for remaining sites in 1992. Trends for fish assemblages in 2012 were similar in terms of the transition from small-bodied acanthurids to small-bodied parrotfishes moving westward across the bay, however, site-level differences were greatly diminished (Table 4). Only site B appeared to have unique fish assemblages due to high occurrences of both small acanthurids and small scarids, perhaps representing a transition between reef habitats influenced by groundwater versus surface water discharge described above. Results of ANOSIM suggested that present fish populations throughout Laolao Bay were more similar to one another when compared to past assemblages (Table 4). This corroborates the decreased abundances of many species of food-fish at sites D, E, and F. Another consistent trend was the low heterogeneity consistently found for site A, where limestone bedrock exists in the watersheds and greater groundwater discharge was reported. In contrast, site C consistently had the highest heterogeneity, which was associated with proximity to the largest freshwater discharge channel associated with volcanic watersheds and runoff. In general, spatial findings were consistent with those of the temporal analysis.

Table 4. ANOSIM results of fish groupings in hierarchal order of site similarity for spatial analysis. Results depicted in the table show that differences in change through time do not significantly follow any specific gradient, however sites with unique habitats.

1992 Site Groups	R-statistic	P-value	2012 Site Groups	R-statistic	P-value
E, F	0.067	0.072	D, E	0.023	0.301
C, E	0.07	0.103	E, F	0.055	0.136
C, F	0.128	0.02	D, F	0.111	0.025
B, E	0.168	0.07	A, F	0.113	0.027
A, B	0.173	0.008	A, B	0.151	0.012
B, C	0.212	0.007	A, D	0.165	0.024
B, F	0.262	0.003	A, E	0.176	0.018
A, E	0.277	0.001	A, C	0.216	0.004
A, C	0.344	0.001	C, F	0.248	0.001
A, F	0.365	0.001	C, E	0.26	0.004
D, F	0.401	0.001	B, C	0.31	0.001
C, D	0.453	0.001	B, F	0.353	0.001
D, E	0.505	0.001	C, D	0.415	0.001
A, D	0.589	0.001	B, E	0.416	0.001
B, D	0.62	0.001	B, D	0.491	0.001

H0$_2$:

Depth Analysis:

The purpose of H0$_2$ was to understand if depth acted as a refuge for the food fish assemblages of Laolao Bay. Although no significant differences were found between food fish assemblages at 5m and 15m depths for both density and biomass(Table 5 & Figure 16, ANOSIM R-stat =0.25, 0.065 , p value =.1% for both), defining attributes between depth were noted. In terms of biomass fish assemblages at 15 m were more homogeneous, as less variation among replicate SPC's existed (PERMDISP = 2.5, p value = .09). This was due to fish assemblages at 15m comprising greater and more consistent biomass and density of *Holocentrids* and the small-bodied *Lutjanids (L. kasmira* and *L. fulvus)*, all of which are considered to be common table fish, and all of which had more uniformed occurrences among SPC's. Assemblages at 5m were generally more heterogeneous (PERMDISP = 4.4, p value = 0.006) due to varying abundances of small- bodied acanthurids, small-bodied parrotfish, *C. sordidus,* and *N. Lituratus* (Figure 17). One exception existed for site B` where relatively high heterogeneity existed due to the varying presence of *N. unicornis, C. sordidus, C. microrhinos, L. monostigma, L. fulvus, S. argenteus,* and mixed Holocentrids. Interestingly, two adjacent sites (E and E`) were both most homogeneous within their respective depth regimes (Figure 17- E). Overall, the lack of differences between assemblages of 5 and 15m suggests that depth does not act as a refuge to food-fish assemblages when considered as a single entity, as both depth strata were consistently dominated by *C. sordidus, C. striatus, S. psittacus,* and *C. urodeta.* Yet, differences in data homogeneity clearly define that depth-related characteristics existed.

Table 5. Results of ANOSIM test in hierarchal order of significance, for each respective sight grouping (H0$_2$). Table suggests that differences in fish assemblages between the respective depths are not significant for any sites throughout Laolao Bay.

Site Group	R-Statistic	P-value
B, B`	0.086	0.07
C, C`	0.113	0.44
F, F`	0.15	0.01
E, E`	0.197	0.005
A, A`	0.266	0.001
D, D`	0.375	0.001

Figure 16. MDS plot of fish populations in multivariate space between the two respective

depth regimes. Vector overlays were included to illustrate fish groups responsible for the

differnces between depths. The plot suggests that although differences exist between

depth, fish assemblages of these two strata are relatively homogenous with one other.
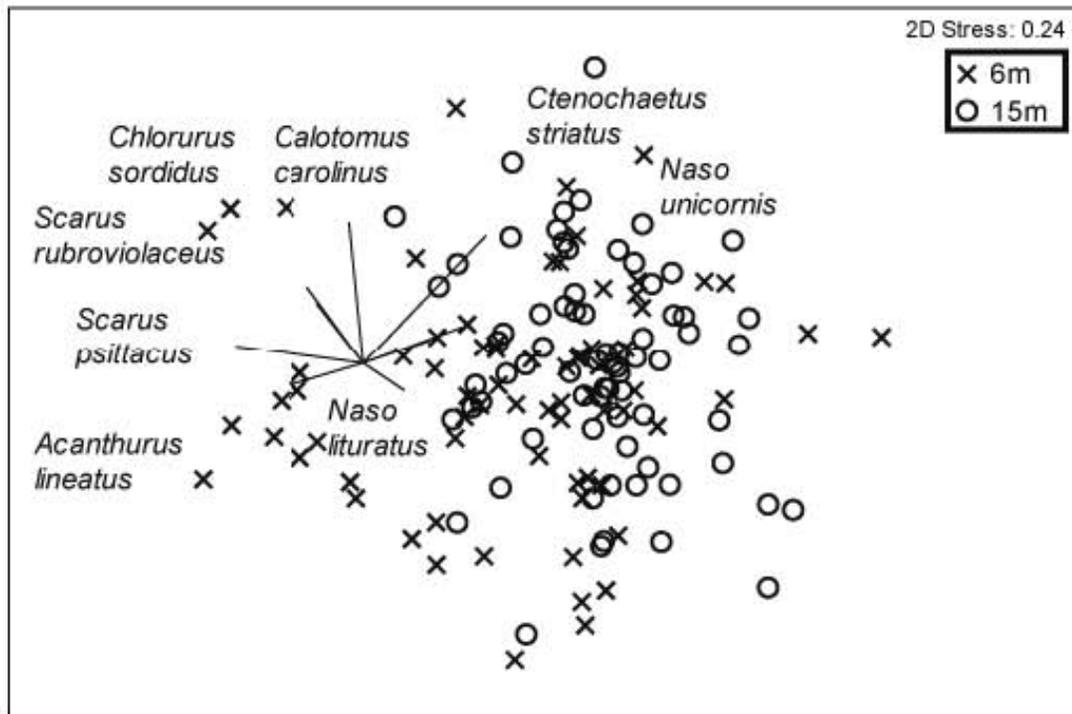
Figure 17A-F. MDS plots with vector overlays depicting differences in fish population biomass between depths throughout Laolao Bay. Plots suggest that differences between fish groups of the respective depths were relatively small.
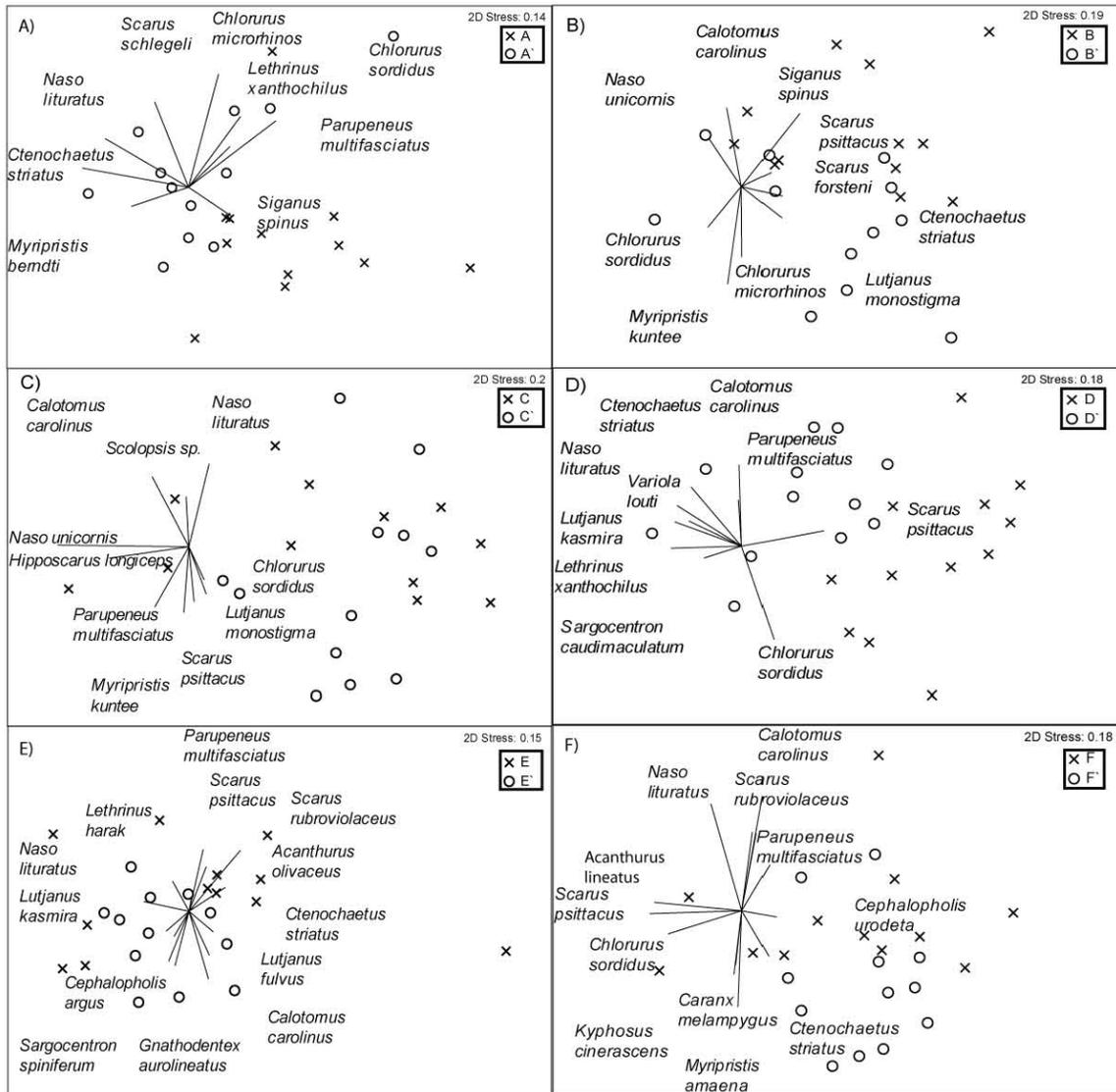
Similar examinations were undertaken across the two depth strata using fish densities instead of biomass. Investigations using fish density revealed the same general trend of greater heterogeneity at shallow depths due mainly to variations in small-bodied acanthurid assemblages (Figure 18). However, contrasting findings across depths were apparent for sites A - A'. Site A` had greater heterogeneity than site A due to high variability in densities of wrasses, small-bodied acanthurids, *L. xanthochilus*, and *L. bohar* at depth (Figure. 18-A). Site B and B` had the greatest homogeneity among all sites due to consistent presences of *N. unicornis, N. lituratus, C. microrhinos,*small-bodied acanthurids, and small-bodied parrotfish (Figure. 18-B).

H0$_3$:

Fish function roles as potential agents of benthic and coral assemblage change across Laolao Bay:

In analyzing factors attributed to changing fish assemblages since 1992, "Fish PCO change", a dependent variable based upon the distance between past and present data-points in multivariate space, was influenced greatest by water quality trends (Figure 19, Table 6, F = 23.01, p = 0.008). These relationships were driven by a strong association between declining water quality (i.e., greater water quality change values, Table 6) and increased densities in small-bodied herbivores, and declining water quality and lower densities of larger-bodied fish (Pearson's moment correlation r-values 0.77 and -0.77, respectively). Expectedly then, there was also a strong, negative association between changes in small-bodied herbivores and larger-bodied fish groups (i.e., acanthurid and scarid species that attain adult sizes less than 25 cm and all other larger fish grouped together). Yet, no relationships existed between water quality change and any of the coral assemblage metrics, such as skewness (p<0.05 for all associations),

Figure 18A-F. MDS plots illustrating the differences in fish assemblage densities between depths, for each sampled site. Vector overlays were inserted to show fish groups responsible for differences in multivariate space.
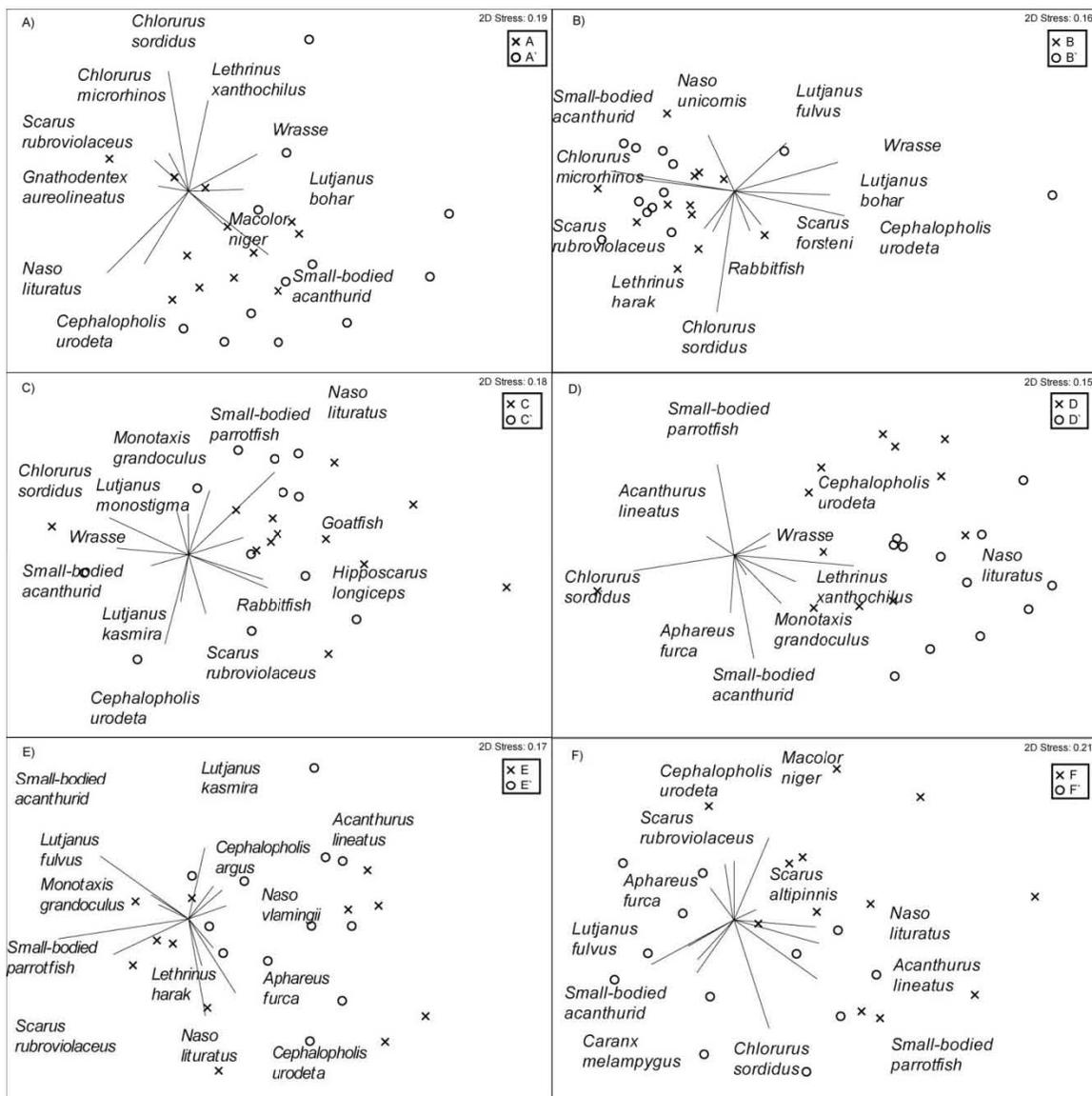
Figure 19. $H0_3$ and $H0_4$ historical regression and correlation diagram. For $H0_3$, only water quality change was found to have a significant relationship with changes in fish assemblages. Greater changes to water quality increases the change in Fish PCO and change in small-bodied herbivore populations, or negative changes to water quality result in increases in small-bodied herbivore population. For coral populations; greater wave exposure translated to a decrease in 3-D coral community structure.
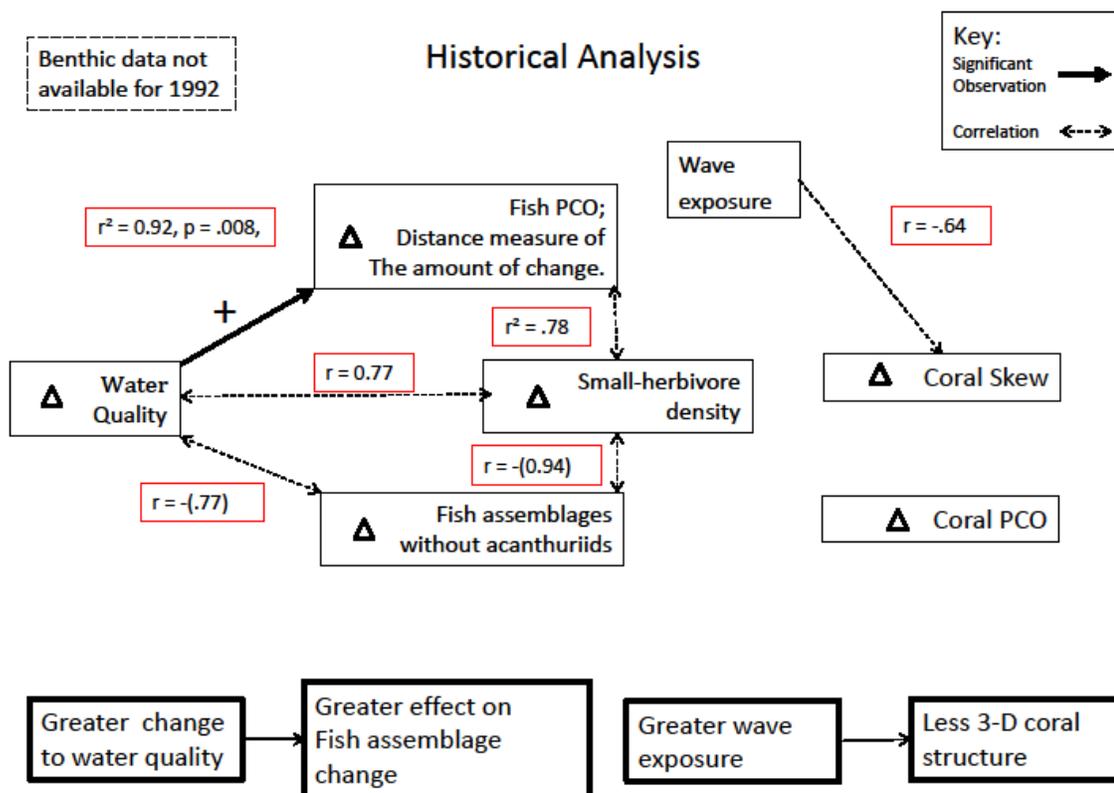
Table 6. Historical regression/correlation table showing variables responsible for driving the greatest amount of variation in fish and coral assemblage change over time. Measure of wave exposure and water quality were found to drive distance-based (i.e., multivariate) metrics of change in fish assemblages. Wave exposure also had a slight influence on coral three-dimensionality (i.e. skew)

Dependent	Equation	Slope(SE)	Intercept (SE)	R^2	P-Value	AIC
1)Fish PCO change	Y = .92 (wq) + .15	±.19	±.42	.81	.008	10.45
2) Fish PCO change	Y = .26 (wq x wave) + .82	±.07	±.38	.71	.02	12.95
3)Coral skew change	Y = -.65(wave) + 3.2	±.38	±.83	.27	.16	18.6

Table 7. 2012 regression/correlation table displaying metrics responsible for the greatest amount of changes to fish and coral assemblages of Laolao Bay. Again, measures of wave exposure were found to influence assemblage dynamics, however water quality did not have any significant effect on these regimes.

Dependent	Equation	Slope(SE)	Intercept (SE)	R^2	P-Value	AIC
1)Fish heterogeneity	Y = .83 (wave) + .33	±.27	±.61	.6	.04	14.9
2)Fish heterogeneity	Y = .34 (wave x wq_pco) + .52	±.07	±.35	.81	.008	10.3
3)BSR (2010)	Y = .89 (wave) + .2	±.22	±.48	.75	.01	12.2
4)BSR (2010)	Y = .81 (fish_hetero) +.37	±.29	±.63	.57	.04	15.4

which were expected intermediary drivers of negative changes in larger fish densities with greater habitat dependence. Similarly, the heterogeneity associated with 2012 fish assemblage data was interactively predicted by both water quality and wave exposure (F = 23.7, P = .008, interactive regression model, Table 7), whereby negative changes to water quality and low wave exposure predicted for fish assemblages that were dominated by small-bodied acanthurids. The consistent linkages found for both temporal and modern fish assemblage dynamics suggested that small-bodied herbivores responded to increased basal resources, and this increase in resources may have been driven by declining water quality and/or diminished larger-bodied herbivores. Modern 2012 data highlighted that the dominance of smaller-bodied herbivores, but not water quality, was associated with declining benthic substrate ratio's across Laolao, purporting a greater emphasis on the latter (Figure 20). The association between wave exposure and higher fish assemblage heterogeneity in 2010 (i.e., more diverse assemblages comprised of both small- and large-bodied species) also supports the latter (Figure 20).

H0$_4$:

Coral assemblages as potential agents of fish assemblage change across Laolao Bay:

In analyzing factors attributed to changing coral assemblages since 1992, wave exposure had the only association with shifting coral skewness (Pearson's moment correlation r-values = -0.64, Figure 19 Table 6), whereby high wave exposure was associated with smallest declines in skewness. No relationships were found between changing water quality and coral assemblages since 1992. Modern data supported these findings and depicted a significant, positive association between wave exposure and benthic substrate ratio's, suggesting wave exposure benefitted calcifying benthic

Figure 20. H0$_3$ and H0$_4$ multiple regression and correlation diagram for 2012. Significant interactive effects of wave exposure and water quality affect fish assemblage heterogeneity. Poor water quality and low wave exposure predict fish assemblages dominated by small-bodied acanthuriids, which in turn predicts dominance of non-calcifying benthic substrate.
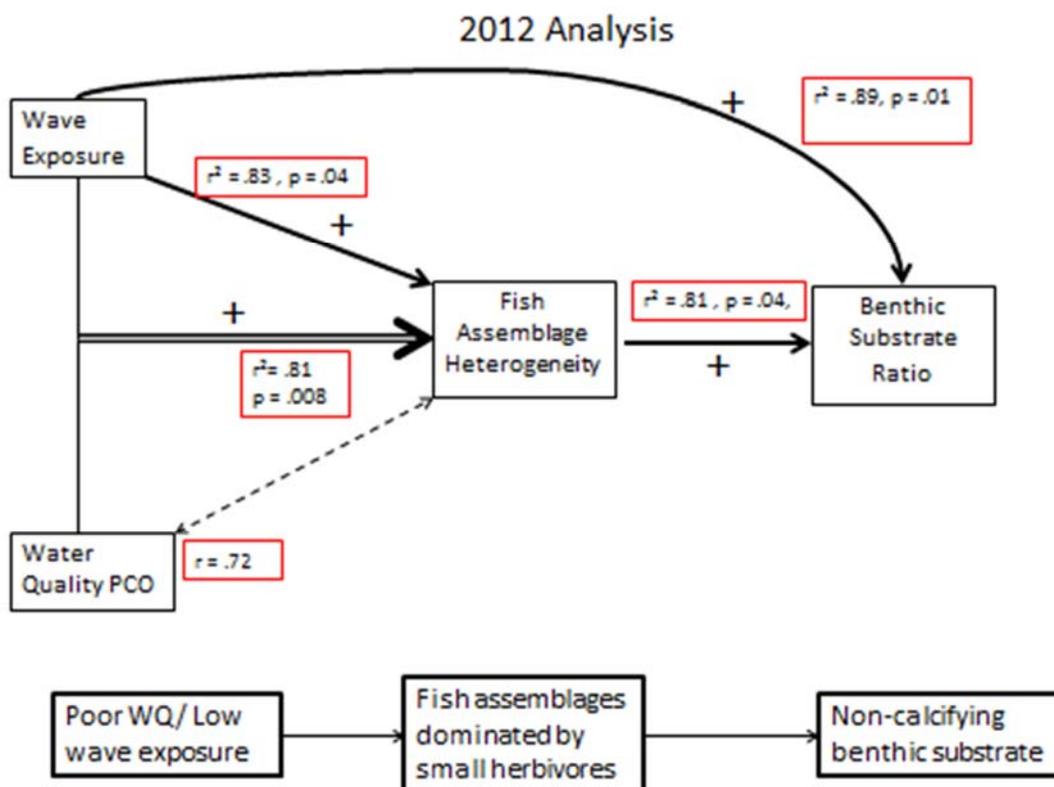
substrates. Modern data also found no associations between water quality and any coral or benthic assemblage metric. Fish assemblages with greater heterogeneity were the only other correlates of calcifying benthic substrates, yet as stated above, there was no evidence for expected intermediary relationships between structural coral loss and fish declines. Hence, there was less evidence to support HO4 because coral loss through time was only associated with low wave exposure (Houk, Okano et al. 2010), and 2012 benthic substrate ratio's declined spatially across Laolao in accordance with changing fish assemblages, but not water quality. The inability to account for changes to the coral communities of Laolao Bay since 1992 may be an artifact of the lack of relevant data, such as measures of fishing pressure and benthic composition through time.

Discussion:

This study examined spatially extensive snapshots of coral and fish assemblages in 1992 and 2012 across Laolao Bay, CNMI, providing a unique look into coral and fish population dynamics for an economically and culturally important reef setting. Temporal analyses found strong evidence for a ubiquitous decline in the majority of food fish densities across Laolao Bay, accompanied by increased densities of a few smaller-bodied, opportunistic counterparts. While consistent trends across all sites through time suggested that the nature of change was ubiquitous, spatial examinations found a gradient associated with the magnitude of change. Both change since 1992 and modern datasets depicted highest densities of small-bodied parrotfishes and surgeonfishes (i.e., the most compromised fish assemblages) to be most pronounced in eastern Laolao Bay, where wave exposure is minimal and karst watersheds provided a greater connection with groundwater discharge. These physical characteristics provided some insight as to what

the plausible drivers of change may be. Moving across the study area from east to west, wave energy increases substantially, with high waves limiting (fishing) access to western Laolao during parts of the year when trade winds produce large swells. Previous studies have found relationships between short time periods when calm weather exists (i.e., low wind and wave periods) and disproportionally successful reef fish landings (Houk, Rhodes et al. 2012), as well as high wave exposure and a lower fishing pressure metric that was derived from opinion surveys taken by CNMI's resource managers (Maynard et al. Reef resilience report). Thus, one perceived driver of the spatial trends was the relationships between wave exposure and fishing pressure. In addition, the easternmost, sub-watershed associated with the karst aquifer had the greatest, consistent contribution of nutrients and largest change in water quality through time. The combined influence of fishing pressure and reduced water quality serves to remove larger-bodied species (Hutchinson and Rhodes 2010) and provide more access to more algal and detrital resources for smaller-bodied counterparts (Jennings, Reynolds et al. 1999), respectively, and enhance the net algal and detrital resource pool (Fabricius, De'ath et al. 2005). In turn, the dominance of small-bodied herbivores and removal of larger-bodied species suggested that compromised grazing capacity became evident (Mumby, Dahlgren et al. 2006, Lokrantz, Nyström et al. 2008), because allometry dictates a non-linear relationship between fish size and function. Lokrantz et al. (2008) showed that a doubling in parrotfish size resulted in a 67% in grazing rate. In support, fish assemblage heterogeneity, which was an indicator of the degree of dominance by small-bodies herbivores, emerged as the strongest covariate of compromised benthic substrates in 2012.

Interestingly, depth analyses suggested that while many unique attributes existed between shallow and deeper fish assemblages, depth did not have a significant influence upon the density or biomass of many key functional groups, in contrast to what has been documented elsewhere (Tyler, Speight et al. 2009, Lindfield, McIlwain et al. 2014). It is speculated that the 15m habitats surveyed may not have been deep enough to show the expected signs of depth refuge, or previously legal (and perceived illegal) SCUBA fishing may have diminished resources at depth (Lindfield, McIlwain et al. 2014).

Benthic and coral assemblages also showed informative dynamics through time with respect to wave exposure, fish assemblages, and water quality. Historic studies suggested a disturbance event during the early phases of the 1992 surveys that was attributed to *Acanthaster planci* populations reported by fishermen, extreme low tides, and/or a nearby passing tropical storm event (Cheenis). Thus, recovery was expected across the two time periods given that no major disturbances have existed since 2003-2006 when *Acanthaster* were more recently documented (Houk, Bograd et al. 2007). The present study reported differences in the change in coral cover and colony density that provided evidence of non-uniform recovery throughout the bay (Figure 9). Although there was a universal increase in colony density throughout, shifts in size-class distributions and species assemblages provided three interesting scenarios. For sites A and B, there was a slight decline in coral cover, a slight increase in population density of smaller opportunistic corals (*Porites rus* in particular), and a significant decline in colony size distributions (Figures 9, 10, and 11). This scenario represented the least desirable case based upon known reef recovery patterns that typically show a return of coral cover manifested by larger colonies of mixed species given longer time periods following

disturbance events (Bellwood, Hughes et al. 2004, Golbuu, Victor et al. 2007). In contrast, coral cover had a slight increase at sites D and E, but population density grew substantially, and significant declines in size-class distributions were again observed. These trends were similar to above, but suggested that reefs were showing higher signs of recruitment, yet recruits were mainly opportunistic corals such as small favids, *Leptastrea*, and *Leptoria*, known to be tolerant to environmental stress (Nyström and Folke 2001, Hughes, Baird et al. 2003). This may also be a result of partial mortality of larger colonies followed by a continued selection against coral growth and recovery (Brodie, Fabricius et al. 2005, Gardner, Côté et al. 2005, Chollett, Mumby et al. 2012). Interestingly, size-class distributions have remained the most consistent through time for sites C and F, while coral cover increased. The positive changes through time were associated with a return to dominance by encrusting *Montipora* corals, and increases in some branching *Acropora* and *Pocillopora* corals that add three-dimensionality to reefs. Thus, the recovery of coral assemblages from these two locales provides an interesting situation compared to others.

Site F had the greatest wave exposure, and site-specific recovery resonated well with an ongoing study. Houk et al. (in review) examined the dynamics of 21 sites around CNMI following the 2003 – 2006 disturbance period associated with high *Acanthaster planci* populations, and found that wave exposure was a primary factor driving recovery. However, herbivore populations and water quality proxies significantly increased the amount of variance explained in a spatially-inconsistent manner, relevant to the synthesis of this thesis presented below. Within Laolao Bay, the highest wave exposure existed at site F, suggesting its role as a primary driver of recovery. In support, a significant

association existed between wave exposure and coral skewness change (i.e., an indicator of coral community structure and function) across all sites (Figure 19). This has similarly been found elsewhere, whereby high-cover, *Montastrea*-dominated reefs in the Caribbean had greatest affinities with wave exposure (Chollett and Mumby 2012). However, recovery at site C was less attributable to wave exposure, as moderate exposure existed, yet recovery was maximal. Noted above, site C had the highest biomass and density of larger-bodied fish, including numerous herbivores, purporting a stronger role of fish assemblages (i.e., grazing) in promoting coral assemblage recovery (Mumby and Harborne 2010). It is speculated that site C represents a unique locale where land-based sediments and reef flat algal build-up have naturally had a strong connection with near-shore reefs due to the presence of the largest hydrodynamic channel in Laolao Bay being adjacent to this site. Hence, this natural geomorphological situation may be facilitating, in part, the presence of larger-bodied herbivore assemblages, with ensuing benefits to the corals.

Benthic data collected in 2012 support the general findings depicted from coral assemblages. Low wave exposure, high groundwater influence, and compromised herbivore populations were associated with a dominance of turf and macroalgae throughout eastern portions of the bay, which are known to impede coral settlement and growth (Keats, Chamberlain et al. 1997, McCook 1999, Mumby, Hastings et al. 2007). In contrast, maximal coral growth was reported at sites C and F, and an overall strong association between wave exposure and heavily-calcifying benthic substrates grouped together existed (combined cover of corals and crustose coralline algae, Figures 8 and 20). Wave exposure has been shown to promote a dominance of calcifying substrates

elsewhere in Micronesia (Houk, Benavente et al. 2012), and also influence reef accretion through time (Grigg 1998). In contrast to wave exposure, water quality did not have a predictable influence upon 2012 benthic substrates across the entire bay, but compromised herbivore assemblages did (Figure 20). Clearly, it seems relevant to contextualize the influences of localized stressors across Laolao Bay while accounting for wave exposure, a driving natural environmental regime.

Correlation analyses and regression examinations indicated that two key environmental drivers of change to Laolao Bay were water quality and wave exposure, both which had linked associations with the fishes, corals, and benthic substrates that suggested plausible pathways for change since 1992, and spatial gradients in 2012. Diminished water quality across space and through time had the similar, positive association with small-bodied acanthurids, and negative association with larger-bodied, mixed species assemblages. Several studies support these results whereby fish assemblages dominated by small-bodied species that can rapidly respond to resource availability become prolific where chronic stress from reduced water quality persisted (Hughes, Rodrigues et al. 2007). In addition, coral loss from disturbances and/or poor water quality has been attributed to reduced reef structure (i.e., loss of large, three-dimensional coral colonies), and a decline in fisheries potential of larger-bodied species with economic potential (Pratchett, Gust et al. 2001, Jones, McCormick et al. 2004). Yet, recent studies in the Seychelles provide alternative lines of evidence. One atoll where fishing has been prohibited for several years was impacted by repeated coral bleaching events over the past decade, yet biomass of most large-bodied species with high fisheries potential remains (Friedlander, Obura et al. 2014). Clearly disturbances have direct

impacts for fishes that are coral obligates (Pratchett 2005), and a major loss of structure would eventually reduce fisheries potential (Jones, McCormick et al. 2004), yet it is important to consider the functional role of fishes in controlling algae and promoting coral growth.

This study reports strong associations between poor water quality and the increased dominance of small-bodied species, but provided no evidence linking water quality to coral assemblages or benthic substrates when considering the gradient among all sites across Laolao. Rather, sessile organisms were best predicted by wave exposure (historical analyses) in combination with herbivore assemblages (2012 spatial gradients). While declines in water quality were inferred through time for two sites (A and E), these may represent site-specific instances where water quality impacts were most substantial, as gradients inclusive of all sites were not significant. Further, these sites had the greatest shifts in coral demography, and the most prolific growth of less-calcifying algae that are known to impede coral recruitment and survival (Antonius 1999, Antonius 2001). Therefore, this study provided less evidence to support $H0_4$, where coral loss from disturbance or water quality was the suspected driver of declining food fish fish resources. In turn, more evidence existed to support $H0_3$, where fish assemblages have shifted through time, and this shift has resulted in the proliferation of compromised assemblages with reduced ecological function. This notion is also supported by Houk et al. (in review) who examined a 12-year dataset from CNMI's long-term monitoring program and found that beyond wave exposure, the process of herbivory appeared to be highly influential in predicting coral assemblage recovery. Laolao Bay represented a low anchor point in their regression models, where recovery was greatly diminished. It

followed that water quality was also a significant predictor of trends, but water quality had a more spatially-restricted influence upon reefs where land-based impacts in the watershed were most observable. Site A was associated with karst watersheds and the development of a golf course following the 1992 study, and Site E has a large watershed that is connected to urban development and road construction in the upper watershed.

Overall, the western portion of the bay held fish assemblages with greater heterogeneity, a trend that was associated with less dominance of smaller-bodied surgeonfishes, and greater abundances of mixed fish assemblages mainly from the herbivore and secondary consumer guilds. The unique attributes of high herbivore biomass at site C were strongly driven by the increase of one species between 1992 and the present (*N. unicornis*), while other species decreased. Thus, heterogeneity for all sites on the eastern part of the bay were diminished, and the strongest explanatory factor was wave exposure. There was also a general gradient of low-to-high ecosystem integrity moving east-to-west across Laolao Bay, depicted by high coral cover and more favorable calcifying benthic substrate, with site C representing the data point in the predictive association where residuals were highest. Fish assemblages with higher diversity and biomass were noted in western compared to eastern Laolao based upon 2012 data, yet comparisons through time revealed a greater decline in both metrics in the western portion of the bay. It is speculated that greater declines in fish abundance in western Laolao may be due to the transfer of fishing effort in the more wave exposed portion of the bay through time as fish resources in the calmer parts of Laolao diminished (sites D, E, and F). 1992 data suggested the relative dominance of smaller-bodied, faster growing species already existed in the eastern portion of the bay, where wave exposure was

minimal, and fishing access greatest (predominantly for day/night spearfishing). Given a greater harvesting potential with increased wave exposure that has been documented for CNMI (Houk, Rhodes et al. 2012), increasing fishing effort on more exposed reefs could have become emergent (Jennings and Polunin 1996, Cinner and McClanahan 2006). Yet, it is problematic that no fishing effort data exists through time to formally develop these themes. This premise is therefore not scientifically grounded, but rather based on personal observation, and local knowledge of fishing practices throughout Laolao Bay. However, understanding gradients in fishing pressure for Laolao Bay, and the entire CNMI, should be considered a priority for resource management agencies.

This study has documented the change in food fish assemblages of Laolao Bay, and was able to address several issues as to how and why these shifts have occurred. The roles of water quality and wave exposure were found to be distributed throughout Laolao Bay in a non-uniform pattern, shedding light on the spatial gradients present within the bay. Specifically, the influence of natural geomorphology (i.e., karst limestone substrate in eastern Laolao, and greater wave exposure in western Laolao) served to drive underlying differences between coral, benthic and fish assemblages of east and west portions of Laolao Bay. Several factors limited this studies ability to explain the role of coral-reef structure on fish assemblage dynamics, the role of depth on fish assemblage structure, and the greater decreases in density to western portions of Laolao despite greater wave exposure. The availability of fisheries dependent and catch effort data, would have served to identify and partition greater amounts of variation explained by the spatial gradients of fishing pressure. Conveniently, these limitations provide clear direction for future fisheries research focused at Laolao Bay. It is also highlighted that

although we draw conclusions about change through time from historical "baseline" data (i.e., 1992 dataset); the resources of Laolao Bay have been subjected to external stressors long before these studies were carried out. This reinforces perceptions that fish and coral assemblages of Laolao Bay have been compromised prior to 1992, consistent with the logic of shifting baselines (Pauly 1995), whereby the lack of understanding of these present regimes stems from the inability to adequately visualize true change through time. In conclusion the analysis of the fish assemblages of Laolao Bay have provided local managers with a statistical documentation of how the synergistic factors of wave exposure, water quality and fishing pressure influence the spatial gradients and recovery patterns of the coral reefs ecosystems of Laolao Bay. Ultimately this study underscored shifting baselines, and the importance of documenting change through time, in hopes that proper management of such economically important resources remains a priority for the sake of the future generations of resource users at Laolao Bay.

Bibliography:

Almany, G. R., et al. (2010). "Research partnerships with local communities: two case studies from Papua New Guinea and Australia." Coral Reefs **29**(3): 567-576.

Anderson, M., et al. (2008). "PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods." Plymouth, UK, 214pp. PRIMER-E, Plymouth, UK, 214pp.

Anthony, K. R. N. and O. Hoegh-Guldberg (2003). "Variation in coral photosynthesis, respiration and growth characteristics in contrasting light microhabitats: an analogue to plants in forest gaps and understoreys?" Functional Ecology **17**(2): 246-259.

Antonius, A. (1999). "Metapeyssonnelia corallepida, a new coral-killing red alga on Caribbean reefs." Coral Reefs **18**(3): 301-301.

Antonius, A. (2001). "Pneophyllum conicum, a coralline red alga causing coral reef-death in Mauritius." Coral Reefs **19**(4): 418-418.

Aronson, R. B., Precht, W.F., Toscano, M.A., Koltes, K.H. (2002). "The 1998 bleaching event and its aftermath on a coral reef in Belize." Coral Reefs.

Bell, P. (1992). "Eutrophication and coral reefs -- some examples in the Great Barrier Reef lagoon." Water Res. **26**(5): 553-568.

Bellwood, D., et al. (2004). "Confronting the coral reef crisis." <u>Nature</u> **429**(6994): 827-833.

Bellwood, D. R. (2003). "Origins and escalation of herbivory in fishes: a functional perspective." <u>Paleobiology</u> **29**(1): 71-83.

Bellwood, D. R. and J. H. Choat (2011). "Dangerous demographics: the lack of juvenile humphead parrotfishes Bolbometopon muricatum on the Great Barrier Reef." <u>Coral Reefs</u> **30**(2): 549-554.

Bellwood, D. R., et al. (2012). "Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs." <u>Proceedings of the Royal Society B: Biological Sciences</u> **279**(1733): 1621-1629.

Bohnsack, J. A. and S. P. Bannerot (1986). A stationary visual census technique for quantatively assessing community structure of coral reef fishes, National Oceanic and Atmospheric Administration Technical Report. **NMFS 41**.

Bonaldo, R. M. and D. R. Bellwood (2008). "Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia." <u>Marine Ecology-Progress Series</u> **360**: 237-244.

Brander, J. A. and M. Scott Taylor (1998). "Open access renewable resources: Trade and trade policy in a two-country model." Journal of International Economics **44**(2): 181-209.

Brodie, J., et al. (2011). "Assessment of the eutrophication status of the Great Barrier Reef lagoon (Australia)." Biogeochemistry **106**(2): 281-302.

Brodie, J., et al. (2005). "Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence." Marine Pollution Bulletin **51**(1): 266-278.

Brown, B. and J. Bythell (2005). "Perspectives on mucus secretion in reef corals." Marine Ecology Progress Series **296**: 291-309.

Bruno, J. F., et al. (2003). "Nutrient enrichment can increase the severity of coral diseases." Ecology Letters **6**(12): 1056-1061.

Bruno, J. F. and E. R. Selig (2007). "Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons." PLoS ONE **2**(8): e711.

Cesar, H., et al. (2003). "The economics of worldwide coral reef degradation."

Cheenis (1991). Cheenis 1991_6 Water Quality. Saipan, CNMI.

Choat, J. H. and D. R. Robertson (2002). Age-based studies on coral reef fishes. Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem (San Diego: Academic Press, 2002). P. Sale. San Diego, Academic Press**: 57-80.

Chollett, I. and P. Mumby (2012). "Predicting the distribution of Montastraea reefs using wave exposure." Coral Reefs **31**(2): 493-503.

Chollett, I., et al. (2012). "Physical environments of the Caribbean Sea." Limnology And Oceanography **57**(4): 1233.

Cinner, J. and T. McClanahan (2006). "Socioeconomic factors that lead to overfishing in small-scale coral reef fisheries of Papua New Guinea." Environmental Conservation **33**(01): 73-80.

Cinner, J. E., et al. (2009). "Socioeconomic Factors that Affect Artisanal Fishers' Readiness to Exit a Declining Fishery." Conservation Biology **23**(1): 124-130.

Company, C. P. (1992). Quantitative marine baseline survey. Biological resources and water quality. Bahia Laulau and Unai Laulau Kattan areas, Saipan, Mariana Islands. C. C. R. M. Office. Saipan, MP.

Connell, J. H. (1997). Disturbance and recovery of coral assemblages, Coral Reefs. **16:** S101-S113.

De'ath, G. and K. Fabricius (2010). "Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef." <u>Ecological Applications</u> **20**(3): 840-850.

De'ath, G., et al. (2012). "The 27-year decline of coral cover on the Great Barrier Reef and its causes." <u>Proceedings Of The National Academy Of Sciences Of The United States Of America</u> **109**(44): 17995-17999.

Dulvy, N., et al. (2004). "Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects." <u>Canadian Journal Of Fisheries And Aquatic Sciences</u> **61**(3): 466-475.

Dulvy, N. K., et al. (2004). "Coral reef cascades and the indirect effects of predator removal by exploitation." <u>Ecology Letters</u> **7**(5): 410-416.

Ekebom, J., et al. (2003). "A GIS-based step-wise procedure for assessing physical exposure in fragmented archipelagos." <u>Estuarine, Coastal and Shelf Science</u> **57**(5): 887-898.

Essington, T. E., et al. (2006). "Fishing through marine food webs." <u>Proceedings of the National Academy of Sciences of the United States of America</u> **103**(9): 3171-3175.

Fabricius, K., et al. (2005). "Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef." <u>Marine Pollution Bulletin</u> **51**(1): 384-398.

Friedlander, A. M., et al. (2003). "Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago." <u>Coral Reefs</u> **22**(3): 291-305.

Friedlander, A. M. and E. E. DeMartini (2002). "Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators." <u>Marine Ecology Progress Series</u> **230**: 253-264.

Friedlander, A. M., et al. (2014). "Coexistence of Low Coral Cover and High Fish Biomass at Farquhar Atoll, Seychelles." <u>PLoS One</u> **9**(1).

Gardner, T. A., et al. (2005). "Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline." <u>Ecology</u> **86**(1): 174-184.

Gilmour, J. P., et al. (2013). "Recovery of an Isolated Coral Reef System Following Severe Disturbance." <u>Science</u> **340**(6128): 69-71.

Golbuu, Y., et al. (2007). "Palau's coral reefs show differential habitat recovery following the 1998-bleaching event." <u>Coral Reefs</u> **26**(2): 319-332.

Graham, N. A. J., et al. (2011). "Coral reef recovery dynamics in a changing world." <u>Coral Reefs</u> **30**(2): 283-294.

Greenstein, B., et al. (1998). "Shifting ecological baselines and the demise of Acropora cervicornis in the western North Atlantic and Caribbean Province: a Pleistocene perspective." <u>Coral Reefs</u> **17**(3): 249-261.

Grigg, R. (1998). "Holocene coral reef accretion in Hawaii: a function of wave exposure and sea level history." <u>Coral Reefs</u> **17**(3): 263-272.

Grigg, R. W., et al. (1984). "Model Of A Coral-Reef Ecosystem .3. Resource Limitation, Community Regulation, Fisheries Yield And Resource-Management." <u>Coral Reefs</u> **3**(1): 23-27.

Halford, A. (1996). "Recovery of a fish community six years after catastrophic marotality event." <u>Proc 8th Int Coral Reef Symp, Panama</u>: 1011-1016.

Houk, P., et al. (2012). "Characterization and evaluation of coral reefs around Yap Proper, Federated States of Micronesia." Biodiversity and Conservation **21**(8): 2045-2059.

Houk, P., et al. (2013). "Coral reef disturbance and recovery dynamics across gradients of localized stressors in the Mariana Islands." In review.

Houk, P., et al. (2007). "The transition zone chlorophyll front can trigger Acanthaster planci outbreaks in the Pacific Ocean: Historical confirmation." Journal of oceanography **63**(1): 149-154.

Houk, P. and C. Musburger (2013). "Trophic interactions and ecological stability across coral reefs in the Marshall Islands." Mar. Ecol. Prog. Ser **488**: 23-34.

Houk, P., et al. (2010). "Water quality and herbivory interactively drive coral-reef recovery patterns in American Samoa." PLoSONE **5**(11): e13913.

Houk, P., et al. (2010). "Water quality and herbivory interactively drive coral-reef recovery patterns in American Samoa." PLoS One **5**(11): e13913.

Houk, P., et al. (2010). Laolao Bay Road and Coastal Management Improvement Project: Ecological and Water Quality Assessment, Pacific Marine Resources Institute.

Houk, P., et al. (2012). "Commercial coral-reef fisheries across Micronesia: A need for improving management." Coral Reefs **31**(1): 13-26.

Houk, P. and R. Van Woesik (2006). "Coral reef benthic video surveys facilitate long-term monitoring in the commonwealth of the Northern Mariana Islands: Toward an optimal sampling strategy." Pacific Science **60**(2): 177-189.

Hubbell, S. P. (1997). "A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs." Coral Reefs **16**: S9-S21.

Hughes, T. P., et al. (2003). "Climate change, human impacts, and the resilience of coral reefs." Science **301**(5635): 929-933.

Hughes, T. P., et al. (2007). "Phase shifts, herbivory, and the resilience of coral reefs to climate change." Curr Biol **17**(4): 360-365.

Hutchinson, N. and K. Rhodes (2010). "Home range estimates for squaretail coralgrouper, Plectropomus areolatus (Ruppell 1830)." Coral Reefs **29**(2): 511-519.

Jackson, J. B., et al. (2001). "Historical overfishing and the recent collapse of coastal ecosystems." Science **293**(5530): 629-637.

Jennings, S. and N. Polunin (1996). "Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities." Journal Of Applied Ecology **33**(2): 400-412.

Jennings, S. and N. V. Polunin (1996). "Impacts of fishing on tropical reef ecosystems." Ambio: 44-49.

Jennings, S., et al. (1999). "Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories." Conservation Biology **13**(6): 1466-1475.

Jennings, S., et al. (1999). "Predicting the Vulnerability of Tropical Reef Fishes to Exploitation with Phylogenies and Life Histories." Conservation Biology **13**(6): 1466-1475.

Johannes, R. E. (1981). Words of the lagoon: fishing and marine lore in the Palau district of Micronesia, Univ of California Press.

Jones, G. P., et al. (2004). "Coral decline threatens fish biodiversity in marine reserves." Proceedings of the National Academy of Sciences of the United States of America **101**(21): 8251-8253.

Keats, D. W., et al. (1997). "Pneophyllum conicum (Dawson) comb nov (Rhodophyta, Corallinaceae), a widespread Indo-Pacific non-geniculate coralline alga that overgrows and kills live coral." Botanica Marina **40**(4): 263-279.

Knowlton, N. and J. B. Jackson (2008). "Shifting baselines, local impacts, and global change on coral reefs." PLoS biology **6**(2): e54.

Kohler, K. E. and S. M. Gill (2006). "Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology." Computers & Geosciences **32**(9): 1259-1269.

Lindfield, S. J., et al. (2014). "Depth Refuge and the Impacts of SCUBA Spearfishing on Coral Reef Fishes." PLoS One **9**(3): e92628.

Lokrantz, J., et al. (2008). "The non-linear relationship between body size and function in parrotfishes." Coral Reefs **27**(4): 967-974.

Loya, Y., et al. (2001). "Coral bleaching: the winners and the losers." Ecology Letters **4**(2): 122-131.

Marubini, F. and P. S. Davies (1996). "Nitrate Increases Zooxanthellae Population Density and Reduces Skeletogenesis in Corals." Marine Biology **127**(2): 319-328.

McClanahan, T. (1995). "A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes." Ecological Modelling **80**(1): 1-19.

McClanahan, T. R., et al. (2011). "Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries." Proceedings Of The National Academy Of Sciences Of The United States Of America **108** (41): 17230-17233.

McClenachan, L. (2009). "Documenting loss of large trophy fish from the Florida Keys with historical photographs." Conserv Biol **23**(3): 636-643.

McCook, L. J. (1999). "Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef." Coral Reefs **18**(4): 357-367.

McCook, L. J., et al. (2010). "Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves." Proceedings of the National Academy of Sciences of the United States of America **107**(43): 18278-18285.

McGoodwin, J. R. (2001). Understanding the cultures of fishing communities: A key to fisheries management and food security, Food & Agriculture Org.

Mumby, P. J., et al. (2006). "Fishing, trophic cascades, and the process of grazing on coral reefs." Science **311**(5757): 98-101.

Mumby, P. J. and A. R. Harborne (2010). "Marine reserves enhance the recovery of corals on Caribbean reefs." PLoS One **5**(1): e8657.

Mumby, P. J. and A. R. Harborne (2010). "Marine reserves enhance the recovery of corals on Caribbean reefs." PLoS ONE **5**(1).

Mumby, P. J., et al. (2007). "Thresholds and the resilience of Caribbean coral reefs." Nature **450**(7166): 98-101.

Myers, R. A. and B. Worm (2003). "Rapid worldwide depletion of predatory fish communities." Nature **423**(6937): 280-283.

Nugues, M. M. and C. M. Roberts (2003). "Coral mortality and interaction with algae in relation to sedimentation." Coral Reefs **22**(4): 507-516.

Nyström, M. and C. Folke (2001). "Spatial resilience of coral reefs." Ecosystems **4**(5): 406-417.

Pandolfi, J. M. and J. B. C. Jackson (2006). "Ecological persistence interrupted in Caribbean coral reefs." Ecology Letters **9**(7): 818-826.

Pauly, D. (1995). "Anecdotes and the shifting baseline syndrome of fisheries." Trends in Ecology and Evolution **10**(10): 430.

Pauly, D. (2008). "Global fisheries: a brief review." Journal of Biological Research-Thessaloniki **9**: 3-9.

Pauly, D., et al. (2005). "Global trends in world fisheries: impacts on marine ecosystems and food security." Philosophical Transactions of the Royal Society B: Biological Sciences **360**(1453): 5-12.

Pratchett, M., et al. (2001). "Consumption of coral propagules represents a significant trophic link between corals and reef fish." Coral Reefs **20**(1): 13-17.

Pratchett, M. S. (2005). "Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef." Marine Biology **148**(2): 373-382.

Rhodes, K. L. and M. H. Tupper (2007). "A preliminary market-based analysis of the Pohnpei, Micronesia, grouper (Serranidae : Epinephelinae) fishery reveals unsustainable fishing practices." Coral Reefs **26**(2): 335-344.

Russel, S. (1998). Tiempon I Manmofo'na: Ancient Chamorro Culture and History of the Northern Mariana Islands. Micronesian Archaeological Survey Report 32. CNMI Division of Historic Preservation**: 179-192.

Salinas-de-León, P., et al. (2013). "Temporal and spatial variability in coral recruitment on two Indonesian coral reefs: consistently lower recruitment to a degraded reef." Marine Biology **160**(1): 97-105.

Starmer, J. and P. Houk (2008). Marine and Water Quality Monitoring Plan for the Commonwealth of the Northern Mariana Islands. C. D. o. E. Q. a. C. R. M. Agency. Saipan, MP.

Sweatman, H., et al. (2011). "Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends." Coral Reefs **30**(2): 521-531.

Talbot, F. H. B. C. R. and G. R. V. Anderson (1978). "   "Coral reef fish communities: unstable, high diversity systems?"." Ecol. Monogr. 48:425-440.

Tyler, E. H., et al. (2009). "Evidence for a depth refuge effect in artisanal coral reef fisheries." Biological Conservation **142**(3): 652-667.

van Beukering, P., et al. (2006). "The Economic Value of the Coral Reefs of Saipan, Commonwealth of the Northern Mariana Islands." Technical Report submitted to the CNMI Coral Reef Initiative, Saipan, MP.

Wilson, S., et al. (2010). "Habitat degradation and fishing effects on the size structure of coral reef fish communities." Ecological Applications **20**(2): 442-451.

Wilson, S. K., et al. (2010). "Habitat degradation and fishing effects on the size structure of coral reef fish communities." Ecological Applications **20**(2): 442-451.

Zeller, D., et al. (2007). "Re-estimation of small-scale fishery catches for US flag-associated island areas in the western Pacific: the last 50 years." Fishery Bulletin **105**(2): 266-277.

Zeller, D., et al. (2006). "Fisheries contributions to the gross domestic product: underestimating small-scale fisheries in the Pacific." Marine Resource Economics **21**: 355-374.