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Title: LINKING PATTERNS AND PROCESSES WITH SHIFTING BASELINES ON CORAL REEFS.

Approved: ______________________________

Peter C. Houk, Chairman, Thesis Committee

Kosrae is a small, sparsely populated Pacific island whose people rely heavily on marine resources and depend on coral-reef resilience. In recent decades, coral-reef degradation has impacted islands across the Pacific, including small islands like Kosrae. Understanding how and why coral-reefs have changed in the last twenty to thirty years is crucial to sustaining coral-reef resilience on these small islands. This study used a unique historical baseline to examine how Kosrae's coral and fish assemblages have shifted since 1986, and examined potential drivers of change. We report substantial shifts in both fish and coral assemblages that amplified natural species distributions between windward and leeward sides of the island. Many food fishes and framework-building corals were historically more abundant on the leeward side of the island, but have become locally depleted and now persist mainly on the windward side, least accessible to humans. Fish declines included reductions in large-bodied predators and large-bodied herbivores such as sharks, snappers, and parrotfishes. These declines have led to dominance by small-bodied, opportunistic species of herbivores and secondary consumers that have smaller home ranges and poorer ecological function. Coral declines included the loss of fast-growing, framework-building (e.g., *Acropora*, Faviidae) species from leeward sites, and subsequent

dominance by slow-growing, sediment-tolerant species (e.g., *Porites, Galaxea*). Windward sites have become increasingly dominated by wave-tolerant assemblages of arborescent and table-forming *Acropora*. We found that fishing access predicted declining fish assemblage condition through time, and that changes in fish assemblages were correlated with changes in coral assemblages, especially in leeward sites. A pollution proxy was further identified as a predictor of coral assemblage condition, but only in the modern timeframe, suggesting that coral assemblages are becoming increasingly afflicted by pollution in densely populated areas. However, the influence of pollution was spatially limited, and did not account for shifting coral assemblages through time. Altogether, fishing access was higher for leeward sites, where fish declines were most severe, while pollution was higher in densely populated areas along the windward side. Overall, it is likely that unsustainable fishing reduced ecosystem resilience, and in-turn fostered the decline of coral assemblages through time. Although we documented substantial shifts in coral-assemblage structure, existing evidence suggests large-scale disturbances have been rare in Kosrae, raising the question: what caused these shifting baselines? Declining coral condition must have been caused by either 1) a large-scale disturbance that was undocumented or 2) the accumulation of small-scale perturbations through time. In either case, lowered ecosystem resilience due to unsustainable fishing, and to a lesser extent pollution, would have prevented coral recovery. Improving Kosrae's marine resources into the future will require prioritized management policies such as fisheries regulations for leeward areas of the island where fishing pressure is highest, while incorporating both fisheries regulations and pollution reduction for windward areas.

LINKING PATTERNS AND PROCESSES WITH SHIFTING BASELINES ON CORAL REEFS

BY

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I dedicate this thesis in memory of Christopher Langel, an adventurous, enthusiastic biologist and gregarious friend, who lost his life doing what he loved.

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Introduction:

Coral-reef ecosystems are under threat from acute disturbances and chronic stressors that alter species composition, trophic interactions, and ecosystem processes (Knowlton 2001, McClanahan 2002, Hughes et al. 2003). Coral bleaching from heat stress and *Acanthaster planci* outbreaks are examples of acute disturbances that impact reefs intermittently, while watershed pollution and unsustainable fishing are chronic stressors that slowly shift reefs from coral to algal dominance. The combined effects of disturbances and stressors are also synergistic. For example, over-exploited fish assemblages lose their functional capacity to restore reefs after widespread coral mortality, however, there is debate about what drivers are most responsible for reef decline (Roberts 1995, Mumby et al. 2007, Hughes et al. 2010, Mouillot et al. 2013, Aaronson and Precht 2001). While coral reefs cover less than 1% of the ocean, their fisheries account for 5% of global fish consumption (Spalding and Grenfell 1997, Pauly et al. 2003). Reefs also provide invaluable ecological services, including shoreline protection from storms and erosion, life-saving pharmaceuticals, and an enormous eco-tourism industry (Birkeland 1997). Coral reefs further contain astonishing biodiversity, with up to 30-40% of the world's fish species (Hixon and Beets 1993). Preventing coral reef degradation is a complex and possibly insurmountable task, yet ensuring reefs provide ecological services is clearly vital. Thus, sustaining coral-reef resilience – the ability to withstand and recover from disturbances and stressors – is critical. Scientists must therefore evaluate coral-reef changes through time and determine the characteristics that maintain healthy reefs, and use this information to enhance resource management.

Coral-reef diversity, function, and resilience:

The exceptional diversity found on coral reefs makes it difficult to distinguish which species, or how many species, are needed to provide the greatest ecological function and resilience (Bellwood et al. 2004). Diversity and functional redundancy are perceived to promote resilience, however, it is unclear how much diversity is necessary to maintain functionality (MacArthur 1955, Nyström et al. 2008). Coral reefs in the Red Sea, Caribbean, and Indo-Pacific all have a similar number of fish functional guilds despite differing in species richness (Roberts and Ormond 1987, Mouillot et al. 2014). Some of the world's most pristine reefs contain exceptionally high fish biomass and coral cover, but have fewer fish and coral species compared with many exploited reefs (Sandin et al. 2008). Even in highly diverse assemblages, some functional roles are supported by many species, while others rely heavily on one or two (Mouillot et al. 2014). For example, Hoey and Bellwood (2009) discovered that *Naso unicornis* was responsible for 90% of *Sargassum* removal across all reef types on Lizard Island, suggesting that some species provide disproportionally higher function. These findings collectively suggest that higher diversity doesn't necessarily equate to higher functionality.

In contrast, Burkepile and Hay (2008) found that herbivore assemblages with more species suppressed algal growth more effectively than assemblages with fewer species due to different feeding mechanisms within caged experiments. A study of herbivore diversity on the Great Barrier Reef found that higher diversity assemblages maintained functionality during environmental fluctuations due to asynchronous species responses (Thibaut et al. 2012). These studies suggested that diverse fish assemblages increase the efficiency of trophic interactions across complex food webs, and in turn buffer disturbance impacts and promote resilience (MacArthur 1955, Odum and Odum 1955, Paine 1966, Polis and Strong 1996, Bascompte et al. 2005).

Maintaining resilient ecosystems therefore requires an understanding of how assemblages function through disturbance-and-recovery cycles, and identifying upon key species, functional groups, and diversity patterns that are associated with long-term stability. Achieving this understanding requires tracking how reefs respond to environmental pressures through time (Ostrander et al. 2000). Characterizing temporal dynamics can identify species or functions that are absent on reefs that have declined, and in turn reveal species and functions associated with resilience.

Disturbance cycles:

Disturbances are natural events in all ecosystems, however, climate change has increased the frequency of natural disturbance cycles, while resource exploitation and degradation prolong recovery (Knutson et al. 2010). In the tropical Pacific, heat-stress from climate change and predator starfish outbreaks represent large-scale disturbances responsible for much of the overall loss in coral cover (De'ath et al. 2012). Generally, reefs recover from acute disturbances in approximately one decade, however local stressors can undermine reef resilience, prolonging or preventing recovery (Golbuu et al. 2005, Graham et al. 2011b, Carilli et al. 2009, Houk et al. 2014). Therefore, many studies have concluded that understanding and managing local stressors is the best strategy for dealing with increasing disturbance frequencies resulting from climate change (Gardner et al. 2003, De'ath et al. 2012, Van Woesik et al. 2012, Gurney et al. 2013). This strategy attempts to preserve ecological function, which fosters reef recovery following disturbances resulting from climate change.

Local stressors – overfishing and pollution:

Healthy reef fish assemblages maintain ecosystem function and resilience, but due to human impacts, they are becoming highly threatened (Jackson et al. 2001, Scheffer et al. 2001, Bellwood et al. 2004). Herbivores and detritivores enhance coral growth and cover by consuming turf and macro-algae that compete with corals for space (Bellwood et al. 2004, Bellwood et al. 2006b, Mumby et al. 2006a, Hughes et al. 2007). They also act as bio-eroders by removing dead corals and carbonate, which opens substrate for coral recruitment (Birkeland 1997, Mumby et al. 2006a, Hughes et al. 2007). The natural grazing capacity of herbivorous fishes is a necessary function to maintain coral dominance and prevent algal-dominated phase shifts, like those that have plagued reefs throughout the Caribbean (Scheffer et al. 2001, Mumby et al. 2006b, Hughes et al. 2007, Welsh and Bellwood 2014a).

Additionally, abundant predators, characteristic of resilient reef-fish assemblages, enhance the functional diversity and stability of lower trophic levels (McCann et al. 1998, McCann 2000, Allesina and Tang 2012, Houk and Musburger 2013b). Reefs with intact shark populations have been associated with high herbivore biomass, herbivore assemblage heterogeneity, and abundances of large-bodied species (Graham et al. 2005, Houk and Musburger 2013b). Predation supports the persistence of many weak interactions among lower trophic levels by preventing competitive dominance (Connell 1961, Paine 1966, McCann et al. 1998, Mellin et al. 2014). Weak interactions, in turn, stabilize food webs because consumer-resource oscillations become diminished when spread across many species (McCann et al. 1998). Additionally McCann et al. (2005) and Rooney et al. (2006) showed that top predators forage across multiple energy channels, coupling prey with fast and slow biomass turnover. This allows predators to asynchronously respond to resource fluctuations, which stabilizes large food webs.

Over-exploitation of coral-reef fisheries disrupts trophic stability and can result in coral-to-algal phase shifts through cascading interactions (Daskalov et al. 2007). Reefs with fewer predators often have smaller, less diverse herbivore assemblages (Dulvy et al. 2004). In turn, compromised herbivore assemblages can reduce coral recruitment, lowering coral cover and diversity (Wilson et al. 2010). In support, Houk et al. (2015) identified fishing pressure as the strongest predictor of compromised fish assemblages across nine islands in Micronesia, which reduced overall ecosystem condition. Pollution was a secondary contributor that was pronounced in some lagoons near high islands.

Watershed pollution discharges nutrient-rich runoff and sediments into coastal waters, which increases turbidity and eutrophication, smothers corals, and feeds algal growth (Brown 1997). Globally, coastal water quality is deteriorating from land clearing and terrestrial runoff, and in developing tropical countries untreated sewage and nutrient-enriched groundwater are major pollution sources (Fabricius 2005). At high levels, nutrient enrichment has been shown to reduce coral cover and diversity, and increase macroalgae abundance (Smith et al. 1981, Edinger et al. 2000). The macroalgae blooms overgrow coral reefs and trap additional sediments, which inhibits coral recruitment. (Walker and Ormond 1982, McCook 1999). Sedimentation and nutrient enrichment have been further shown to reduce crustose coralline algae cover, which further inhibits coral recruitment and reduces reef calcification (Kendrick 1991).

Together with overfishing, sediments and nutrients from terrestrial runoff reduce reef resilience, however, the relative contribution of these stressors influences how reefs change through time (Houk et al. 2010, Graham et al. 2011b). Just as overfishing can facilitate coral loss, coral loss diminishes fish assemblages through habitat degradation. Identifying the extent to which overfishing and pollution contribute to local coral reef decline is crucial for resource management (Hughes 1994, Jones et al. 2004, Wilson et al. 2006). A deeper understanding of the relative contribution of these stressors can inform resource managers which local stressors require prioritized management actions, demanding science-to-management frameworks that benefit from examining ecosystem targets alongside gradients in local stressors (Houk et al. 2014).

Baselines:

Historical baselines provide invaluable insight into reef changes through time. Reefs change slowly, and often the combination of large disturbances and local stressors causes severe change through time. Yet, historical baselines are rare and often difficult to compare with modern datasets due to changing data collection methods. Therefore, novel approaches are often needed to draw comparisons between baselines and modern times. For instance, McClenachan (2009) quantified fishery landings from historical photographs to evaluate changes in fish size and catch composition over 50 years. Some historical coral-reef assessments used qualitative rankings to describe resource abundances (i.e., DACOR:

dominant, abundant, common, occasional, rare) (Maragos et al. 2004). While not as desirable as quantitative, long-term datasets, DACOR surveys by expert observers provide a means to compare resource abundances across known environmental gradients. Comparing resource abundances along environmental gradients through differing time periods can provide an alternative means to evaluate how resources have shifted through time despite the continuous improvement in protocols and technology. This approach offers resource managers a powerful method for incorporating historical baselines into their modern understanding of why reefs are changing, and what management options might best ameliorate reef decline.

Study Aims and Study Area:

Kosrae, Federated States of Micronesia, is an ideal location to examine fishery-induced changes in reef assemblages through time because it is a small island with low human population and land-development, yet fishing is a major source of both food and income. Kosrae is representative of many small Pacific islands, where human populations and land-development are minimal, but people rely heavily on fisheries. This study investigated the spatial distribution of coral and fish assemblages around Kosrae, and how the magnitude of spatial gradients have shifted since a baseline study was conducted in 1986 (Kosrae Coastal Resource Inventory, U.S. Army Corps of Engineers). To approach causation, this study assessed the contribution of environmental factors and local stressors in predicting the magnitude of biological gradients during both time frames, then compared whether gradients became more or less magnified, and identified biological consequences.

Specifically, the present thesis: 1) examined biological datasets gathered by the US Army Corps of Engineers in 1986 and characterized the spatial distribution of corals and fishes across natural environmental and local stressor gradients, 2) collected modern biological datasets and conducted similar spatial investigations, 3) identified key species, trophic guilds, and ecological attributes (e.g., assemblage heterogeneity and species dominance distribution curves) that underpin the observed temporal changes, and 4) compared the strength of predictive relationships between biological attributes and environmental factors across both time frames. In order to do this, the following hypotheses were tested sequentially:

H01: The relative composition of fish and coral assemblages were not predicted by wave energy, watershed size, fishing access, or pollution in 1986 or in 2015, and were similar between both time frames.

H02: Latent variables describing the condition of fish and coral assemblages (described in methods) were not be influenced by wave energy, watershed size, fishing access or pollution.

H03: Correlations between individual metrics and their respective latent variables were equal in both time frames.

H04: Changes in fish and coral latent variables were not spatially coupled.

H05: The difference between normalized fish and coral condition scores across time frames was not predicted by wave energy, watershed size, fishing access, or pollution.

Methods:

Study Area:

The islands of the Federated States of Micronesia (FSM) contain over 5000 km^2 of coral reefs that provide a critical source of both food and income (George et al. 2008). Kosrae is the easternmost of the Federated States of Micronesia, located 600 km north of the equator, approximately midway between Guam and Hawaii. Kosrae is a small (110 km^2) high island covered in forested watersheds, lined with mangroves, and surrounded by a fringing outer reef (USACE 1989). Although the island has a small population (6,616), human density per reef area is moderately high (130 individuals per km^2 reef), and the local population has a strong connection to the ocean and uses resources heavily.

Kosrae's position near the equator and at the Eastern end of the Caroline Islands minimizes typhoon impacts, as typhoons usually form in the Eastern Pacific, and move Westward (Gray 1968). The only recorded *Acanthaster planci* outbreak occurred in 1994 on the Western side of Kosrae, and resulted in notable coral mortality, however no outbreaks have been reported since (George et al. 2008). In 2013, Kosrae suffered a moderate bleaching event followed by localized coral mortality. Formerly, the only documented bleaching event was localized to *Acropora* corals along the northeast side of the island (George et al. 2008). Thus, available records and anecdotes suggest that large-scale disturbances have had little impact in Kosrae, however, standardized monitoring across Micronesia has revealed relatively low fish biomass in Kosrae (Houk et al. 2015). Given the moderate human population per land area (60 individuals per km^2 in Kosrae; 148 individuals per km^2 in FSM on average), but high human population per reef area (approximately six times higher than FSM on average), this study hypothesized that fishing pressure is the most influential local stressor on Kosrae's reefs.

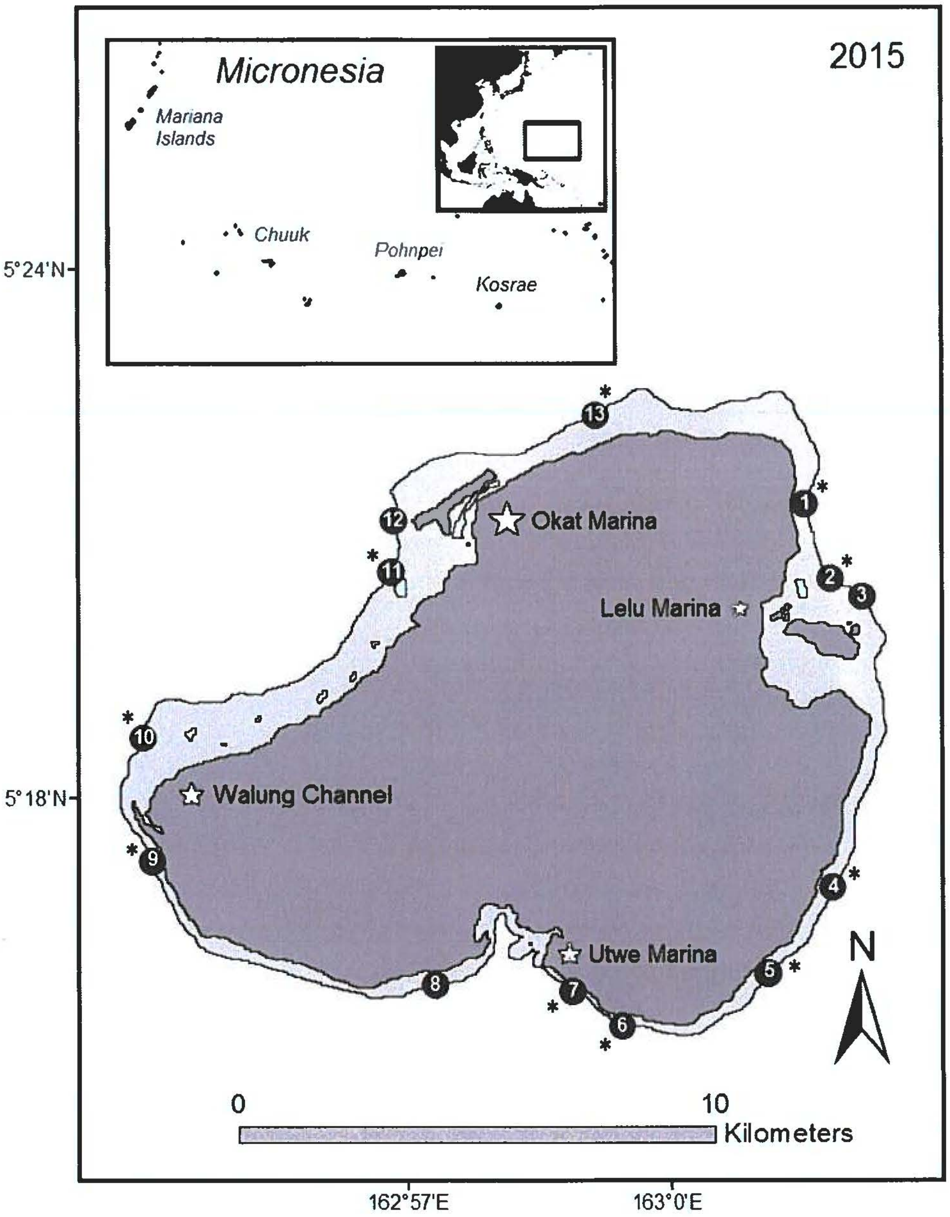
The goals of this study were to: (i) evaluate how coral and fish assemblages around Kosrae may have shifted since a baseline survey 25 years ago, (ii) assess whether natural environments and local stressors account for biological changes, and (iii) identify key species or trophic guilds that underpin change to infer compromised ecological processes, and determine priority management targets.

Modern coral-reef assessments:

To assess the present ecological state of Kosrae's reef slopes, quantitative fish and coral data were collected from 13 representative sites around the island, with the exception of site 3, where only fish data were collected, and site 12 where only coral data were collected (Figure 1). All sites were marked with global positioning system coordinates and mooring buoys that were installed during a community conservation effort in 1995. Corals and fishes were surveyed at the 8 m depth contour following standardized protocols (Houk and Van Woesik 2013).

Fish observers entered the water first and laid five 50-m transects while conducting replicate fish counts, beginning at the mooring buoy and running parallel to shore. Fish assemblages were assessed using twelve stationary point counts (SPC) spaced equally over 250 m. During each SPC the observer recorded the species and estimated size of all food-fish occurring within a 5 m radius, for 3 min. Food-fish were defined as acanthurids, scarids, serranids, carangids, labrids, lethrinids, lutjanids, balistids, kyphosids, mullids,

Figure 1. Map of sites surveyed in 2015. Asterisks indicate sites with overlap in 1986 that were used to compare coral and fish condition score changes through time. Marinas are indicated with stars, and star size corresponds to the number of fishing boats residing within each marina.



holocentrids, and sharks. All size estimates were converted to biomass (kg) using established length-weight coefficients from both FishBase (www.fishbase.org) and fishery-dependent data collected across Micronesia (Cuetos-Bueno and Hernandez-Ortiz unpublished).

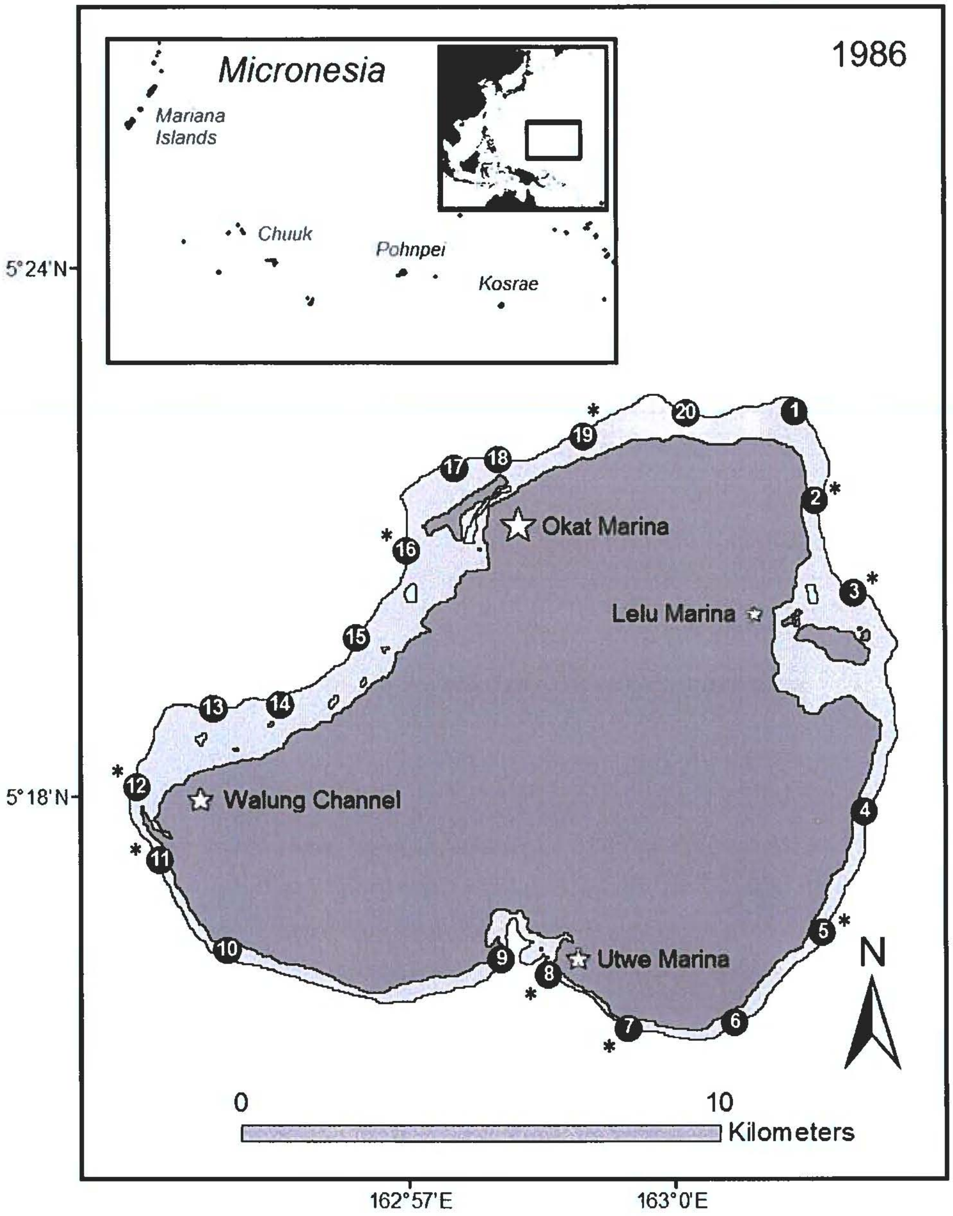
To account for the disparity between modern survey methods that are limited to a 5-m radius and historical surveys that had no distance limitation, a second fish observer swam alongside the primary observer and recorded fish densities for larger food-fish that were less frequent within the 5 m radius, using no distance boundaries. This excluded small surgeonfishes and parrotfishes, but included a consistent set of larger species of food-fishes.

Coral assemblages were assessed using standard 1-m^2 quadrats placed at 25-m intervals along the transect lines (n=10). Coral colonies whose center point was inside the quadrat were recorded to species level and measured across the widest diameter and the diameter perpendicular to the largest. When colonies were too small to distinguish species, they were recorded to genus level and denoted as juveniles.

Historical Status – DACOR:

A total of 52 sites were surveyed in 1986, including 26 reef slopes. Of these, 20 were considered to have similar spatial coverage as modern surveys, and 9 of those overlapped with modern survey locations (Figure 2). During each survey, observers qualitatively recorded the abundance of organisms by assigning each species to an abundance category. For corals these were: dominant (D), abundant (A), common (C),

Figure 2. Map of sites surveyed in 1986. Asterisks indicate sites with overlap in 1986 that were used to compare coral and fish condition score changes through time. Marinas are indicated with stars, and star size corresponds to the number of fishing boats residing within each marina.



occasional (O), and rare (R). For fishes these were abundant (A), common (C), occasional (O), and rare (R).

Data collected in 1986 were qualitative and could not be directly compared with present data. To overcome this limitation, we compared the spatial distributions of both fish and coral assemblages with respect to environmental conditions and local stressors. Using this approach, we were able to consider differences in both spatial distributions and the magnitude of relationships between environmental factors and biological assemblages. When examining the spatial distribution of fishes and corals, we assigned numbers to each of the corresponding DACOR categories using information provided in the historical report for fishes, or natural breaks in coral-species abundance patterns that persisted across Micronesia (Figure 3-4).

Quantifying DACOR data:

Corals:

In order to assign abundance values on DACOR datasets, we examined natural breaks in coral abundances from modern datasets for Kosrae, and three nearby islands that represent a gradient of 'pristine' to human impacted reefs (Pohnpei, Namdrik Atoll, Rongelap Atoll). Modern datasets were used to determine consistent, natural breaks in coral abundances associated with the 5 DACOR categories. This approach provided an objective means to estimate Kosrae's historical coral abundances in a categorical manner, reflecting the 1986 protocol.

Figure 3. Outlined process for estimating 1986 DACOR coral abundances and validating the approach taken for data analyses.

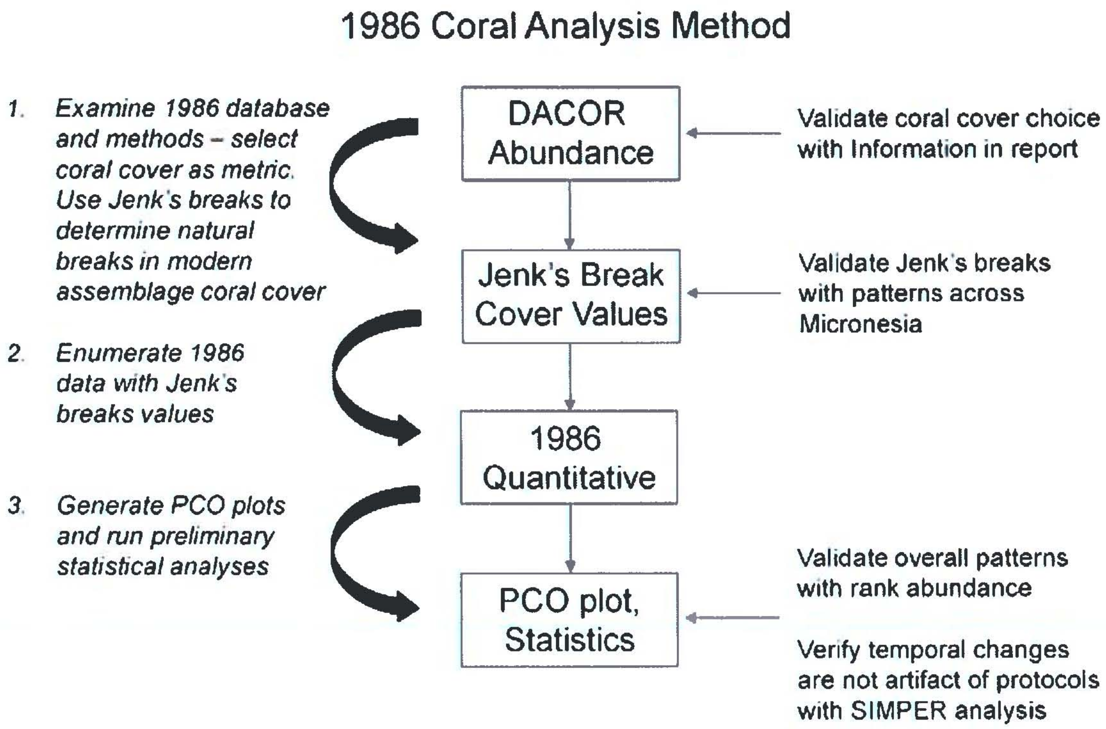
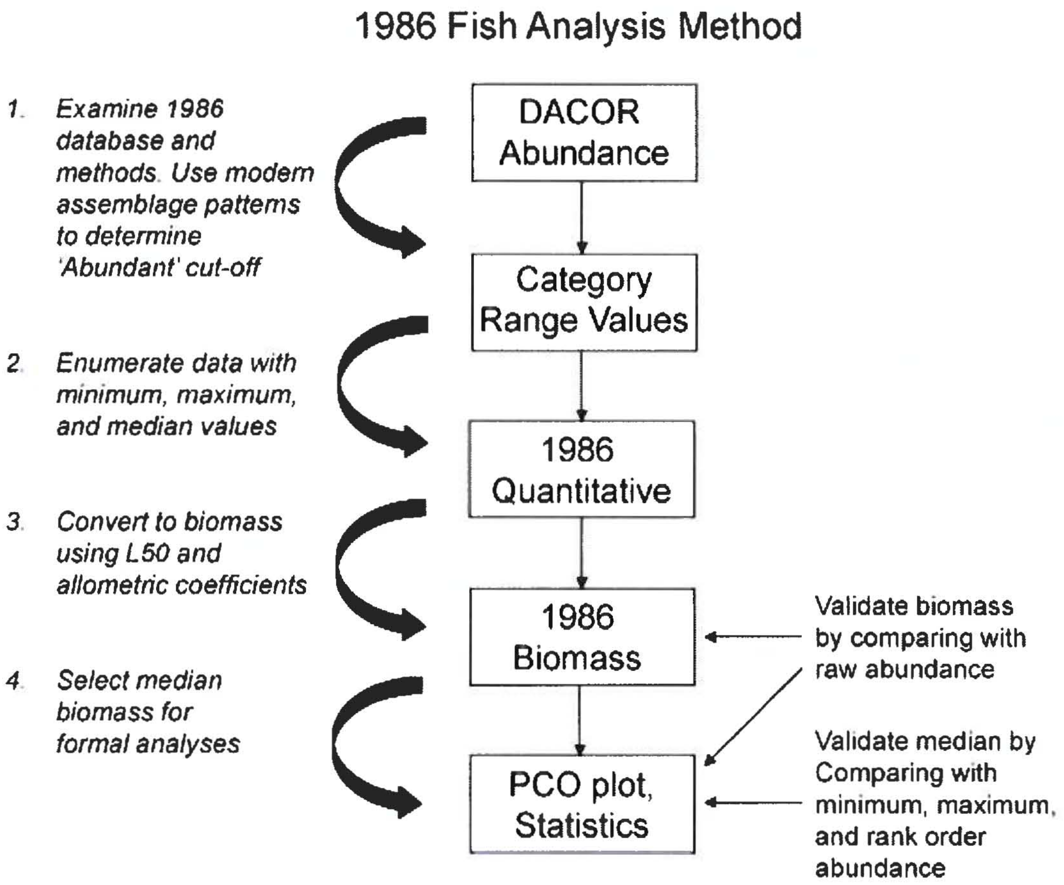


Figure 4. Outlined process for enumerating 1986 fish qualitative abundance categories and validating the methods.



Expert observers in 1986 used DACOR abundance categories to estimate the total coverage of any particular coral species, with no dependence on colony size. This was evidenced by equal DACOR rankings for corals that attain large colony sizes but are few in number (e.g. *Acropora hyacinthus*) and corals that have small colony-sizes, but are prolific on reefs across Micronesia (e.g. *Leptastrea purpurea*). Jenks Natural Breaks Optimization procedures (hereafter referred to as Jenk's breaks) were used to define optimal abundance categories for coral species from modern datasets associated with Kosrae, Rongelap, and Namdrik atolls, Republic of the Marshall Islands, and Pohnpei, FSM. In all cases, coral abundance data were collected using the same protocols noted in modern surveys. Jenk's breaks clustered coral-species abundance data into 5 categories (matching DACOR) by minimizing intra-class variation while maximizing inter-class variation (Jenks 1967). This process revealed a similar, exponential relationship between species-based coral cover and Jenk's breaks for all islands (Figure 5). We determined the values for D, A, C, O, and R by taking the mean coral cover between sequential breaks, D= 11.83%, A = 4.70%, C = 2.40%, O = 1.0%, R = 0.16% (Figure 6). We assigned these values to the 1986 coral dataset and compiled coral cover data at the species level and functional group level (e.g. branching *Acropora* or massive *Porites*) for data analyses. No direct temporal analyses were conducted using the assigned coverage values, rather coverage was used to examine spatial gradients in biological metrics as described below. To ensure validity, initial multivariate plots of species abundance distributions were compared using both these estimated coral cover values and rank order abundance values. Differences were non-significant, however rank abundance data diminished multivariate

Figure 5. Boxplots showing the range of coral cover cut off values from Jenk's Natural Breaks Optimization for each island. Six cut offs were generated to create end points for five individual classes, representing the range of values between the cut off values. Similar, power-law relationships were found for each island, indicating the inherent nature of coral abundance categories throughout Micronesia.

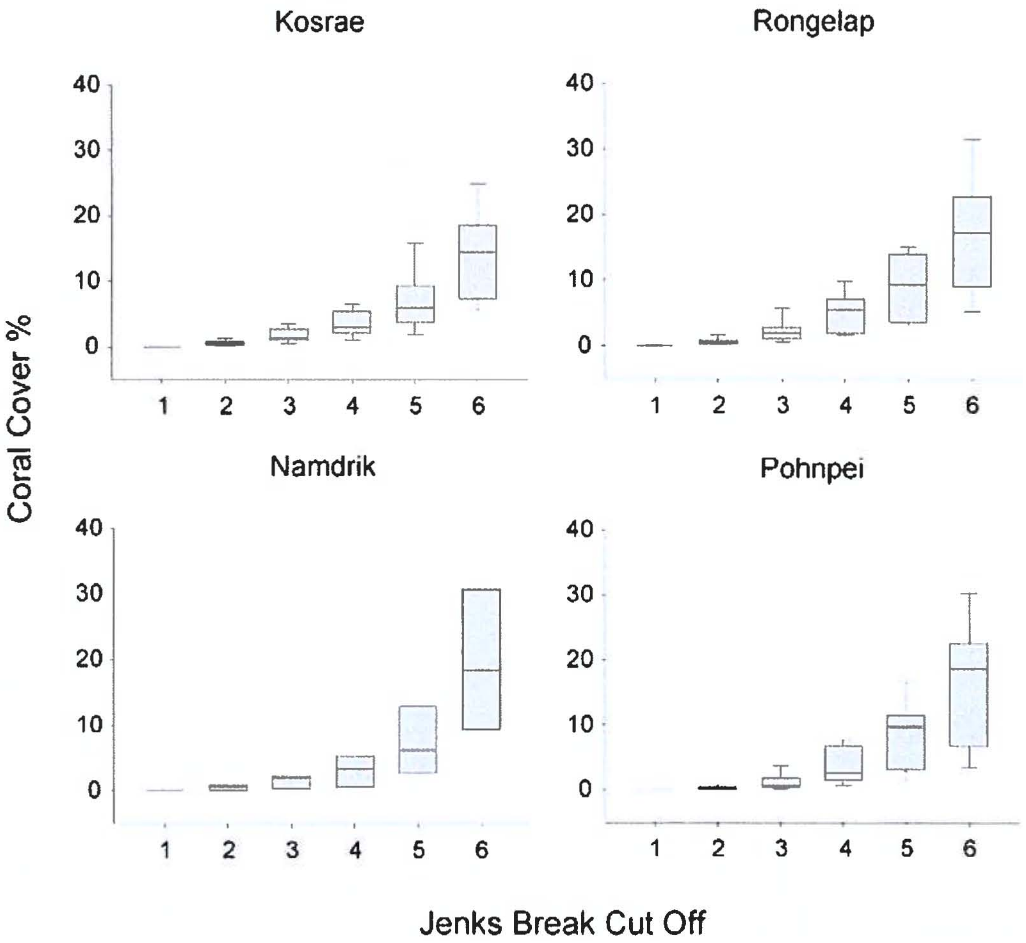
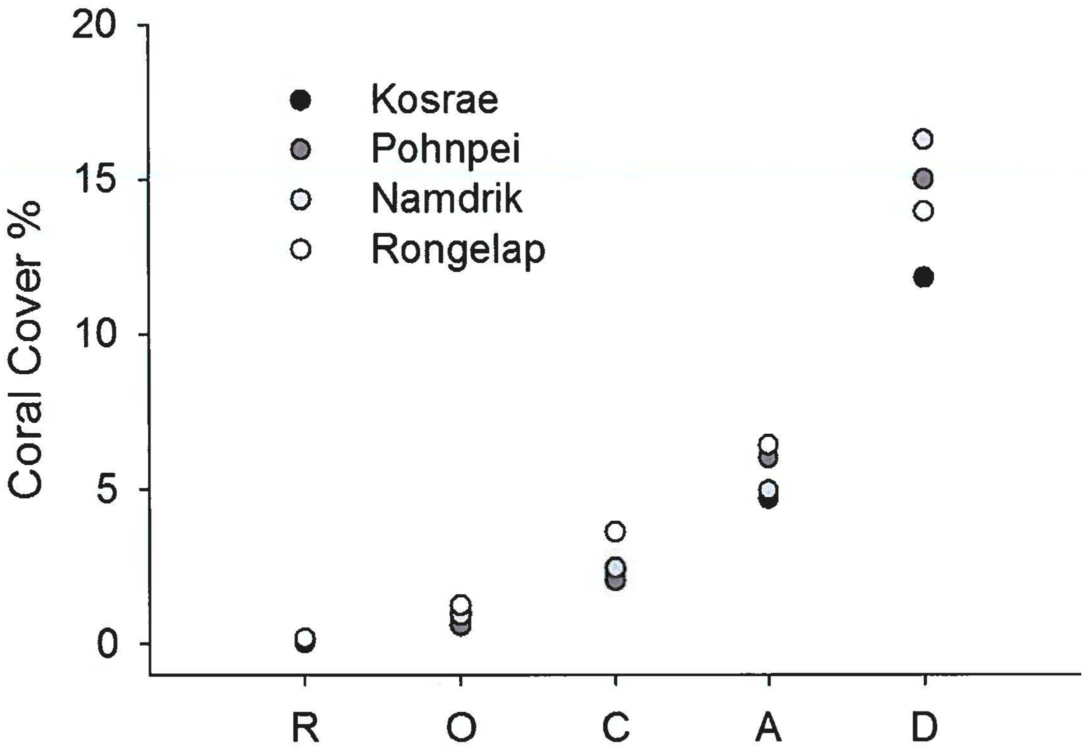


Figure 6. Estimated values of coral cover for the five coral abundance classes across Micronesia. Coral cover for O, C, and A categories represent means between Jenks breaks (Figure 3). Coral cover for R represents the mean between 0 and the mean of the second category, while cover for D represents the mean between the second-to-last category and one standard deviation above the last category. This method was chosen to include variance associated with the tails without including outliers, and to prevent data-overlap between classes.



separation between contrasting coral assemblages, due to reduced cover estimates of prolific coral species.

Fish:

For both 1986 and modern fish datasets, rare encounters of species with extremely high numeric densities were removed from the present analyses because they disproportionately influence overall composition and represent species that are not site-specific (appendix 1). During the 1986 surveys fish abundances for each site were reported in the following ranges (number of fishes): abundant (A) = 15 or more, common (C) = 5-14, occasional (O) = 2-4, and rare (R) = 1. We defined an upper cut off value for the abundant category using the maximum density observed in fish surveys conducted over similar areas from modern data across Micronesia (44 fishes); therefore A = 15-44. In order to examine the sensitivity of our fish abundance categories, initial multivariate comparisons were conducted using the minimum, maximum, and median values for each abundance category. Initial tests were also conducted using rank order abundance. In all instances, non-significant differences in spatial patterns were observed, with the similar finding that rank-order abundance diminished the magnitude of multivariate separation. Given non-significant differences, we logically used median abundance values for each category, therefore we assigned A = 30, C = 10, O = 3, and R = 1.

Abundance data, or numeric density, fails to represent overall fish assemblage composition, because all species are not equal in biomass. To overcome this limitation we chose a standard size estimate for each species to convert density to biomass; while assuming individual species of fish were uniform in size ignored obvious intra-specific variation, it emphasized clear size differences between species, such as large-bodied and small-bodied herbivores. The standard size estimate used was the size at first maturity (L_{50}) based upon equations from FishBase and asymptotic lengths from ongoing fisheries-dependent datasets. L_{50} was chosen because it is a universal measure pertaining to life-history for all fishes, and again emphasized inter-specific size differences.

Environmental Factors:

Wave energy values were generated for each site in both time frames using a 10-year record of wind-speed, fetch distance, and angle of wind exposure (Quicksat wind data sets from 1999 to 2009; https://winds.jpl.nasa.gov, Houk et al. 2015). Wind and wave patterns were assumed to be unchanging through time, thus the same method was used to generate wave energy values for both time frames. Natural influences (terrestrial nutrient and freshwater input) from watersheds were also considered for each site by measuring adjacent watershed sizes (km^2) in ArcGIS using United States Geological Survey topographic maps base layers.

A proxy for fishing access was derived from local fishing pressure and boat-based fishing pressure, as well as wave energy. Local fishing pressure was estimated by multiplying the standardized values for: 1) the estimated number of fishers residing in the municipality adjacent to a site (2010 FSM Census, http://www.sboc.fm/), and 2) linear distance to the nearest access point or human residence. Boat-based fishing pressure was determined by multiplying the standardized values for: 1) the number of fishing boats housed within each marina (Okat Marina, Lelu Marina, Utwe Marina, and Walung Channel), and 2) the distance from each site to each marina. For both local and boat-based fishing pressure, distances were negatively scaled so that increasing distance yielded lower fishing access scores. The overall proxy to fishing access was then calculated by adding local and boat-based fishing pressure scores, and multiplying this by the proportion of days per year considered accessible for fishing based on wave energy parameters (unfishable conditions defined as wind speeds >6 m/s with fetch distances ≥20 km).

In addition, a pollution proxy was calculated by estimating: 1) the total area of altered land in the adjacent watershed (barren urban, urbanized vegetation, developed infrastructure), 2) human population in the adjacent watershed, and 3) the distance from a site to the nearest discharge point (Houk et al. 2015). As with fishing access, distances were negatively scaled so that increasing distance from discharge yielded lower pollution scores. Altered land area was derived using United States Forest Service land-use data (United States Forest Service, http://www.fs.usda.gov/r5). The same pollution proxy was used for both time frames based on the assumption that the population distribution around Kosrae has not changed through time, and because human population per watershed was unavailable for 1986. (1986 FSM Census, 2010 FSM Census, http://www.sboc.fm/, Table 1).

Table 1. Population distribution of Kosrae in 1986 and 2010.

	1986	2010
Total Population	6607	6166
Tafunsak	1755	2173
Lelu	2422	2160
Malem	1354	1300
Utwe	1076	983

Data Analysis:

Multivariate spatial composition:

The spatial distribution of both coral and fish assemblages were assessed during each time frame using standard multivariate approaches (Anderson et al. 2008). During both time frames, spatial differences were assessed with respect to wave energy, watershed size, fishing access, and pollution (H01). In all instances, coral cover and fish biomass data were aggregated by functional group (i.e., arborescent *Acropora*, massive *Porites*, large-bodied parrotfishes, etc.), log-transformed and Bray-Curtis similarity coefficients were calculated between each pair of sites. Bray-Curtis dissimilarities were depicted using principal coordinate ordination (PCO) plots. The influences of environmental gradients and local stressors were determined using redundancy analysis. Redundancy analysis is the multivariate analog of multiple regression modeling, and examines independent predictors for their ability to explain multivariate species-abundance separation. Significant environmental factors were overlaid on the PCO plots using vectors that were associated with each axis, as fitted by the process of redundancy analysis.

Initial results indicated that spatial differences in coral assemblages existed between high and low wave energy zones (i.e. east and west sides of the island), with a higher degree of difference in 2015. Analysis of similarity (ANOSIM) was therefore used to determine if separation between high and low wave energy zones was greater in 2015 than 1986. Next, In order to determine if these findings were an artifact of different survey methods, SIMPER tests were used to determine species that contributed most to high and low wave energy sites. Larger differences between coral assemblages in high-versus-low energy could be due to smaller-scale quadrat surveys in 2015 compared to DACOR observations in 1986. This would be true, for instance, if corals that were common on reefs with high wave energy were absent on reefs with low wave energy based upon 2015 quadrat data, while the same differences were less pronounced in 1986 (i.e. common-to-rare, with fewer species absences given the broader DACOR protocols). Taking this approach, species with the largest contributions to the SIMPER analyses were examined across wave energy conditions during both time frames. For these analyses, sites with average wave energy values above 800 J/m3 (i.e., eastern exposure) were categorized as high, while sites lower than 800 J/m3 (i.e., west exposure) were categorized as low.

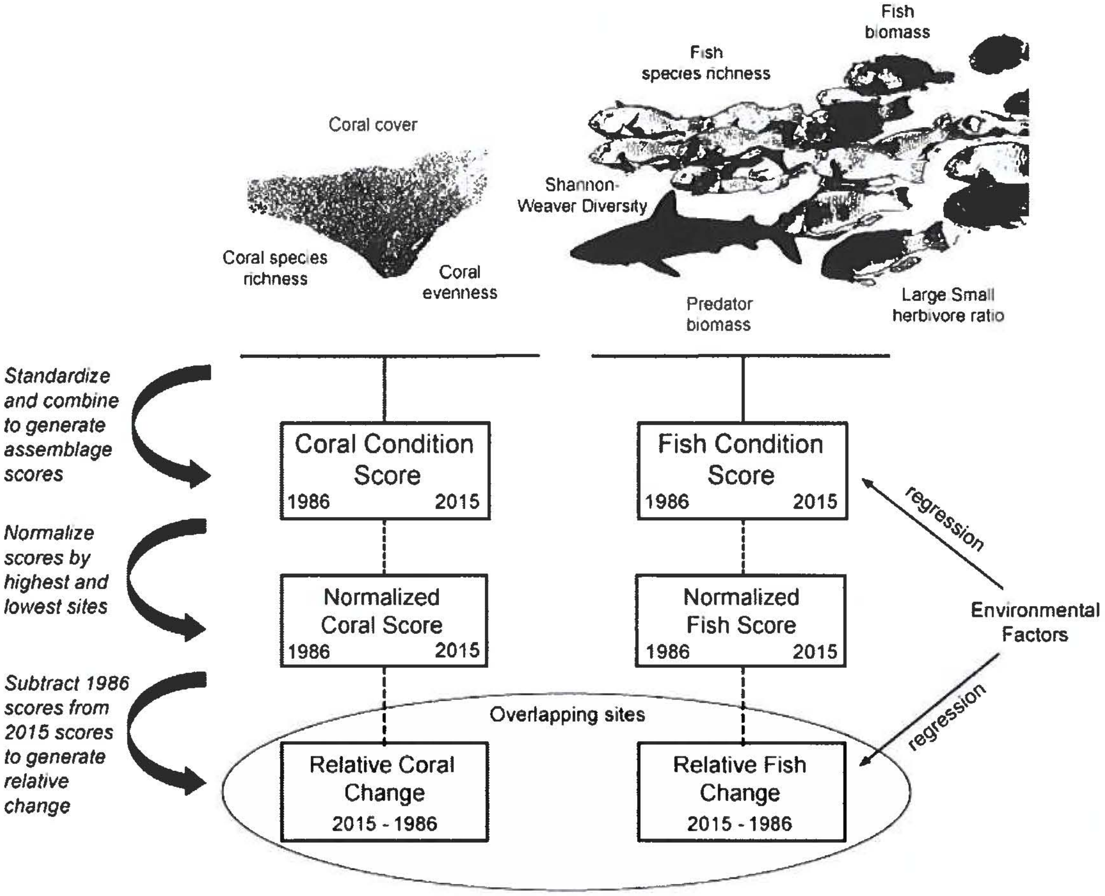
Diversity indices:

Statistically, the influences of wave energy, watershed size, fishing access, and pollution on fish and coral Shannon-weaver diversity were investigated using linear regressions (H01).

Latent variables and assemblage condition:

Beyond spatial differences in multivariate species abundances and species evenness patterns, this study last created latent variables for fish and coral assemblages during both time frames to depict their condition (Figure 7). Ecological attributes used to generate fish latent variables were fish assemblage biomass, predator biomass, ratios of large-to-small bodied herbivores, Shannon-Weaver diversity, and species richness. Large herbivore species were defined as those with estimated asymptotic lengths over 40 cm, while small

Figure 7. Fish and coral condition evaluation depicting the individual ecological attributes used to generate scores. Ecological attributes that were available in both time frames were standardized and averaged to create overall condition scores for both fish and corals.



herbivore species were defined as those with asymptotic lengths under 40 cm (based upon unpublished fisheries dependent datasets from Micronesia, Cuetos-Bueno and Hernandez-Ortiz). Individual attributes were standardized and averaged to generate latent variables. The ecological attributes used to generate latent variables to depict coral assemblage condition were: 1) coral cover, 2) Shannon-Weaver diversity, and 3) species richness. Attributes were standardized and averaged to create latent variables

Validating modern fish surveys:

To examine potential bias due to differing fish survey protocols used in 1986 and 2015, we compared key ecological attributes between modern fish observers, one using standard stationary point count protocols, and a second using a method similar to the 1986 survey (i.e. abundance counts without spatial restrictions). Ecological attributes considered were: 1) fish-assemblage biomass, 2) predator biomass, and 3) Shannon-Weaver diversity. Other attributes were not considered for comparisons because the secondary observer only observed a subset of the overall food fishes that are larger, heavily targeted, and less represented using modern protocols. Pearson's moment correlations were used to determine the nature of these relationships.

Environmental influences:

Using the latent variables for fish and coral assemblages as dependent variables, this thesis examined the influence of wave energy, watershed size, fishing access, and pollution using multiple regression modelling. (H02). Resultant models were examined for residual normality using Shapiro-Wilk tests, and evaluated by their explanatory power (R^2 values), p-values, and Akaike Information Criteria (AIC).

Given significant relationships between environmental factors and condition scores, sensitivity analyses were performed to determine which individual metrics were most sensitive to environmental gradients. Sensitivities were calculated as correlations between individual ecological metrics of the coral and fish assemblages and their overall latent variable values (H03). The rationale behind these comparisons was to assess whether different ecological attributes had become more or less pronounced through time, and to identify underlying processes that may have compromised ecological function.

Relative changes in fish and coral condition:

Last, this study examined the relative changes in fish and coral scores through time using the differences in normalized values (i.e., 0 – 100) between each time frame, based upon a subset of overlapping sites. Ten of the 2015 survey sites overlapped with a corresponding site from the 1986 survey sites, with estimated distances between 2015 and 1986 sites ranging between 0.1 – 1.3 km. The normalized scores for the 1986 sites were subtracted from their 2015 pairs, yielding relative change values (Table 2). Positive values indicated that sites' relative condition scores have increased through time, while negative values indicated they have declined through time. To determine if relative changes in fish and coral scores (2015 relative score – 1986 relative score), were spatially linked through time Pearson's moment correlation was used (H04). To determine if environmental factors

Table 2. Normalized fish and coral scores for overlapping sites in 1986 and 2015, with relative score changes.

2015 Site #	1986 Site #	1986 Fish Score	2015 Fish Score	Fish Score Change	1986 Coral Score	2015 Coral Score	Coral Score Change
1	2	0.21	0.34	0.13	0.62	0.46	-0.16
2	3	0.23	1	0.77	0.33	1	0.67
4	5	0	0.05	0.05	0.59	0	-0.59
5	5	0	0.23	0.23	0.59	0.09	-0.50
6	7	0.38	0.40	0.01	0.29	0.47	0.18
7	8	0.13	0.04	-0.09	0	0.72	0.72
9	11	0.30	0.63	0.32	0.30	0.70	0.40
10	12	1	0	-1	1	0.47	-0.53
11	16	0.67	0.08	-0.59	0.06	0.33	0.28
13	19	0.84	0.65	-0.19	0.52	0.40	-0.29

may have driven shifting ecological scores, multiple regression modeling was performed. Similar independent variables (wave energy, watershed size, fishing access, and pollution) were regressed against the relative change in fish and coral condition scores (H05). Resultant models were evaluated with the same criteria stated above.

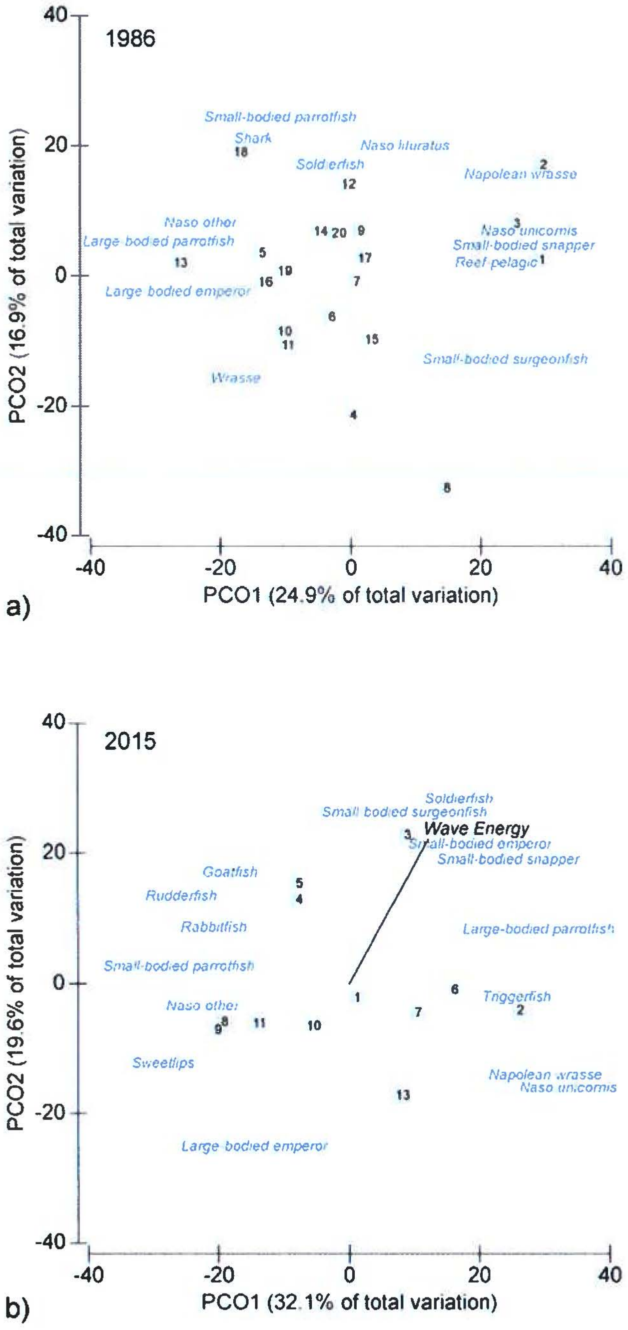
Results:

Multivariate spatial composition:

Redundancy analysis (DISTLM) revealed that neither wave energy nor watershed size predicted fish assemblage structure in 1986, suggesting similar fish assemblages existed across all environmental regimes (Figure 8). In contrast, wave energy predicted fish assemblage structure in 2015, with fish assemblages differing strongly between sites in high and low wave energy zones (DISTLM, $p<0.05$). In 2015, high wave energy zones were distinguished by soldierfishes, small-bodied surgeonfishes, small-bodied emperors, and small-bodied snappers, while low wave energy zones were distinguished by large-bodied emperors and sweetlips (Figure 8). These results suggested that fish assemblages were rather uniform across wave energy zones in 1986 but have become spatially differentiated over time. SIMPER analyses were used to better depict the difference between fish functional groups across wave energy regimes.

Sites with high wave energy in 2015 contained greater biomass of large-bodied parrotfishes, Napoleon wrasses, orange-spine unicornfishes, rudderfishes, and both small and large-bodied snappers compared with low wave energy sites (SIMPER analyses, species that cumulatively contributed 60% of significant differences between wave energy

Figure 8. Principal component plot of fish assemblage structure with wave energy, watershed size, and associated functional groups overlaid. 1986 fish assemblages were not predicted by any environmental factor (a). 2015 fish assemblages were predicted only by wave energy (b).



regimes in modern time frame, Figure 9). This pattern was similarly found in 1986 for Napoleon wrasses and rudderfishes. Interestingly, the opposite pattern was found for large-bodied parrotfishes, which had greater biomass in low wave energy sites in 1986. Orange-spine unicornfish and large and small-bodied snappers had relatively even biomass across wave energy zones in 1986. Low wave energy sites on the other hand, contained greater biomass of large-bodied emperors in both time frames. In sum, many desirable food fishes became less prominent in wave sheltered areas through time. One concern with these results was the potential influence of differing survey protocols, even though we only examined relative trends during each time frame. To address this issue, in part, we examined relationships between modern fish surveys using spatially-restricted SPC methods and spatially-unrestricted methods; positive correlations existed between both modern observations of fish assemblages (Figure 10). These findings suggest spatial trends within each time frame were less likely to be an artifact of different survey methods, and represented shifting species abundance patterns across Kosrae through time.

Both wave energy and watershed size predicted coral assemblage structure in 1986 (DISTLM, wave $p<0.05$, watershed $p<0.005$, Figure 11). Correlation testing revealed that wave energy and watershed size had a moderate, negative association ($r=0.59$, $p<0.05$) suggesting the two factors did not necessarily act independently on coral assemblages. Coral assemblages associated with high wave energy and small watersheds were characterized by species with encrusting and massive growth forms, including *Hydnophora*, *Goniastrea*, and *Favia stelligera*. Coral assemblages in low wave energy zones near large watersheds were characterized by corals commonly known to tolerate, or

Figure 9. SIMPER analysis showing percent differences between fish functional groups in high and low wave energy zones in 1986 and 2015 fish assemblages. The functional groups shown have the greatest dissimilarity between high and low wave energy zones, with overlap in both time frames.

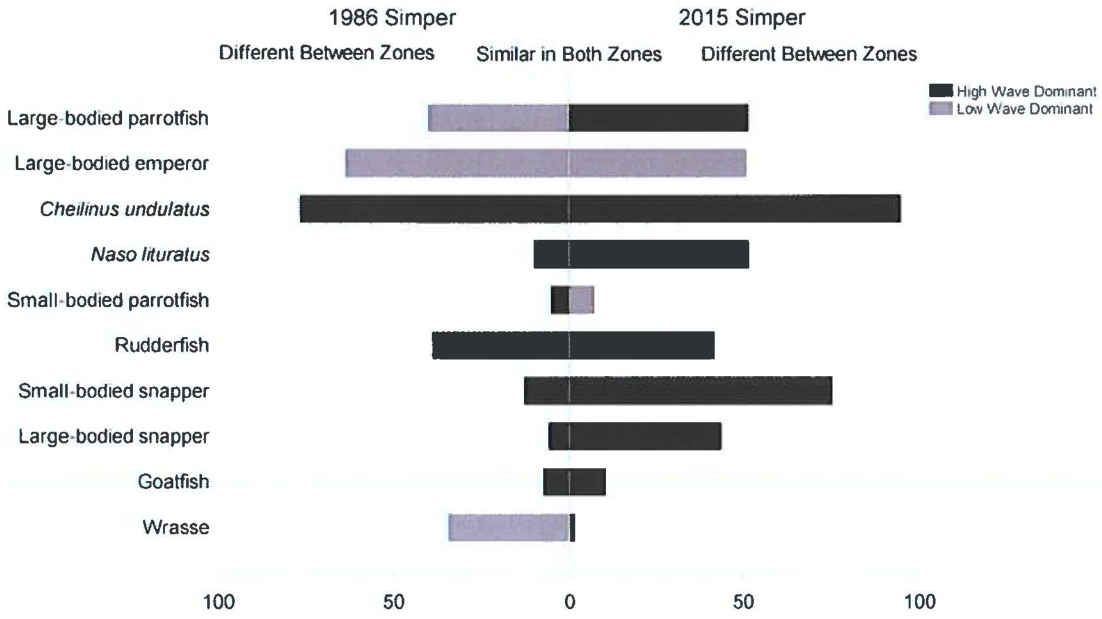


Figure 10. Correlation between fish biomass (a), predator biomass (b), and Shannon-Weaver diversity (c) recorded by a fish observer using the standard, modern method, and a second fish observer replicating the historical DACOR method. The solid lines indicate the correlation with all sites included, while the dashed lines indicate a conditional correlation with one (circled) site removed.

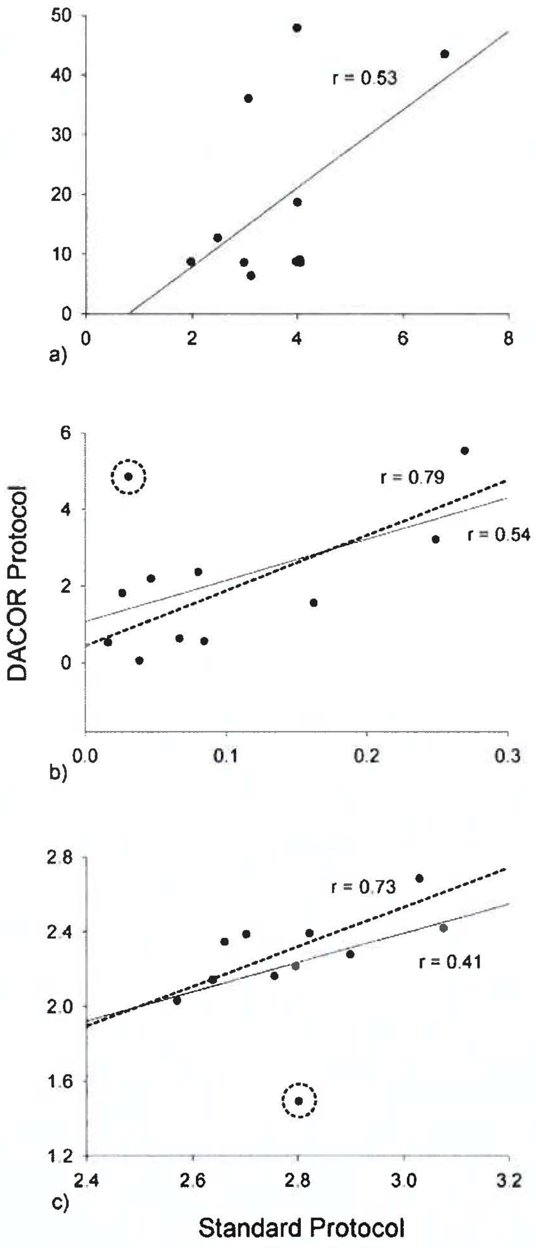
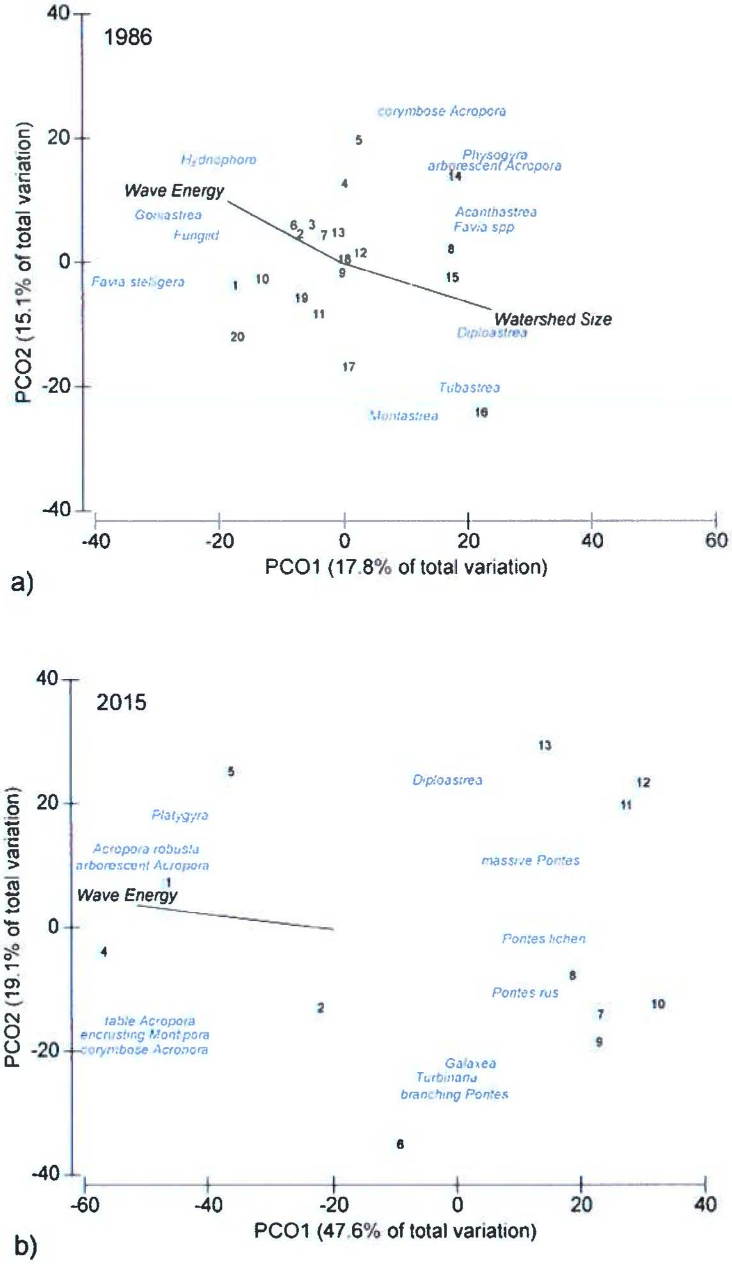


Figure 11. Principal component plot of coral assemblage structure with wave energy, watershed size, and associated functional groups overlaid. 1986 coral assemblages were predicted by both wave energy and watershed size (a). 2015 coral assemblages were predicted only by wave energy, and spatial differentiation has increased between coral assemblages in different wave energy zones (b).



benefit from, sediments and nutrients including *Diploastrea*, *Tubastrea*, and *Porites*. Coral assemblages in intermediate wave energy zones or near intermediate-sized watersheds included a mixture of these corals (Figure 11). Interestingly, *Acropora* were not characteristic of any single environmental regime in 1986, and were spatially consistent around Kosrae. In contrast, spatial patterns in 2015 became amplified for *Acropora* and many other corals. Wave energy alone predicted coral assemblage structure in 2015, with distinct assemblages existing between high and low wave energy zones (DISTLM, $p<0.05$, ANOSIM, 1986 $R=0.12$, 2015 $R=1.0$, Figure 11). High wave energy zones were characterized by *Acropora* and *Montipora* while low wave energy zones were characterized by *Porites* and *Galaxea*. In sum, wave energy was the only environmental influence affecting coral assemblage structure during both time frames, and differences between high and low wave energy assemblages became more pronounced through time.

SIMPER analyses were used to further highlight the differences in species composition based on wave energy, and also to distinguish if these findings may have been an artifact of different survey methods. SIMPER comparisons further highlighted major differences in coral assemblages between the time frames. In 2015, high wave energy predicted high cover of arborescent *Acropora*, table-forming *Acropora*, and *Acropora robusta* (100% higher than low wave zones for arborescent *Acropora* and *Acropora robusta*), as well as encrusting *Montipora* (Figure 12). Conversely, low wave energy predicted high cover of *Heliopora*, *Galaxea*, *Turbinaria*, and all *Porites* groups. Results from 1986 revealed that coral assemblages in high wave energy sites also had higher cover of *Acropora robusta* and table-forming *Acropora*, as well as encrusting *Montipora*, with *Acropora robutsta* cover 36% higher in highly wave-exposed sites, on average. Low wave

Figure 12. SIMPER analysis showing percent differences between coral functional groups in high and low wave energy zones in 1986 and 2015 coral assemblages. The functional groups shown have the greatest dissimilarity between high and low wave energy zones, with overlap in both time frames.

sites were likewise characterized by disproportionately higher cover of *Heliopora*, *Turbinaria*, *Porites lichen*, and massive *Porites*, which all had over 25% higher coral cover in low wave energy zones. *Galaxea*, *Porites rus*, and arborescent *Acropora* were also more abundant in low wave sites. For all functional groups except arborescent *Acropora,* spatial differences were similar through time, yet these differences have become more pronounced.

The increasing separation of multivariate coral assemblages with wave energy since 1986 did not appear to be biased by protocols (spatially-restricted versus non-restricted in 2015 and 1986, respectively). For example, arborescent *Acropora* were frequently reported as abundant and common in 1986 on the leeward side of the island, while they were not seen on the leeward side of the island in 2015. However, many other corals reported as common in 1986 were found to have a consistent presence in 2015 (e.g. *Leptoria*, *Platygyra*, *Pavona*). Thus, the 100% difference values reported for several species across the time frames did not appear to be an overweighed artifact of survey protocols, but rather an indication of shifting species assemblages through time. Further, iconic arborescent *Acropora* corals were actually documented in higher abundance in low wave energy sites in 1986, where they were no longer observed in 2015; many other *Acropora* species were also documented as abundant and common in low wave sites in 1986 (Table 3).

Table 3. 1986 categorical abundance summary for *Acropora* functional groups from low-wave energy sites. *Acropora* functional groups were a major driver of spatial differences between high and low wave energy sites in 2015. To determine if these results were merely an artifact of modern survey methods overlooking rare corals, we examined the 1986 abundance frequencies for *Acropora* functional groups. *Acropora* functional groups were most frequently considered common in the 1986 survey, indicating that our modern methods did not merely overlook rare corals, but rather depicted actual change through time.

Functional Group	Dominant	Abundant	Common	Occasional	Rare	Absent
Table *Acropora*	1	8	7	0	0	0
Arborescent *Acropora*	0	1	6	2	0	3
Corymbose *Acropora*	0	2	12	2	0	5
Acropora robusta	0	4	10	1	0	2

Diversity indices:

Relationships between environmental factors and univariate metrics of the fish and coral assemblages complimented the noted multivariate differences. Linear regression modelling revealed that Shannon-Weaver diversity indices for fish assemblages were not predicted by wave energy, watershed size, or pollution in 1986. Although wave energy predicted fish assemblage structure in 2015, wave energy did not predict fish assemblage Shannon-Weaver diversity. Likewise, Shannon-Weaver diversity was not predicted by watershed size, fishing access, or pollution in 2015.

Although wave energy predicted coral assemblage structure in 1986, it did not predict coral assemblage Shannon-Weaver diversity. Watershed size, on the other hand, did predict coral Shannon-Weaver diversity in 1986 ($R^2=0.48$, $p<0.005$, Figure 13). This relationship followed was unimodal, indicating that intermediate-sized watersheds enhanced species richness the most, and very small or large watersheds predicted lower richness. Coral diversity indices were not predicted by wave energy, watershed size, fishing access, or pollution in 2015.

Latent variables and assemblage condition:

Environmental influences:

Fishing access was the only significant predictor of overall fish condition score in 1986, whereby increased fishing access was associated with a higher overall fish assemblage score ($R^2=0.22$, $p<0.05$, Figure 14). Thus, favorable fish assemblages existed on the leeward side of the island with greater human access. In contrast, there was a non-,

Figure 13. Polynomial regression depicting the relationship between 1986 coral assemblage Shannon-Weaver diversity and watershed size. Watershed size predicted coral assemblage Shannon-Weaver diversity, where large and small watersheds was had similar diversity, and medium-sized watersheds had the highest diversity.

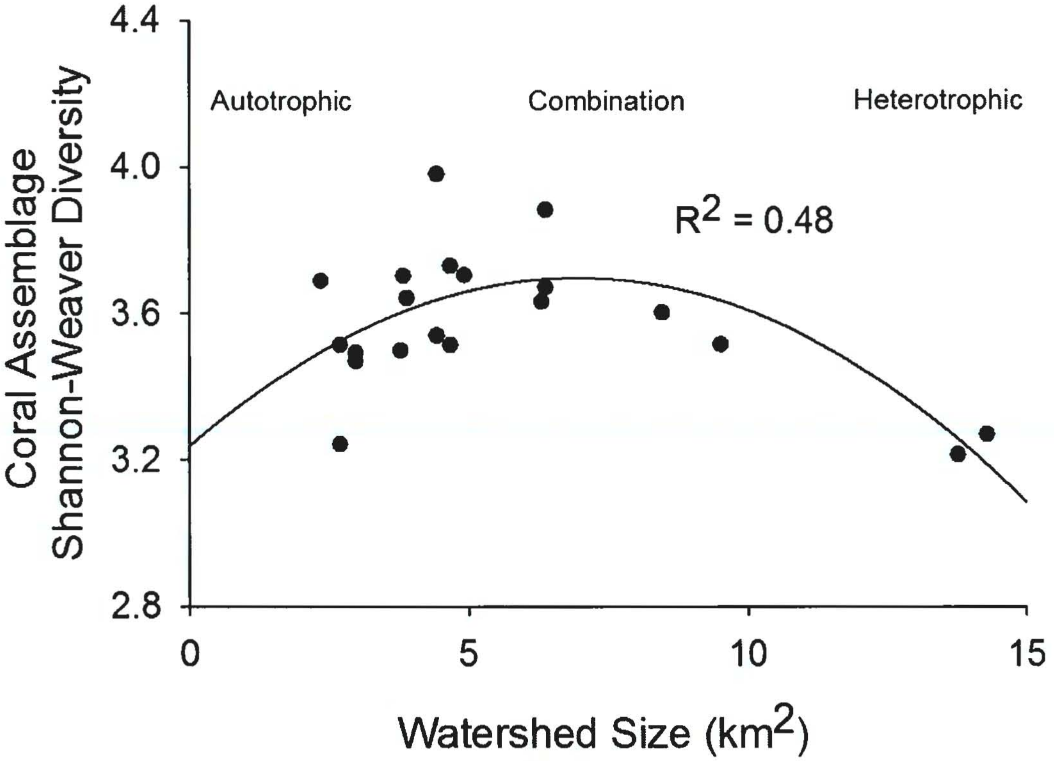
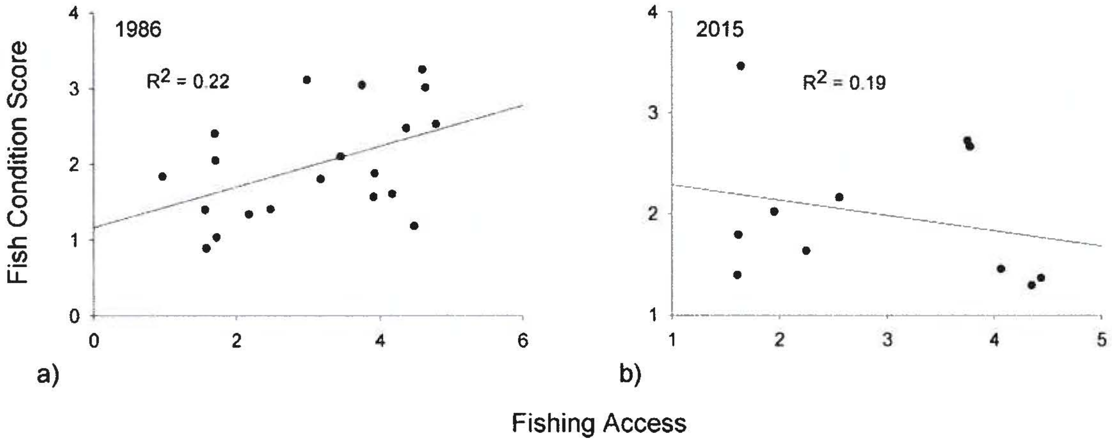


Figure 14. Linear regressions depicting the relationship between fishing access and fish assemblage condition scores in both time frames. Increased fishing access predicted higher fish assemblage scores in 1986 (a), as desirable food-fishes existed in high abundance nearest fishing marinas on the Western side of the island. In 2015 (b), this relationship has shifted to a non-significant, negative association where more favorable fish assemblages no longer exit near fishing marinas.



significant, negative association between fishing access and fish assemblage score in 2015 (R^2=0.18, p=0.19, Figure 14), as favorable fish assemblages currently exist on the windward side. For corals, watershed size predicted overall condition score in 1986, with highest scores being associated with medium-sized watersheds, and a decline for both larger and smaller watersheds, similar to the results for diversity indices (R^2=0.43p<0.005, Figure 15). In contrast, the proxy to pollution was the only negative predictor of coral scores in 2015 (multiple regression modelling, R^2=0.36, p<0.05, Figure 16), suggesting a potential shift from prevailing environmental influences to anthropogenic stressors, similarly found for fish assemblages. Wave energy alone did not predict fish or coral scores in either time frame.

Sensitivity analysis furthered that fish species richness, Shannon-Weaver diversity indices, and assemblage biomass had the largest contributions to the latent variable for overall fish assemblage score in 1986, indicating that these attributes were positively correlated and highly influential (r=0.9, r=0.82, and r=0.79 respectively, Figure 17). Predator biomass and the ratio of large to small herbivores, had lower and more unique contributions to the fish assemblage score (r=0.57 and r=0.55 respectively). In contrast, the relative influence of individual attributes shifted in 2015, as predator biomass, Shannon-Weaver diversity, and species richness all had the highest correlation contributions (r=0.79, 0.75, 0.74, respectively). Thus, declining predator abundance was a major driver of fish assemblage change through time. Fish assemblage biomass and the ratio of large to small herbivores, had lower but unique contributions (r=0.62 and r=0.6 respectively).

Figure 15. Polynomial regression depicting the relationship between 1986 coral assemblage condition score and watershed size. Watershed size predicted coral assemblage condition score, where large and small watersheds was had similar coral condition, and medium-sized watersheds had highest coral condition.

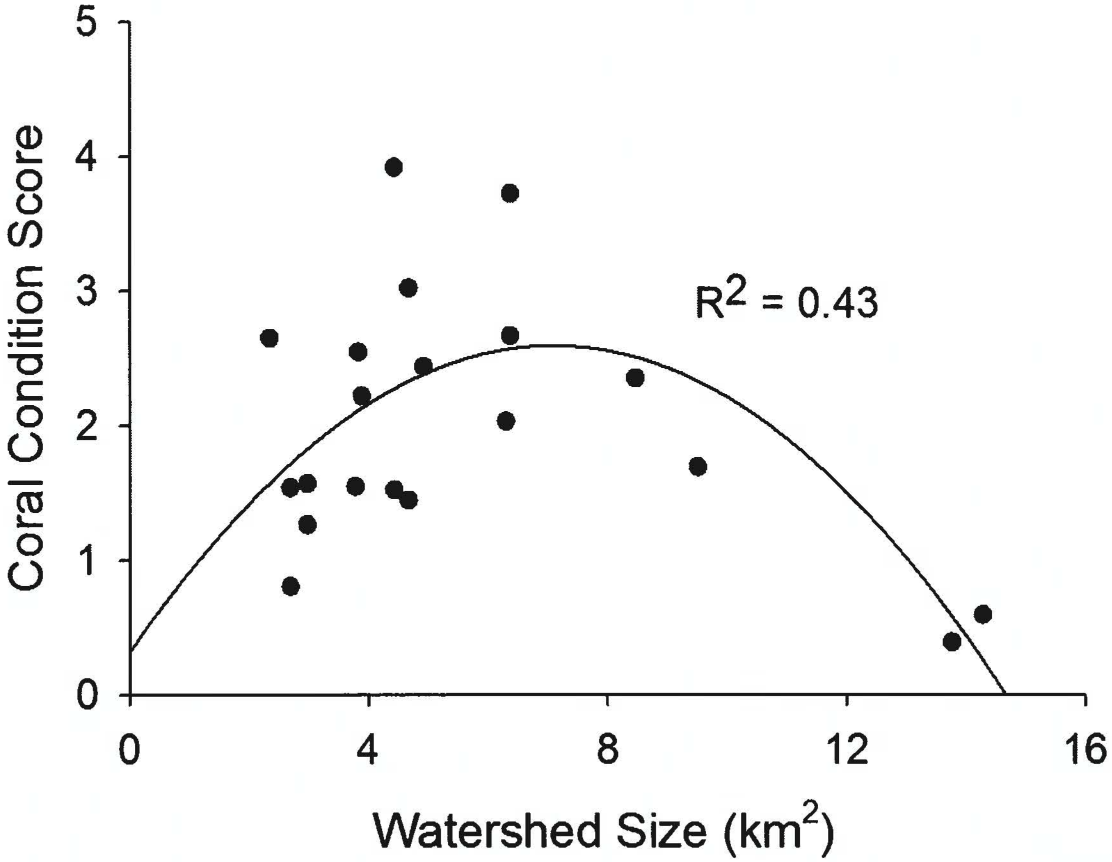


Figure 16. Linear regression depicting the relationship between 2015 coral assemblage condition score and the pollution proxy. Pollution predicted coral assemblage condition score, where increasing pollution was associated with decreasing coral condition.

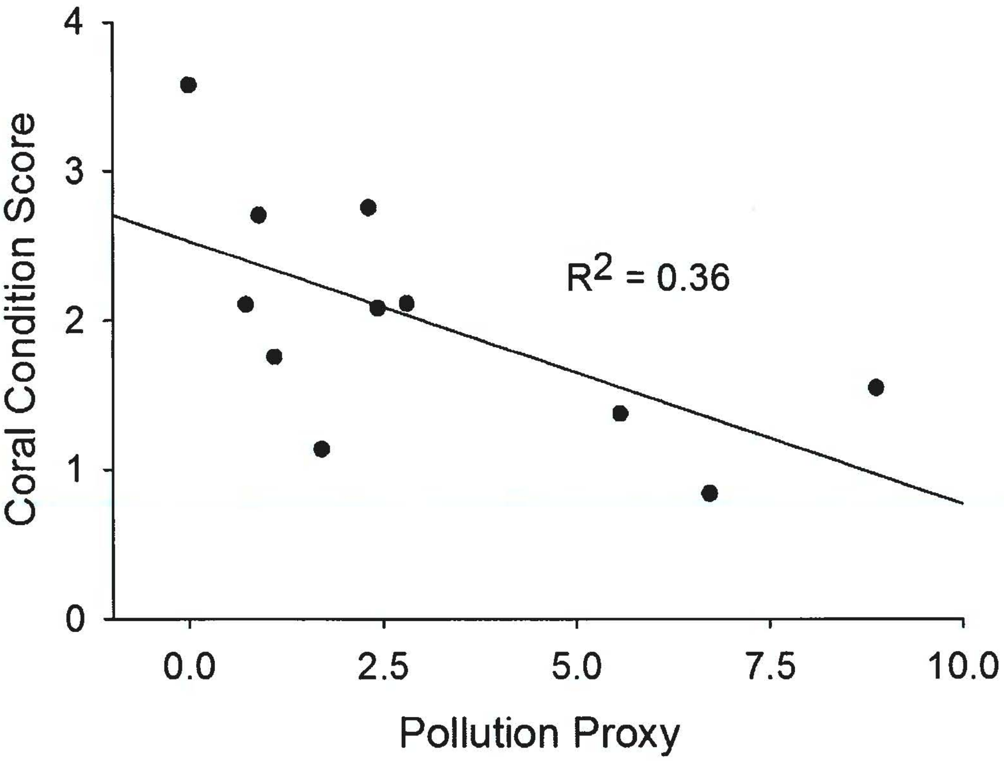
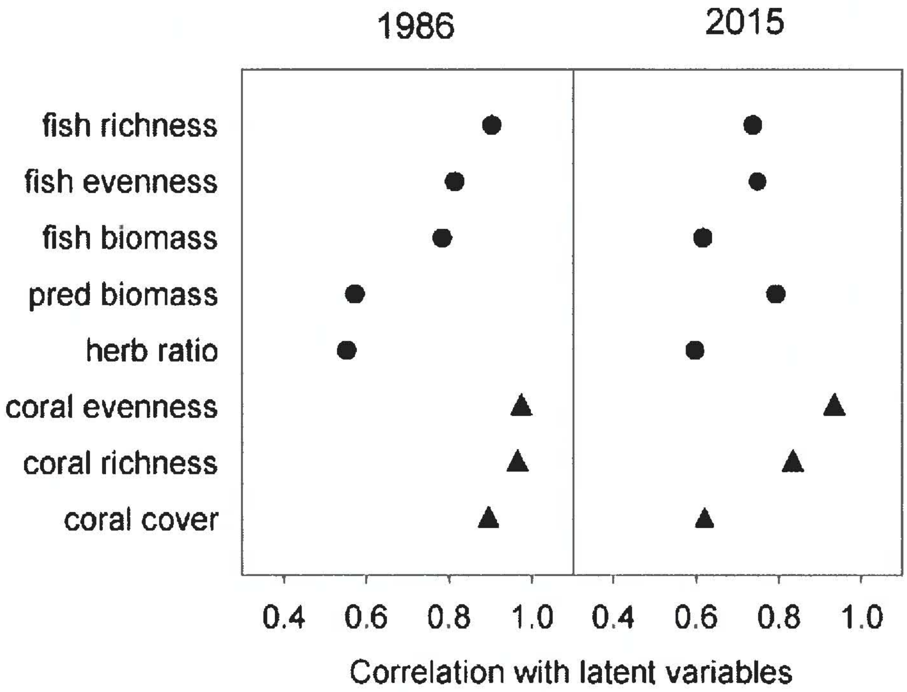


Figure 17. Sensitivity of fish and coral condition scores depicted by correlation coefficients between individual ecological attributes and their corresponding latent variables

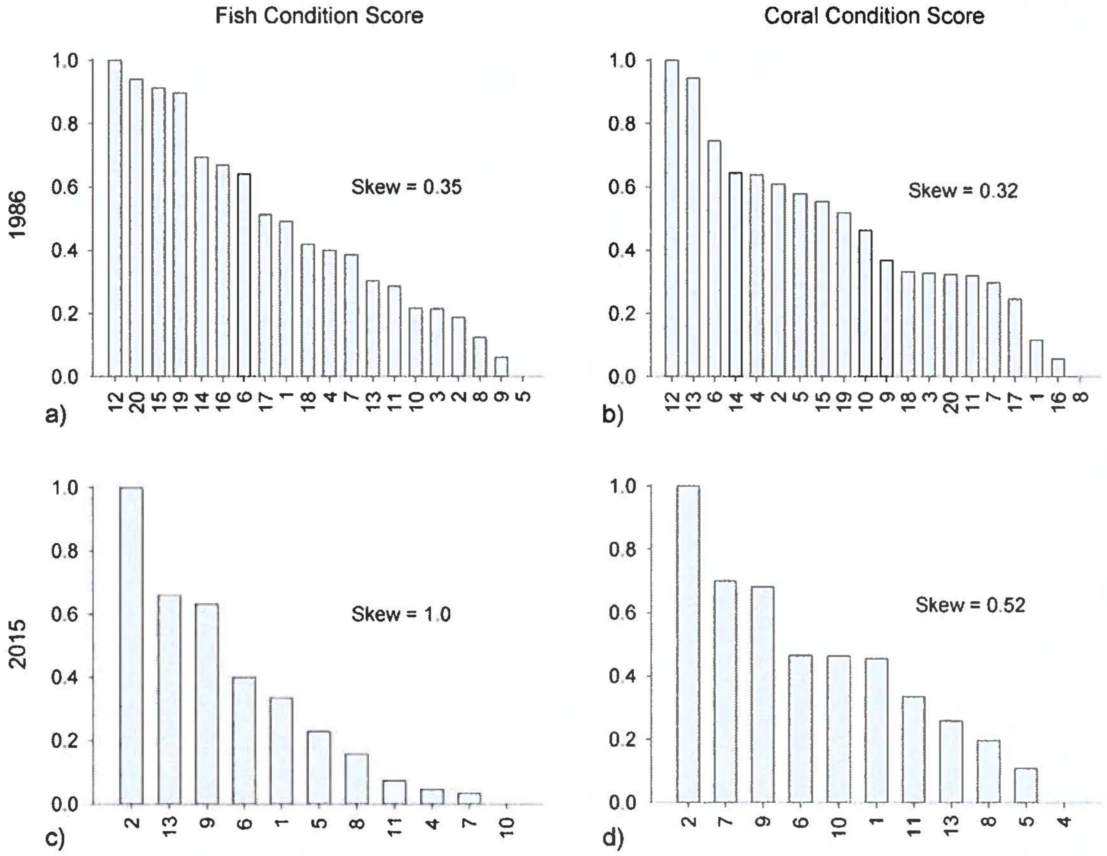


Sensitivity analyses for coral assemblages found that Shannon-Weaver diversity indices and species richness had similar influences on overall coral score in 1986, indicating that these attributes were positively correlated and highly influential (r=0.97 in both cases). Coral cover had a weaker influence on the coral assemblage score, but had positive association with both Shannon-Weaver diversity and species richness (r=0.9). In 2015, Shannon-Weaver diversity indices remained the most influential attribute to overall coral score, while species richness and coral cover had weaker contributions (r=0.93, r=0.83, r=0.62, respectively). Thus Shannon-Weaver diversity was the strongest driver of overall coral assemblage score in both time frames, while coral cover became much less influential through time.

Relative changes in fish and coral condition:

To better understand temporal changes through time, assemblage scores for all sites, and overlapping sites were normalized during both time frames by the highest and lowest site values. Histograms of normalized scores revealed that both fish and coral scores had lower skew in 1986 compared to 2015, indicating that scores were historically more consistent across sites, and that the disparity between high and low condition has increased through time (Figure 18). Further, the relative change in overlapping site normalized fish and coral scores were weakly positively correlated when considering windward and leeward sides individually. In both instances, fish and coral assemblage changes had strong correlation coefficients, but dividing these sides reduced sample size beyond significance. This was necessary, because in leeward sites, fish changes were more pronounced than coral changes, while in windward sites coral changes were more pronounced than fish

Figure 18. Normalized Fish and coral condition scores ranked from highest to lowest. The skew of fish and coral condition rankings across sites is lower for 1986 than 2015, suggesting that scores were more consistent across sites.



changes. These conflicting relationships resulted in an overall non-significant correlation between relative change in normalized fish and coral scores. However, the correlation coefficients between the relative change of fish and coral scores for each regime suggest spatial changes in fish and coral assemblages were coupled through time (Pearson's moment correlations, leeward r=0.74, p=0.16, windward r=0.8,p=0.10, Figure 19). Lastly, fishing access alone negatively predicted the relative changes in normalized fish scores through time, indicating that human fishing pressure was the strongest driver of fish assemblage decline through time (Figure 20, multiple regression modelling, $p<0.05$). In turn, because fish and coral changes appear spatially coupled, it is likely that fishing pressure also indirectly reduced coral condition through time, as coral changes were not predicted by any other environmental factor.

Discussion:

This study reported predictable distributions of fish and coral assemblages around Kosrae that were historically driven by natural environmental influences, but have become increasingly influenced by human stressors through time. While coral-reef declines are intuitive in densely populated islands with heavy pollution and overfishing, such declines are more puzzling in remote, sparsely populated islands around the Pacific. Kosrae is a small island with a modest population and intact primary forests, yet negative changes in coral and fish assemblages were documented through time. Similar reef declines are becoming common even in remote islands around the Pacific (Hoegh-Guldberg et al. 2007). Therefore, identifying the major causes of coral-reef decline in Kosrae might help explain similar patterns and reveal testable hypotheses for other small Pacific islands.

Figure 19. Pearson's moment correlation depicting the relationship between the relative change in coral and fish scores from 1986 to 2015 on leeward and windward sides. Relative changes in fish and coral assemblages were weakly correlated when considered by windward and leeward site individually.

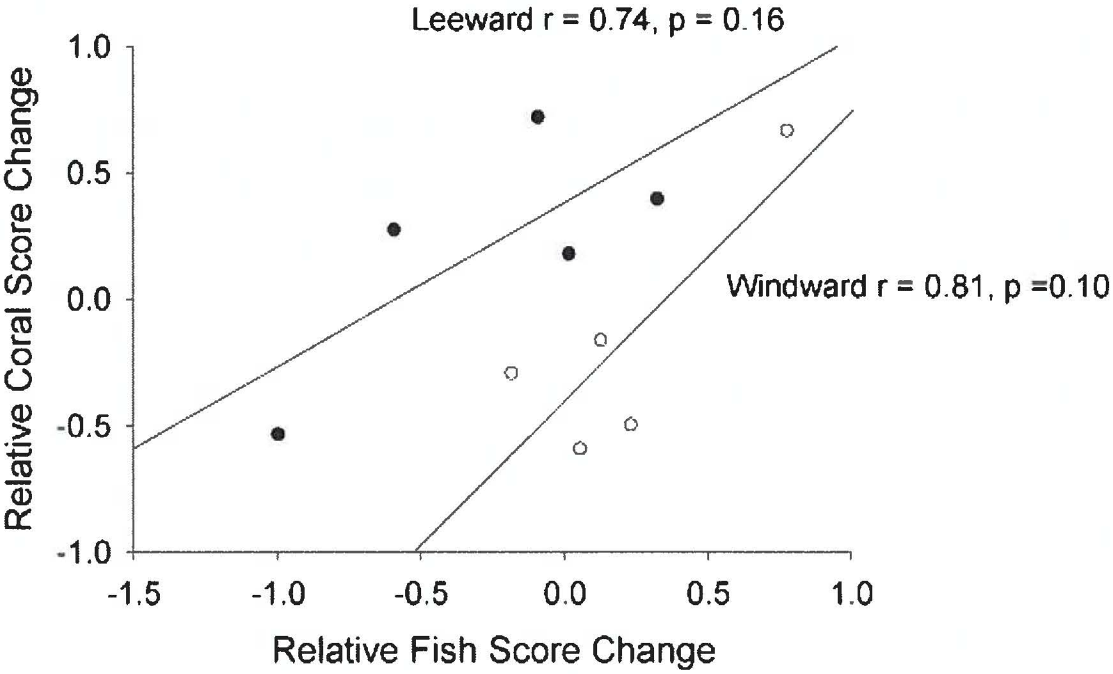
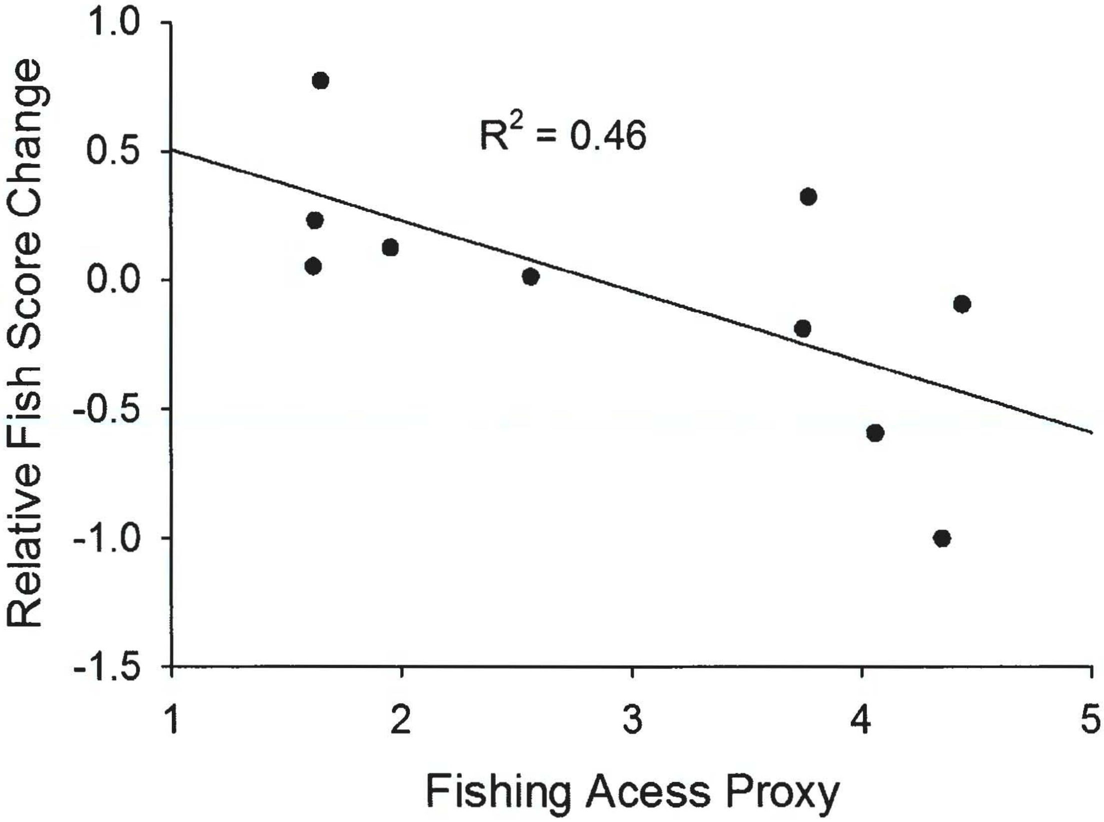


Figure 20. Linear regression depicting the relationship between the relative change in fish assemblage score from 1986 to 2015, and the proxy for fishing access. Fishing access predicted the relative change in fish assemblage score, where increasing fishing access was associated with decreasing fish assemblage condition.



This study reported multiple scenarios that may explain coral reef decline in Kosrae, but ultimately, decline was linked to the removal of key fish groups and fish functionality.

Fish assemblages:

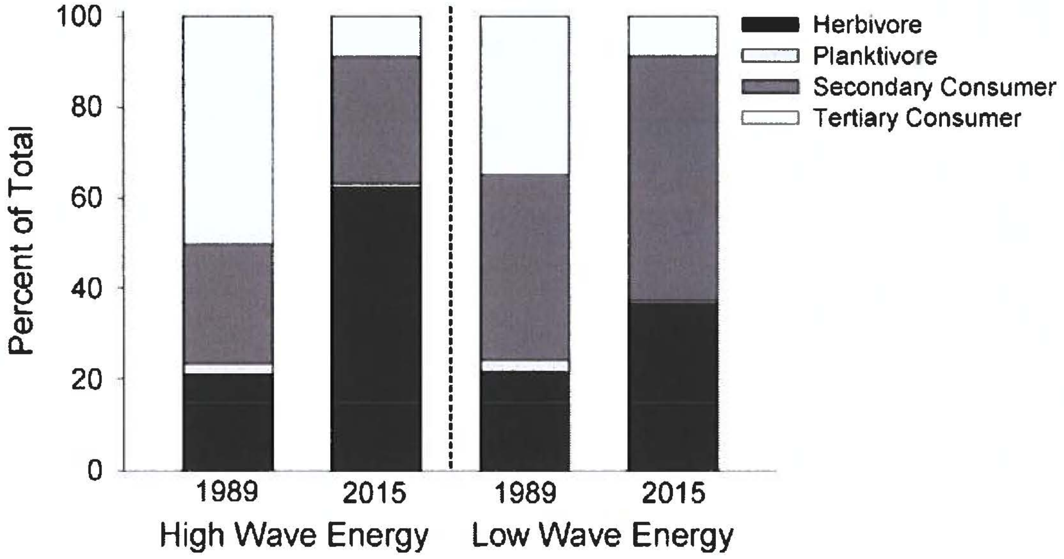
Historically, fish assemblages were well-mixed around Kosrae, with little difference in species abundances between major environmental regimes. In 1986, large predators, including *Carcharhinus amblyrhynchos* and *Triaenodon obesus*, were common in Kosrae, as were larger-bodied, longer-lived herbivores such as *Kyphosus vaigiensis*, *Scarus rubroviolaceus*, *Chlorurus microrhinos*, and *Scarus altipinnis.* Given the linear relationship between body size and home range, larger fishes would increase population connectivity (Harestad and Bunnel 1979). A few species and functional groups were not evenly distributed, including some emperorfishes, snappers (*Lutjanus bohar*), and large-bodied parrotfishes which were more abundant on the leeward side, and Napoleon wrasses and rudderfishes, which were more abundant on the windward side. Additionally, Bumphead parrotfishes were only observed on the leeward side of the island. However, these differences did not distinguish overall assemblage structure around Kosrae in 1986, and were likely the result of environmental preferences or natural variability (Bell and Gazin 1984, Fabricius et al. 2005). Therefore, fish assemblages in 1986 likely represented a well-connected metapopulation with little disruption from human influence (Hanski 1998, Armsworth 2002, Saenz-Agudelo et al. 2011).

In contrast, we report distinct spatial differences in fish assemblages between high and low wave energy zones in 2015, suggesting a marked shift in overall fish assemblage structure over the past 29 years. These patterns were driven by declines in large-bodied predators and herbivores, which were most pronounced in low wave energy zones. Modern assemblages have few predators, and herbivore biomass is dominated by small-bodied, short-lived species with small home ranges. These declines have amplified differences between high and low wave energy zones that were slightly apparent in 1986. In 1986, fish assemblages on the leeward side had slightly higher fish condition scores, but in 2015, these scores have plummeted. Due to low wave energy and high fisher populations near Okat Marina and Walung Channel, leeward sites had higher fishing access. Not surprisingly then, fishing access was the strongest driver of declining fish assemblages through time (i.e., declining normalized scores on the leeward side compared with windward).

The cumulative changes in fish assemblages shifted the proportional biomass of different trophic groups from 1986 to 2015. While differing sampling protocols could obviously impact the biomass distribution across trophic levels, modern fish surveys used both spatially-restricted and unrestricted methods. Comparisons with modern data collected from unconstrained survey areas supported our results, and found decreases in predator fish biomass (including sharks, which were observed at the majority of sites in 1986, but never once observed in 2015), coupled with increases in the proportional composition of herbivore and secondary consumer biomass (Figure 21).

Given the unchanging population of Kosrae over the past three decades, it is likely that the number of fishers has remained similar, and increases in fishing pressure have come from technological advancement. Larger boats and engines, modern fishing tackle and spear guns, and underwater flashlights have increased fish harvest on coral-reefs world-wide (Jackson et al. 2001, Kennelly and Broadhurst 2002, Sabetian and Foale 2006).

Figure 21. Mean trophic-level fish biomass between high and low wave exposure zones for 1986 and 2015. 2015 data shown was collected using unconstrained survey methods similar to those used in 1986.



It is also plausible that historical fishing pressure was unsustainable, but the results of this stress had not yet manifested. Over the course of 29 years, unsustainable fishing could have led to the dramatic shifts in fish assemblages we have found, while gradual changes would be less noticeable from year to year, especially without continuous monitoring. These gradual changes support the concept of shifting baselines on coral-reefs, where successive generations notice slight differences in resources year to year, but over decades, major changes become apparent. In this manner, gradual over-harvesting leads to major reductions in fish assemblages over large timescales. In addition, there has been a growing market for fish sales in recent decades. Historically, fish harvest focused on subsistence, while new generations have begun to harvest fish to earn income (William personal communication).

Coral Assemblages:

Historically, coral assemblages appeared to have been shaped by natural influences. Both wave energy and watershed size predicted coral assemblage distributions, and had unimodal relationships with coral cover and species richness, where cover and richness were highest in intermediate wave energy and watershed sizes. Wave energy is known to dictate the structure of coral-reefs through water turbulence, flushing, and light penetration (Stoddart 1969, Roberts 1974, Dollar 1982). High wave energy promotes colonization by tolerant, fast-growing species that can take hold before being damaged by turbulence and sediment-scour (Hubbard 1997). High flushing also reduces the accumulation of sediments and detritus, enhancing gas and nutrient exchange. We found that coral assemblages in highly wave exposed areas are indeed characterized by many fast-growing species that tolerate water turbulence, however, moderate wave energy zones contained an optimal balance between species richness and coral growth.

Alternatively, watershed size dictates the amount of land-based sediments, nutrients, and freshwater that drains into coral-reef ecosystems. In Kosrae, the majority of watersheds are dominated by primary forests that generate large amounts of particulate organic matter and inorganic nutrients, which fuel primary production when added to the marine ecosystem (Vitousek and Sanford 1986, Hatcher 1990, Gleason and Ewel 2002, Devlin and Brodie 2005). This study found that large watersheds were associated with coral species that tolerate turbid, nutrient-rich water and can feed heterotrophically, while small watersheds favored zooxanthellate species that are more common to oligotrophic waters and derive most of their energy from symbiosis (DeVantier et al. 2006). Intermediate watershed sizes had both types of corals, with maximum species richness and coral cover. Interestingly, watershed sizes and wave exposure were inversely related. The largest watersheds were found on the leeward side of the island with low wave energy. Therefore, both intermediate wave exposures and watersheds acted together to dictate coral assemblage structure. Moderate environmental regimes also predicted the highest overall coral condition scores that were derived by integrating coral cover, species richness, and evenness. This pattern reinforced that a moderate input of nutrient-rich water and organic matter from terrestrial ecosystems, and moderate flushing from wave energy, supported a mixture of species with heterotrophic and autotrophic preferences. Similar patterns have previously been observed for environmental factors, including watershed discharge, where diversity is highest when influences are moderate. For example, DeVantier et al. (2006) examined coral assemblages at 599 sites along the Great Barrier Reef and documented that coral species richness was similar nearshore and on the outer continental shelf, but peaked at the mid-continental shelf. Thus, moderate environmental influences appear to provide the most favorable environments for coral-reef growth.

Modern coral assemblages are now strongly predicted by wave energy. While historical coral assemblages had spatial differentiation between high and low wave energy zones, this pattern has become amplified through time. For example, leeward sites contained notable *Acropora* presence in 1986, including more arborescent *Acropora* compared with windward sites, yet *Acropora* corals were rarely encountered in 2015. It appears that the majority of *Acropora* corals have vanished from leeward reefs, which is alarming given that the 1986 survey reported most *Acropora* groups as being common and abundant. In contrast, the contribution of *Porites* and *Galaxea* corals increased dramatically, now making up 59% of coral cover across leeward sites. Furthermore, the 1986 survey reported "the most pristine, diverse, and abundant coral communities off the ocean-facing slopes of Kosrae occurred along Section 4 [leeward]." This was supported by 1986 sites #12 and 13, which had the highest coral condition scores. Overall, 1986 coal condition scores were slightly higher on the windward side of the island, and in 2015 were slightly higher on the leeward side, however coral assemblages in both regimes have become substantially differentiated due to declining species richness and evenness. These findings highlight a dramatic shift from healthy, diverse coral assemblages along the leeward side of Kosrae, to assemblages devoid of many fast-growing, reef-building species, and dominance by few, slow-growing species tolerant of disturbances and stressors. Alternatively, coral assemblages on the windward side have become dominated by few, fast-growing species. These dramatic findings raises the question: what scenarios explain Kosrae's coral-reef decline through time?

Potential mechanisms behind shifting baselines:

In the fall of 2013, Kosrae experienced a thermal stress event that caused localized coral mortality. Before and after surveys from ongoing monitoring efforts found that mortality was mild for most reefs, but severe in one instance (site 8). Data collected prior to this event (2011, 2012, 2014) indicate that the overall impacts of thermal stress did not lead to significantly different coral assemblages prior to and post bleaching for other sites around Kosrae (i.e., comparisons of assemblages before and after the event had greater Bray-Curtis similarities compared with spatial patterns during all timeframes). It is possible that coral mortality from this event exacerbated the overall coral-reef decline we have documented, however, spatial patterns remained similar pre-and-post bleaching.

Given that coral and fish changes were weakly spatially correlated and that fishing pressure was a negative predictor of fish assemblage change through time, the collective findings imply that fishing pressure through time compromised the functional roles of fishes, which eventually led to the decline in coral condition. Pollution was also identified as a predictor of coral condition score in 2015, but not a predictor of coral condition change between the two timeframes. We summarize that coral assemblages are currently afflicted by pollution in densely populated areas alone the east side of Kosrae, but that the influence of pollution through time was not spatially extensive.

While fishing pressure was identified as the strongest influence over coral-reef change through time, fish harvesting does not generally cause direct coral mortality (excluding destructive fishing practices that do not occur in Kosrae) (Aronson and Precht 2006). Sedimentation and pollution have been reported to directly smother living coral, however, pollution was not identified as a driver of coral assemblage change through time. Therefore, the question remains: what caused large-scale coral mortality? Previously published studies, technical reports, and personal communication with resource management agencies suggest that large-scale disturbances have been minimal, with no major bleaching events, crown of thorns starfish outbreaks, or recent typhoons documented. This is puzzling because many studies have noted declining coral condition in areas with exploited fisheries, but only after a large-scale disturbance induces mortality; following coral mortality, exploited fish assemblages do not provide the essential functions that aid coral recovery (Nyström et al. 2000). As additional disturbances occur, reef decline continues. It therefore appears that coral mortality resulted from two possible sources. First, large-scale disturbances have occurred that caused considerable coral mortality, but these disturbance events were either unnoticed or undocumented. Second, the culmination of small-scale perturbations, such as storm surges, mild thermal stress, or land-based discharge, caused coral mortality over time with compromised recovery. Anecdotal reports from local business owners informed us that a strong storm surge in 2008 killed a large amount of living coral, however this event was not officially documented because no tropical cyclone made direct contact with the island. The culmination of small, localized events such as these, which are rarely documented, could have led to the observed coral mortality over time (Done 1992, Nystrom et al. 2008).

Over-fishing coral reefs has repeatedly been shown to shift fish assemblage structure from natural, predator-rich systems with large-bodied herbivores, to assemblages where smaller-bodied species of herbivores and secondary consumers become dominant (Nystrom et al. 2000, Dulvy et al. 2004, Houk et al. 2015). Beyond metapopulation structure, fish assemblages dominated by larger bodied species offer disproportionally greater function to reef ecosystems. Herbivores graze algae and scrape carbonate material providing clean substrates for coral recruitment. Predators stabilize food webs through top-down control and promote herbivore diversity by feeding asynchronously across a wide variety of prey (Paine 1966, Rooney et al. 2006). Allometry dictates that these processes are related to fish size through power-law functions that yield exponential increases with size (Birkeland and Dayton 2005, Lokrantz et al. 2008). Together, high predator biomass and large herbivore dominance create functional fish assemblages capable of maintaining reef resilience (Mumby et al. 2006a, Lokrantz et al. 2008, Houk and Musburger 2013b). Thus, 29 years ago, reef-fish assemblages in Kosrae appear to have been highly functional and to have maintained heterogeneous, resilient coral-reefs prior to the accumulation of modern stressors. Modern fish assemblages have suffered the loss of these key functional guilds through the accumulation of fishing pressure and the availability of new fishing technologies. Kosrae's reefs are now dominated by small-bodied herbivores and secondary consumers like surgeonfishes and small snappers. Such fish assemblages are highly indicative of overexploitation (Jackson et al. 2001, Knowlton and Jackson 2008, McClanahan et al. 2008, Sandin et al. 2008). Available data suggest this shift in fish assemblage composition has reduced overall reef resilience, leading to the failed recovery of many leeward coral assemblages, and the overall coral-reef decline depicted here.

Unfortunately, it appears that many of Kosrae's healthy coral assemblages are in danger of phase shifts if struck by major disturbances. Some areas appear to have already undergone phase shifts (1986 site #13), while others may be in jeopardy from the recent thermal stress event (2015 site #8). Disturbances to coral reefs are predicted to increase in frequency and severity as global temperatures and carbon dioxide levels rise (McGowan et al. 1998, Scavia et al. 2002). Kosrae, in particular, is expected to experience higher seawater temperatures and damaging coral bleaching events in the future (Van Woesik et al. 2012). If Kosrae's fish assemblages continue suffering unsustainable fishing pressure, coral assemblages will likely degrade as well, leading to further declines in coral cover, richness, and reef structure that can impact both resources users and tourism operators.

In order to prevent such catastrophic phase shifts, Kosrae must manage local stressors that degrade coral-reef reef resilience. While large-scale disturbances are unavoidable, we provide evidence suggesting coral-reef decline was mainly linked with unsustainable fishing while pollution was a secondary influence, and therefore polices to improve fish stocks will best enhance resilience, especially on the leeward side of Kosrae where fish condition has declined the most. Coral assemblages declined more on the windward side of the island, which was likely driven by the combination of fishing pressure and localized pollution in densely populated areas (e.g. modern sites 4 and 13). Thus management efforts should prioritize fisheries regulations for leeward sites, and both fisheries regulations (to a lesser extent) and pollution reduction for windward sites. Given that predators and large-bodied herbivores are the primary targets for management, restoring the diversity and biomass of these key functional groups should be a priority. Healthy fish assemblages with high predator biomass and large herbivores have been shown to ameliorate coral-reef decline (Selig and Bruno 2010). Additionally, species richness and evenness contributed greatly to overall fish condition score in both timeframes, suggesting that increased diversity leads to healthier fish assemblages, therefore it appears that managing key fish assemblage aspects (species richness, predator biomass, herbivore ratio) should be the first step. Modern site #2 is a promising example of how in-tact, healthy fish assemblages can not only ameliorate coral-reef decline, but can help reefs recover following major disturbances. This site was damaged by a storm-surge in 2008, but only seven years later this site had the highest fish and coral species richness, along with the highest biomass of predators and large herbivores. Managing other areas to capture this resilience is key to protecting Kosrae's reefs into the future. While impeding fish harvest would damage the economy and livelihood of Kosrae's people, who depend heavily on their resources, fisheries management can act to mitigate exploitation to key fish species and functional guilds through seasonal fish bans, catch quotas, and size windows. Restructuring the nature of fish harvest can help create sustainable fisheries with increased functionality, which in turn will increase overall coral-reef resilience and mitigate the ongoing coral-reef decline seen throughout the Pacific.

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Appendix 1. Fish species recorded in each survey. 2015a represents the stationary point count method, while 2015b represents the spatially unrestricted method.

Species	1986	2015a	2015b
Acanthurus blochii	X	X	X
Acanthurus guttatus	X	X	
Acanthurus leucocheilus		X	
Acanthurus lineatus	X	X	
Acanthurus nigricans	X	X	
Acanthurus nigrofuscus	X		
Acanthurus olivaceous	X		
Acanthurus pyroferus	X	X	
Acanthurus triostegus	X		
Acanthurus xanthopterus	X	X	X
Aethaloperca rogaa	X		
Anyperodon leucogrammicus	X		
Aphareus furca	X	X	X
Aprion viriscens	X	X	X
Balistoides viridescens		X	
Bolbometopon muricatum	X		
Calotomus carolinus		X	
Carangoides ferdau		X	X
Caranx ignobilis			X
Caranx melampygus	X	X	X
Caranx sexfasciatus	X		
Caranx sp.	X		
Carcharhinus amblyrhynchos	X		
Cephalopholis argus	X	X	X
Cephalopholis urodeta	X	X	
Cetoscarus bicolor	X		
Cheilinus chlorourus	X		
Cheilinus fasciatus	X	X	

Cheilinus trilobatus	X	X	
Cheilinus undulatus	X	X	X
Chlorurus frontalis		X	X
Chlorurus japanensis		X	X
Chlorurus microrhinos	X	X	X
Chlorurus sordidus	X	X	
Ctenochaetus striatus	X	X	
Decapterus sp.	X		
Epibulus insidiator	X	X	X
Epinephelus fuscoguttatus	X		
Epinephelus merra	X		
Epinephelus polyphekadion	X		
Epinephelus sp.	X		
Gymnosarda unicolor	X		
Hipposcarus longiceps	X	X	X
Kyphosus bigibbus			X
Kyphosus cinerascens	X	X	
Kyphosus sp.	X		
Kyphosus vaigiensis	X	X	X
Lethrinus harak	X	X	
Lethrinus microdon	X		
Lethrinus miniatus	X		
Lethrinus obsoletus			X
Lethrinus olivaceus		X	X
Lethrinus xanthochilus		X	X
Lethrinus sp.	X		
Lutjanus argentimaculatus		X	X
Lutjanus bohar	X	X	X
Lutjanus fulviflamma	X		
Lutjanus fulvus	X	X	X
Lutjanus gibbus	X	X	X
Lutjanus kasmira	X		

Lutjanus monostigma	X		X
Lethrinus semicinctus		X	X
Lutjanus sp.	X		
Macolor macularis		X	X
Macolor niger	X	X	X
Monotaxis grandoculis	X	X	X
Mulloidichthys flavolineatus	X	X	
Mulloidichthys vanicolensis		X	
Myripristis adusta	X		
Myripristis berndti	X		
Myripristis murdjan	X		
Myripristis sp.	X	X	
Myripristis violacea	X		
Naso brevirostris	X	X	
Naso hexacanthus	X		
Naso lituratus	X	X	X
Naso thynnoides	X		
Naso unicornis	X	X	X
Naso vlamingii	X	X	X
Neoniphon sammara	X		
Neoniphon sp.	X	X	
Parupeneus barberinus	X	X	
Parupeneus bifasciatus	X	X	X
Parupeneus cyclostomus	X	X	
Parupeneus indicus	X		
Parupeneus multifasciatus	X	X	
Pempheris oualensis	X	X	
Platax orbicularis	X		
Plectorhinchus albovittatus		X	X
Plectorhinchus lineatus		X	X
Plectorhinchus nigrus	X		

Plectorhinchus pictus	X		
Pseudobalistes flavimarginatus		X	
Pygoplites diacanthus	X	X	
Sargocentron caudimaculatum	X		
Sargocentron spinniferum	X		
Sargocentron tiere	X	X	
Scarus altipinnis	X	X	X
Scarus dimidiatus	X	X	
Scarus festivus		X	
Scarus forsteni		X	
Scarus frenatus	X	X	X
Scarus ghobban	X	X	X
Scarus globiceps	X	X	
Scarus hypselopterus	X		
Scarus niger	X	X	X
Scarus oviceps	X	X	
Scarus ovifrons	X		
Scarus prasiognathus	X		
Scarus psittacus	X	X	
Scarus rivulatus	X	X	X
Scarus rubroviolaceus	X	X	X
Scarus schlegeli	X	X	
Scarus sp.	X		
Scarus spinus	X	X	
Scarus tricolor	X		
Siganus argenteus		X	X
Siganus doliatus		X	X
Siganus puellus	X		
Siganus virgatus	X		
Sphyraena barracuda	X		
Trachinotus blochii	X		
Triaenodon obesus	X		
Uindentified Mullid	X		
Unidentified carangid	X		

Unidentified Lutjanid	X
Unidentified Scarid	X

Appendix 2. Coral species recorded in each survey.

Species	1986	2015
Acanthastrea echinata	X	
Acropora abrotanoides		X
Acropora aculeus		X
Acropora acuminata	X	
Acropora austera		X
Acropora cerealis	X	X
Acropora cytherea	X	X
Acropora delicatula	X	
Acropora digitifera	X	
Acropora echinata	X	
Acropora florida	X	X
Acropora formosa	X	
Acropora gemmifera	X	
Acropora hebes	X	
Acropora humilis	X	
Acropora hyacinthus	X	X
Acropora irregularis	X	X
Acropora macrostoma		X
Acropora microclados		X
Acropora monticulosa	X	
Acropora nasuta	X	X
Acropora polystoma		X
Acropora robusta		X
Acropora squarrosa	X	
Acropora syringodes	X	
Acropora tenuis		X
Acropora valida	X	
Acropora variabilis	X	
Acropora vaughani	X	
Alveopora allingi	X	
Alveopora verrilliana	X	
Barabattoia amicorum	X	
Coscinaraea columna	X	
Cyphastrea microphthalma	X	X
Cyphastrea serailea	X	X
Danafungia repanda	X	
Diploastrea heliopora	X	X

Distichopora violacea	X	
Echinophyllia aspera	X	
Echinopora gemmacaea		X
Echinopora lamellosa	X	X
Euphyllia cristata	X	
Favia favus	X	
Favia laxa	X	
Favia matthaii	X	X
Favia pallida	X	
Favia rotundata	X	
Favia stelligera	X	X
Favites abdita	X	X
Favites complanata		X
Favites flexuosa	X	
Favites halicora	X	X
Favites pentagonia	X	X
Favites russelli	X	X
Fungia fungites	X	X
Fungia repanda		X
Fungia scutaria		X
Galaxea astreata		X
Galaxea fasicularis	X	X
Gardineroseris planulata	X	
Goniastrea pectinata	X	X
Goniastrea retiformis	X	X
Goniopora columna	X	X
Goniopora djiboutiensis	X	
Goniopora fruticosa		X
Goniopora lobata	X	
Goniopora minor		X
Goniopora somaliensis	X	
Halomitra pileus	X	
Heliopora coerulea	X	X
Hydnophora exesa	X	
Hydnophora microconos	X	X
Hydnophora rigida	X	X
Isopora cuneata	X	
Isopora palifera	X	
Leptastrea bottae	X	
Leptastrea purpurea	X	X

Leptastrea transversa	X	
Leptoria phrygia	X	X
Leptoseris explanata	X	
Leptoseris incrustans		X
Leptoseris mycetoseroides	X	
Leptoseris scabra	X	
Lobophyllia corymbosa	X	
Lobophyllia hemprichii	X	X
Merulina ampliata	X	
Millepora dichotoma	X	
Millepora exaesa	X	
Millepora platyphylla	X	
Millepora tuberosa		X
Montastrea curta	X	X
Montipora caliculata	X	X
Montipora digitata	X	
Montipora efflorescens		X
Montipora ehrenbergii	X	
Montipora floweri	X	X
Montipora foliosa	X	
Montipora foveolata	X	
Montipora granulosa	X	
Montipora grisea		X
Montipora hispida	X	
Montipora hoffmeisteri	X	X
Montipora informis		X
Montipora lobulata		X
Montipora marshallensis	X	
Montipora monasteriata	X	X
Montipora patula		X
Montipora tuberculosa	X	X
Montipora turgescens		X
Montipora verrilli	X	
Montipora verrucosa	X	X
Mycedium elephanotus	X	
Oulophyllia crispa	X	
Oxypora glabra		X
Oxypora lacera	X	X
Pachyseris rugosa	X	
Pachyseris speciosa	X	

Pavona clavus	X	
Pavona divaricata	X	
Pavona duerdeni		X
Pavona explanulata	X	
Pavona varians	X	X
Physogyra lichtensteinii	X	X
Platygyra daedalea	X	X
Platygyra lamellina	X	
Platygyra pini	X	X
Plerogyra sinuosa	X	
Plesiastrea versipora	X	
Pleuractis paumotensis	X	
Pleuractis scutaria	X	
Pocillopora ankeli		X
Pocillopora brevicornis	X	
Pocillopora damicornis	X	
Pocillopora elegans		X
Pocillopora eydouxi	X	
Pocillopora meandrina	X	X
Pocillopora verrucosa	X	X
Porites attenuata		X
Porites australiensis	X	X
Porites cylindrica	X	X
Porites lichen	X	X
Porites lobata	X	X
Porites lutea	X	X
Porites murrayensis	X	
Porites rus	X	X
Porites solida	X	X
Porties nigrescens	X	
Porites vaughani		X
Psammacora contigua	X	
Psammacora digitata	X	
Psammacora nierstraszi	X	X
Sandalolitha robusta	X	
Stylocoeniella armata	X	X
Stylocoeniella guntheri	X	X
Symphyllia recta	X	
Symphyllia valenciennesii	X	
Tubastrea coccinea	X	

Tubipora musica	X	
Turbinaria reniformis		X
Turbinaria stellulata	X	X
Verrillofungia concinna	X	

Appendix 3. Environmental factors used for data analyses in 2015

2015 Site #	GPS Y	GPS X	Wave Energy (J/m3)	Watershed Size (km^2)	Fishing Proxy	Pollution Proxy
1	592400	280990	2372.30	3.83	1.95	8.65
2	590883	281512	2388.20	3.78	1.64	0
3	590465	282179	2387.40	3.78	1.74	0
4	584519	281554	2382.20	4.92	1.61	17.48
5	582746	280232	2350.74	3.31	1.62	7.00
6	581642	277193	788.60	4.67	2.55	9.54
7	582358	276178	127.50	3.35	4.43	8.42
8	582503	273344	239.80	4.76	2.25	5.57
9	585054	267521	156.80	4.43	3.77	4.68
10	587580	267346	200.40	4.43	4.34	4.10
11	591012	272464	122	14.27	4.10	6.56
12	592076	272499	131.73	14.27	3.87	4.12
13	594250	276670	813	3.89	3.74	21.58

Appendix 4. Environmental factors used for data analysis in 1986

1986 Site #	Wave Energy (J/m3)	Watershed Size (km²)	Fishing Proxy	Pollution Proxy
1	2556.68	2.69	1.70	12.97
2	2383.54	3.83	2.17	8.19
3	2363.12	3.78	1.56	0
4	2361.68	2.34	0.96	8.18
5	2378.43	4.92	1.57	19.58
6	2396.34	4.67	1.69	9.54
7	609.68	4.67	3.17	10.23
8	91.24	13.76	4.48	17.31
9	54.92	9.51	1.72	6.73
10	231.28	6.30	2.47	6.03
11	153.81	4.43	3.91	3.49
12	176.03	4.43	4.59	3.85
13	141.07	6.37	4.17	0
14	128.48	6.37	4.78	4.37
15	126.66	8.47	3.75	2.58
16	129.43	14.28	4.37	3.44
17	968.35	2.97	3.45	0
18	1159.42	2.97	3.92	0
19	422.75	3.89	4.63	21.03
20	2322.79	2.69	2.98	9.41