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Oceanographic Controls on Coral Reef Habitats in Present and Future Climates

A dissertation submitted in partial satisfaction of the requirements for the degree
Doctor of Philosophy

in

Oceanography

by

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The Dissertation of Lauren Amelia Freeman is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Co-chair

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University of California, San Diego

2013

DEDICATION

To the wild and ever changing sea.

EPIGRAPH

How inappropriate to call this planet Earth when it is so clearly Ocean

Arthur C Clarke

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ABSTRACT OF THE DISSERTATION

Oceanographic Controls on Coral Reef Habitats in Present and Future Climates

by

Lauren Amelia Freeman

Doctor of Philosophy in Oceanography

University of California, San Diego, 2013

Arthur J Miller, Chair
Richard D Norris, Co-Chair

Coral reef ecosystems are under threat from a myriad of stressors, ranging from direct human stress (e.g. fishing) to global climate change (e.g. warming sea surface temperatures). Climate change will shift the fundamental habitats in which coral reefs reside. To better understand coral reef survival likelihood in future climate scenarios, these habitats are assessed in both present and future conditions. Classification of Pacific coral reefs by physico-chemical environment shows that there is in fact great complexity in coral reef habitat. Sea surface temperatures, aragonite saturation state, storm frequency, nutrient levels, and current speeds are all critical factors in determining physico-chemical habitat. A case study in the Hawaiian Islands indicates that these habitats are in part reflected in coral reef ecology, although it is difficult to tease apart the effects of ocean environment considering the myriad of human stressors to coral reefs. Future coral reef habitats are assessed for two climate change scenarios. Non-uniform habitat constriction is found worldwide. Reefs in the Caribbean Sea are particularly vulnerable to climate change. Reefs in the Indian Ocean are currently experiencing conditions quite similar to projected conditions worldwide, and are ideal candidate regions to select corals for re-wilding and translocation efforts. Finally, case study of regional oceanography in French Polynesia provides further insights into downscaling global projections to individual islands.

CHAPTER 1

Introductory Material

1.1 Coral Reefs

Coral reef ecosystems are amongst the most biodiverse on earth, described as the “rainforests of the sea” [e.g. Knowlton & Jackson 2008]. They provide many ecosystem services, including coastal protection, recreation and tourism, new substances used by the pharmaceutical industry, and natural beauty [Costanza et al. 1997; Moberg & Folke 1999]. Furthermore coral reef fisheries are responsible for 10% of the seafood consumed by humans worldwide [Smith 1978]. Tens of millions of people depend on coral reefs for protein and livelihood in coastal nations [Salvat 1992]. Reefs are mainly built by corals of the order Scleractinia, in symbiosis with photosynthetic dinoflagellates. The coral-algae system is extremely efficient, with over 80% of its energy coming from the sun fueling photosynthesis by the symbiotic algae. The coral animals capturing planktonic prey in the water column make up the remainder. The coral animal secretes a calcium carbonate skeleton, which over time builds up massive structures that we know as coral reefs. These reefs house the tropical ecosystems that humans know and love [Spalding et al. 2001]. Biodiversity estimates range from 0.5-9 million species worldwide [Reaka-Kudla 1997; Bouchet 2006], including over a 35% rare or endemic species [Plaisance et al 2011].

The ability for coral reefs to persist in the next century is under threat from direct human stress. These stressors include artisanal and commercial fishing pressure, nutrient runoff, and pollution [Pastorok and Bilyard 1985; Hughes 1994; Sebens 1994; Jackson et al. 2001; Pandolfi et al. 2003; Pandolfi et al. 2005]. Coral reefs are further under threat from climate change. Two consequences of rising atmospheric CO_2 have been well documented in terms of their adverse effects on coral reefs. Rising sea surface temperatures result in a breakdown of the coral-algae symbiosis where the dinoflagellates are ejected from the coral (coral bleaching), often resulting in disease or mortality to the coral [Glynn 1996, Hoegh-Guldberg 1999, 2011]. In addition, increased carbon dioxide in seawater drives a decrease in pH (ocean acidification) and an associated decrease in aragonite saturation state, which makes it harder for corals to calcify and build up skeletons [Langdon et al 2000, Hoegh-Guldberg et al 2007, Hoegh-Guldberg 2011]. At some point if this trend continues, this will actually cause existing reefs to erode faster than coral and other calcifiers can deposit more structure.

Coral reef organisms have some capacity to adapt to climate change. For example, corals have been shown to shifts towards more heat-tolerant zooxanthellae in recovery following bleaching episodes [Baker et al., 2004] as well as in response to gradually increasing heat stress [Berkelmans & Van Oppen, 2006]. I suggest that the resilience of reef communities to long-term global change will be shaped by their preconditioning to historical environmental conditions: long-term temperature changes, short-term temperature anomalies, varying nutrient levels, and other fluctuating physical oceanographic variables.

1.2 Climate Change

Increased anthropogenic carbon dioxide (CO_2) emissions will have a myriad of effects in the surface ocean. Critically for coral reef ecosystems, sea surface temperatures (SSTs) will rise worldwide. The increase in maximum tropical SSTs will be between 0.4-4.8°C between the years 2010-2100 for the business-as-usual scenario in the National Center for Atmospheric Research (NCAR) Community Earth System Model (CESM1), and this change is distributed non-uniformly around the world (Figure 1.1).

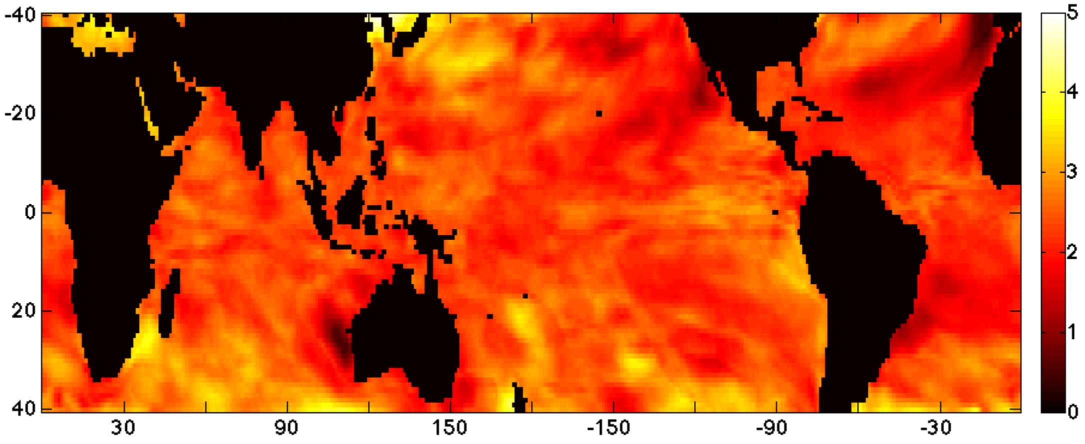


Figure 1.1: Difference in average maximum sea surface temperatures from time period 2006-2010 to 2096-2100, calculated from five-year averages from the NCAR CESM1 RCP8.5 scenario. Scale indicates magnitude of change from low (dark red) to high (white) in °C. Landmasses are black.

In addition to changes in mean temperature, temperature variability and anomalies will also shift. Regions that previously experienced static conditions year-round may suddenly be subject to large swings in temperature. Of particular importance for coral reefs are high temperature anomalies. These extremes are often quantified as degree heating weeks (DHW), which are calculated as a rolling summation of temperatures that exceed the climatological mean by more than one degree Celsius. Temperature anomalies such as DHWs are correlated with coral bleaching [Mumby et al 2004].

Increased atmospheric CO_2 will also result in increased dissolved CO_2 in the ocean through mixing at the air-sea interface. Approximately half of the anthropogenic CO_2 released in the previous two centuries is dissolved and stored in the oceans [Sabine et al 2004]. The dissolved CO_2 reacts with seawater, producing carbonic acid molecules that further react with water to produce bicarbonate and hydrogen ions. The addition of hydrogen ions (H^+) ultimately reduces ocean pH. This phenomenon is commonly known as 'ocean acidification.' Coral reefs deposit calcium carbonate skeletons as the mineral aragonite. We are thus concerned here with the saturation state of aragonite in seawater (Ω_{arag}), which decreases with decreasing pH [Kleypas et al 1999a, Doney et al 2009]. CO_2 dissolves more readily in cooler water, meaning that decreasing Ω_{arag} is a more serious concern at higher latitudes, limiting coral reef habitation poleward [Kleypas et al 1999b, Guinotte et al 2003].

Rising temperature tends to be the most commonly studied aspect of how climate change impacts marine ecosystems, and ocean acidification is increasingly recognized for its potential to cause a range of impacts on marine organisms and ecosystems [Harley et al 2006]. However, many other aspects of basic oceanic habitats will also shift. Ocean current patterns will change, resulting in shifts of upwelling zones and transport pathways. Near islands and landmasses, rainfall will alter terrestrial runoff frequency and patterns affecting nutrient levels in the near-shore. Atmospheric cyclones are projected to increase in intensity and possibly frequency [Emanuel 2005; Knutson et al. 2010; Emanuel 2013], further affecting the shallow seas.

1.3 Motivation

Because coral reefs hold intrinsic economical and aesthetic value [Costanza et al. 1997; Moberg & Folke 1999], there are often efforts to protect them via fishing controls, marine protected areas, underwater parks or reserves, and other management strategies. Notable examples include Australia's Great Barrier Reef Marine Park and the Northwest Hawaiian Islands and Remote Pacific Islands National Monument [e.g. Fernandes et al. 2005]. These management strategies are always in effort to minimize one or more of the many stressors to coral reefs.

Stressors to coral reef ecosystems can be classified in two ways, as shown in Table 1.1. The first classification is based on whether the stressor can be changed by local management efforts. The second classification is based on whether or not ocean and climate models can accurately project future states of a particular stressor. Almost all abiotic (physical and chemical) variables can in fact be predicted with reasonable accuracy, including sea surface temperature and aragonite saturation state. However, none of the direct anthropogenic stressors such as fishing or pollution can be modeled to the same level of accuracy 50, 100, or 500 years in the future.

Table 1.1: Classification of stressors to coral reefs by both predictability and ability to manage with local controls.

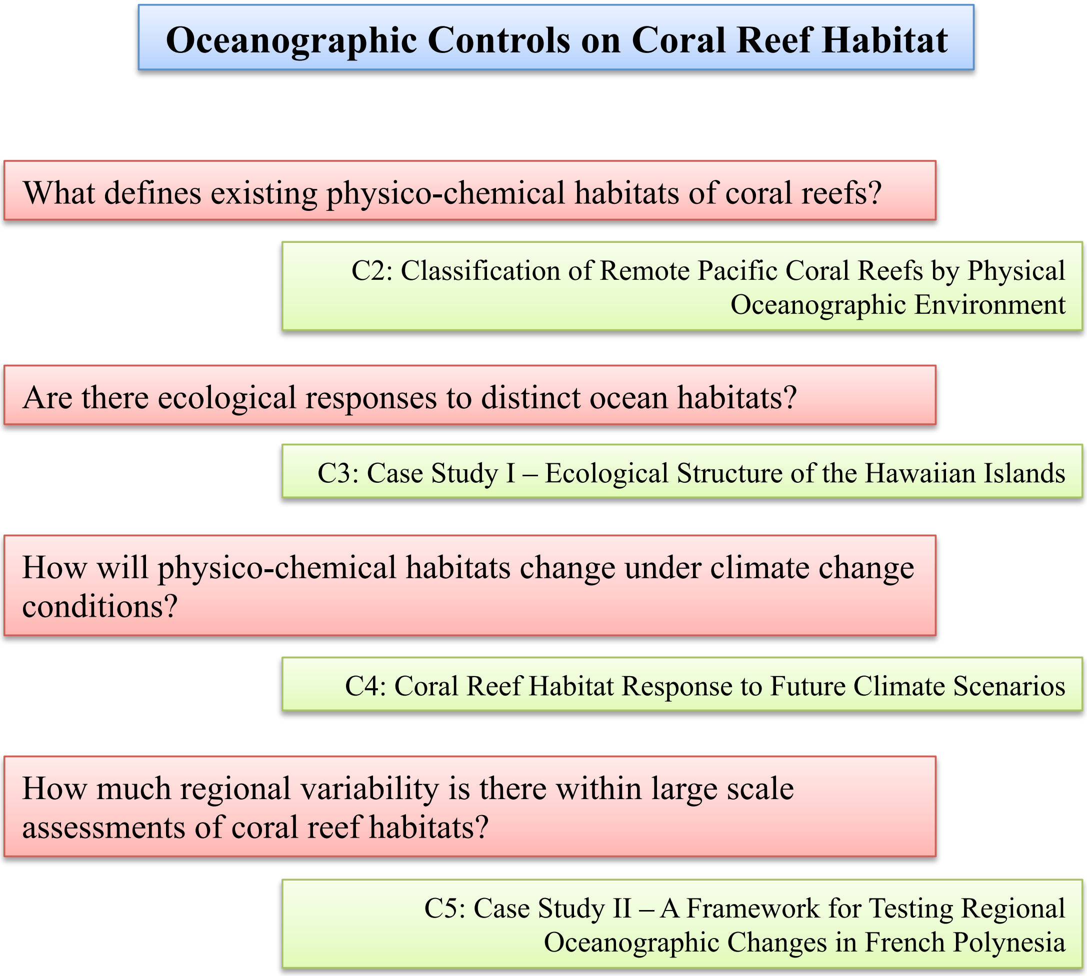
		Can be predicted by ocean/climate models	
		Yes	**No**
Can be controlled or changed by local management efforts	**Yes**		• Artisanal/local fishing pressure • Nutrient runoff from agriculture • Pollution • Tourism
	No	• Sea surface temperature • Sea surface pH • Sea surface temperature variability	• Commercial fishing pressure

This gap in knowledge leads to a series of scientific questions. How do the physical and chemical variables affect coral reef ecosystem state and existence? How can ocean environment alone, as defined by these variables, predict reef characteristics? How will the physical and chemical parameters change in future climate scenarios? What are the likely impacts on coral reef existence of these physical and chemical changes? Are particular ocean regions likely to be less affected by climate change? What regions of the ocean are most similar to the future state of oceans worldwide?

Answering the last two questions will naturally inform conservation strategies. Regions that are less likely to be affected by climate change are excellent locations to focus management efforts now, accounting for all of the stressors in Table 1.1 except for commercial fishing. Such efforts could include implementation of marine protected areas and underwater parks, fishing regulations, and limiting access. Another more controversial conservation strategy is to actively transplant corals from one reef to another. Such species translocations would be used to either a) ensure the survival of a particular species that is in danger of being squeezed from its habitat by moving it to locations where it cannot colonize naturally [Richardson et al. 2009; Schwartz et al. 2012; Hellmann 2013]; or b) to purposefully introduce a species as a functional replacement for a species that is no longer viable [Kreyling 2011; Schwartz et al. 2012]. In either case, selecting the hardiest genetic strains of a species from regions that are currently experiencing conditions most like future climate projections, gives translocation strategies the best chance of success. Other suggestions for creating resilient marine protected areas include large spatial coverage, protecting several examples of each habitat type, and selecting regions in a variety of ocean habitats to minimize risk from climate change stress [McLeod et al. 2008].

1.4 Summary of Key Points

The overarching goal of this dissertation is to understand the fundamental oceanographic controls on coral reef habitats, and how these habitats shift in future climate scenarios. The scientific questions addressed in subsequent chapters are additionally driven by policy and management considerations. I ultimately find results that may guide the two conservation strategies discussed previously.



Oceanographic Controls on Coral Reef Habitat

What defines existing physico-chemical habitats of coral reefs?

C2: Classification of Remote Pacific Coral Reefs by Physical Oceanographic Environment

Are there ecological responses to distinct ocean habitats?

C3: Case Study I – Ecological Structure of the Hawaiian Islands

How will physico-chemical habitats change under climate change conditions?

C4: Coral Reef Habitat Response to Future Climate Scenarios

How much regional variability is there within large scale assessments of coral reef habitats?

C5: Case Study II – A Framework for Testing Regional Oceanographic Changes in French Polynesia

Figure 1.2: Schematic of overarching scientific questions addressed in this dissertation (red) and scientific chapters (green).

Chapter 2 specifically counters the previous assumption that coral reefs occupy a similar oceanographic habitat worldwide, and tests the hypothesis that there may be considerable variation in physico-chemical environments that coral reefs occupy in the Pacific Ocean. I find that there are seven unique habitats in the remote tropical Pacific occupied by reefs, each characterized by different ranges of temperature, degree heating weeks (temperature extremes), aragonite saturation state, dissolved oxygen, nutrient levels, storm frequency and intensity, and salinity. A comparison of percent coral cover between these habitats shows significant differences. The habitats tend to be clustered geographically, but are not singularly a function of latitude. This partially answers the first scientific question: *How do physical and chemical variables affect coral reef existence and state?*

Chapter 3 investigates the effect of oceanic habitat on coral reef ecology with a case study in the Hawaiian Islands. Forty-two ecological metrics were collected during a field expedition in 2012 to four of the Northwest Hawaiian Islands and four of the main Hawaiian Islands. The eight islands occupy two different oceanic habitats, and several differences in ecological metrics were found between the habitats. The effect of position around an island, exposure, and marine reserve status on these ecological metrics was also tested. I found that the biggest difference in ecology is between the Northwest Islands and the main islands, suggesting that oceanic habitat or regime is a fundamental control of the ecology of coral reef ecosystems as suggested by the oceanographic classification of reef settings described in Chapter 2. These results further underscores the importance of carefully planning placement of marine reserves and protected areas, considering oceanic environment. Chapter 3 answers the scientific questions: *How do physical and chemical variables affect coral reef ecosystem state and existence? How can ocean environment alone, as defined by these variables, predict reef characteristics?*

Chapter 4 tests the persistence of coral reef habitats in future climate scenarios. We considered two such scenarios, RCP4.5 or RCP8.5. RCP4.5 represents moderate to significant action taken to control greenhouse gas emissions and/or to sequester carbon. RCP8.5 represents business as usual, or the worst-case scenario. A bioclimatic envelope model (Maxent, Phillips et al. 2006) was used to calculate habitat suitability of the tropical sea for coral reefs in present and future climates. Suitable habitat was found to decline worldwide in both climate scenarios, and more in RCP8.5 (82%) than in RCP4.5 (43%). Particular areas that experienced fewer declines included equatorial regions of the Indian Ocean, much of the Coral Triangle region in the western Pacific, French Polynesia, and the northeast Brazilian shelf east of the Amazon River. These regions are thus excellent areas to focus conservation efforts now. Furthermore, we found that reefs in the Indian Ocean were actually experiencing ocean habitats in the present climate that are extremely similar to projected habitats in future climate scenarios in the Indian Ocean as well as the tropical Atlantic and Pacific. Thus we suggest that reefs in the Indian Ocean, are prime candidates from which to select particular corals for re-wilding and transplantation efforts. The final four questions are addressed in Chapter 4: *How will physical and chemical parameters change in future climate scenarios? What are the likely impacts on coral reef existence of these physical and chemical changes? Are particular ocean regions likely to be less affected by climate change? What regions of the ocean are most similar to the future state of oceans worldwide?*

Chapter 5 considers a second case study in French Polynesia to better understand regional oceanography around islands. I use a regional ocean model (ROMS) to construct a framework to assess the oceanic environment of remote coral reefs at a finer scale than the results of Chapters 2 and 4 were able to resolve. This more detailed look at the abiotic factors from Table 1.1 creates a framework to assess regional changes to these factors under future climate scenarios. We found regular eddy shedding by islands to the west, which periodically created a potential pathway from upstream islands to downstream islands. This pathway could be a means by which coral larvae migrate from one island to another after mass spawning events. We also found persistent upwelling and a cool 'wake' to the south and west of the islands. These cooler waters may provide a local refuge to coral reefs from heat stress. A 20-year model run gives us insight to the seasonal cycle of these observations. Future work will involve using surface forcing from climate model forecasts of the next century in this regional modeling framework.

1.5 Glossary of Concepts and Terms

Because of the cross-disciplinary nature of this dissertation, I include here a list of terms with their definitions to clarify for the various readers what these terms mean in the context of this research.

- **Coral Bleaching** describes a physiological response by the coral-algal system, where algae vacate a stressed coral in response to chemical cues. The coral is still alive, but without the algae living in its transparent tissue. This causes a coral colony to appear white not only from the loss of algae, which provide color to the tissue, but also because the transparency of the tissue reveals the white underlying calcium carbonate skeleton, hence the name 'bleaching.'

Coral bleaching often results in increased coral disease, reduced calcification, and in worse cases, mortality of the corals.

- **Ocean Acidification** refers to a reduction in pH of the ocean over an extended period, typically decades or longer, caused primarily by the uptake of carbon dioxide from the atmosphere. Ocean acidification can also be caused by other chemical additions or subtractions from the oceans that are natural (e.g., increased volcanic activity, methane hydrate releases, long-term changes in net respiration) or human-induced (e.g., release of nitrogen and sulphur compounds into the atmosphere). Anthropogenic ocean acidification refers to the component of pH reduction that is caused by human activity [IPCC 2011].
- **Climate Change** in this dissertation, refers specifically to anthropogenic climate change, or shifts in the global air and sea climate caused by human activity. Since the industrial revolution in the late 1800s, human activities that burn fossil fuels have increased dramatically, resulting in increased atmospheric CO_2. Atmospheric CO_2 concentrations recently surpassed 400ppm (www.keelingcurve.ucsd.edu). This concentration is not unprecedented in geologic time, however the rate of change is.
- **CESM1** is the Community Earth System Model Version 1, the atmosphere-ocean global climate model developed and run by the National Center for Atmospheric Research (NCAR). This is a fully coupled model, meaning that

both the atmosphere and the ocean are modeled realistically and dynamics are able to feed off of one another.

- **RCP Scenarios** are the emissions scenarios used by the most recent set of climate model runs. Representative Carbon Pathways (RCPs) are calculated from the difference in forcing at the top of the atmosphere in watts/meter^2 at the end of the 21st century compared to preindustrial levels. So for example, RCP4.5 has a 4.5 W/m^2 increase in forcing by 2100.
- **Habitat,** in this dissertation, refers specifically to the chemical and physical variables of particular parts of the ocean that have a bearing on coral reef existence and state. This is also referred to as **physico-chemical environment.**
- **Bioclimate Models,** also known as maximum entropy models and ecological niche models, these programs consider environmental variables (such as sea surface temperature) at sites where a species or community of species is known to exist (presence data), and from this information calculates habitat suitability over a larger area seeking the solution with maximum entropy, or closest to a random distribution. Maxent is the bioclimate model used in this dissertation.
- **Ecological Metrics** describe all biotic data considered in this dissertation. This includes, but is not limited to, percent coral cover, number of predatory fish, number of invertebrates, and reef rugosity.

- **Rugosity** is a measure of structural complexity (of a coral reef). It is the true distance a particle would have to travel if following the precise bathymetry to travel ten meters in a straight line (as the fish swims, if you will).

CHAPTER 2

Classification of Remote Pacific Coral Reefs by Physical Oceanographic Environment

2.1 Abstract

The oceanographic environment is a key element in structuring coral reef ecosystems by setting the range of physical and chemical conditions in which coral reef-builders live. A cluster analysis of physical and chemical oceanographic data is used to classify coral habitats in the remote tropical and subtropical Pacific ocean based on average temperature, temperature seasonal cycle, nutrient levels, salinity, aragonite saturation state, storm frequency, intense hurricane hits, and dissolved oxygen as well as temperature anomalies in degree heating weeks. The resulting seven geographic habitats are stable to perturbations in types of data used in the cluster analysis. Based on recent coral reef survey data in the area, coral cover was related to the identified geographic regions. The habitats tend to be geographically clustered, and each is characterized by a unique combination of oceanographic conditions. Previous studies suggest coral reef habitats are associated with a uniform array of oceanographic conditions, while our results demonstrate that finer-scale variations in physical variables may control coral reef environments. The results better define the physical environment of remote coral reefs, forming a foundation for future work addressing physical habitat perturbation and anthropogenic impacts on reefs.

2.2 Introduction

A classical paradigm for coral reefs is that they grow in a fairly uniform oceanic environment - warm, oligotrophic, and low kinetic energy [*Stoddart*, 1969]. However, decades of research in both coral reef ecology and tropical oceanography have suggested that there is truly a large dynamic range of physical oceanographic conditions in which they can thrive [Ando and McPhaden, 1997; Glynn and Colgan, 1992; Glynn and Ault, 2000; Johannes et al., 1983; Rosen, 1988; Wyrtki, 1975; Zhang, 1996; 2005].

A cursory view of the physical and chemical oceanographic conditions around where reef-building corals grow indicates that there exists a broad range of ambient nutrient levels, sea-surface temperature (SST), annual variability, storm intensity and frequency, and other factors. For instance, hermatypic coral reefs are known from a broad array of temperatures (17-29°C), and nitrate concentrations (0-13 mmol/m^3). Anomalies in the physical environment can result in stress on the ecosystem. This is best documented with temperature. In fact, changes in the physical environment are included in ecological definitions of disturbance (i.e. disturbance can be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" [Pickett and White, 1985]). To assess such anomalies, one must first understand the average climatology for a region.

Temperature is a fundamental control on coral reef ecosystems. Temperature variability, in particular prolonged abnormal warm temperatures, result in coral bleaching [Glynn, 1996], which often leads to mortality and subsequent reduction in coral cover. Coral reef locations are strongly controlled by temperature, and reefs do not grow where mean SST drops below 17°C. There are likely large differences in ecosystem structure between reefs with low and high temperature variability, as with terrestrial biomes. For this reason, our analysis includes annual mean SST (which sets the upper latitudinal limits of coral reefs), annual seasonal cycle, and daily anomalies in the form of DHW. The mean and seasonal cycle information relates directly to the 'mean' ecosystem state, while DHW relates to stress events and disturbance.

Aragonite saturation state (Ω-arag) tends to be higher in warmer water and lower at higher latitudes. It is a key determinant of the upper reach of coral reef development. Corals produce aragonite skeletons and Ω-arag is directly related to rates of calcification. In current conditions, most reefs grow slowly (~1 cm per year), and decreases in Ω-arag from increased CO_2 emissions are a serious concern for future coral reef development [Hoegh-Guldberg, 2011; Hoegh-Guldberg et al., 2007].

Nutrients (phosphate, nitrate, silicate) and oxygen are limiting factors for photosynthesis (nutrients only) and respiration (both nutrients and oxygen)and the relative concentrations of these resources will partially dictate whether ecosystems are dominated by autotrophs or heterotrophs. We hypothesize that both nutrient levels and oxygen levels are fundamental in structuring the physical environment for coral reef ecosystems. Nutrients are of particular interest as corals are adapted to thrive in low nutrient environments [Muscatine and Porter, 1977], and may suffer a competitive disadvantage to faster growing algae in the case of increased local nutrient availability [Szmant, 2002].

Cyclones have been documented as intermittent, severe stress events on coral reefs. While storms are relatively rare, and catastrophic storms are extremely rare, the damage that they cause is long lasting. Major effects on coral reefs include debris from land, increased sedimentation from land that may smother corals, and physical breaking and repositioning of coral reef superstructure [Bythell et al., 1993; Bythell et al., 2000; Dollar and Tribble, 1993; Edmunds and Witman, 1991; Gardner et al., 2005; Harmelin-Vivien and Laboute, 1986; Woodley et al., 1981]. We theorize that storm frequency is related to reef morphology, where massive boulder corals likely dominate reefs with high incidence of storms and reefs with rare storms are likely dominated by faster growing but more delicate branching corals. In addition to morphology, storm events may be related to biodiversity and ecosystem function via the intermediate disturbance hypothesis [Connell, 1978; Rogers, 1993] where the highest diversity of reef corals would be expected in areas with intermediate levels of storm frequency and/or intensity. Furthermore, there is evidence that cyclone intensity and damage will increase with continued anthropogenic climate change [*Emanuel*, 2005].

The environmental context of coral reefs must be recognized in order to objectively compare and contrast geographically disparate sites. We attempt to address this issue here by objectively identifying coral reef habitats based on physical and chemical oceanographic data. We use a cluster analysis that includes SST, DHW, Ω-arag, cyclone, nutrient, oxygen, and storm metrics. We restrict our analysis to the

Pacific Ocean because of the remoteness of coral reefs in this basin. This analysis for current climate conditions can then serve as a baseline for estimating coral reef survival capabilities in studies of future climate scenarios.

In previous research, Kleypas et al. [1999b] attempted to identify the range of conditions in which hermatypic reefs can survive in order to identify "marginal reefs" which are near the edge of their reach and may be threatened by changing environmental conditions. They used a cluster analysis to identify such reefs, which they determined were best described by extremes of high temperature, low light availability and low Ω-arag. They also identified "no worries reefs" which were situated in less severe environmental conditions. In the Pacific Ocean, the "no-worries" reefs covered essentially the entire remote open ocean area, which is the subject of the current study.

Here we explore the oceanographic diversity of the Kleypas et al. [1999b] "no worries reefs" in the Pacific by considering variations within the broad window of environmental variables in which coral reefs grow. We expand the list of variables previously used by Kleypas et al., [1999b], and instead of identifying marginal reefs at risk of decline from a changing environment we seek to understand the current oceanographic state of reefs in the tropical Pacific, and the variability of oceanographic conditions between reefs.

The only variable omitted from our study that was included in the Kleypas study was light availability. Kleypas et al., [1999b] found that low light availability was indicative of marginal reef environments. In the Pacific, these marginal reefs were almost entirely coastal and likely related to terrestrial sedimentation influx. We have already excluded the reefs characterized by Kleypas et al [1999b] as light-limited from our study by removing coastal reefs. The only two exceptions occurred at high latitude in the South Pacific, but these reefs are strongly differentiated from other locations by low temperature, strong seasonal cycle, and low Ω-arag in the current study.

It is well known that coral reefs are declining due to many factors [Hoegh-Guldberg, 1999] including climate change and associated variability. These climate induced impacts have been documented extensively both in laboratory experiments and in the field [Hoegh-Guldberg, 2009]. It is also known that coral reefs have some ability to adapt to climate change. For example, corals adapt better to gradual environmental changes than extreme events, as seen in shifts towards more heat-tolerant zooxanthellae and recovery following bleaching episodes [Baker et al., 2008; Baker et al., 2004]. However, the resilience of reef communities may also be linked to synergistic effects of an individual reef's environment: long-term temperature changes, short-term temperature anomalies, varying nutrient levels, and other fluctuating physical oceanographic variables.

We suggest that the first-order structure of reef communities (e.g. abundance of reef building corals) is likely set by the physical environment—both the mean conditions of temperature, nutrients, and salinity as well as the range of environmental variability and propensity toward extreme conditions in different oceanic environments. We start with this assumption to conduct a quantitative classification of the physical environment around Pacific coral reefs and then examine coral cover data to test our assumption.

2.3 Materials and Methods

The physical and chemical variables of interest are outlined in Table 1.1 along with all open-ocean coral sites from ReefBase in the Pacific. A cluster analysis of the physical variables at the coral sites is then performed to identify similar reef environments. Coral cover is then independently compared to the habitats identified by the clusters.

Physical and chemical oceanographic data from the World Ocean Atlas (WOA) and National Oceanic and Atmospheric Administration (NOAA) were obtained on a uniform global grid of 1° latitude by 1° longitude (180x360, 110 km x 110 km) resolution. This grid was selected to match the finest resolution climatology product available from WOA. Sea surface data including temperature, phosphate, dissolved oxygen, and salinity were incorporated [Antonov et al., 2006; Garcia et al., 2006a; b; Locarnini et al., 2006]. The seasonal range of temperature was calculated as absolute value of summer-winter difference from WOA seasonal climatology. Phosphate is used as a proxy for all nutrients, as it is the most completely measured nutrient in the WOA and is correlated with nitrate [Cooper, 1937]. We considered nutrients from WOA to be more representative of upwelling patterns than a dataset obtained by calculating regional upwelling from Ekman stress.

Table 2.1: Description of physical and chemical oceanographic variables used in the cluster analysis

Variable	Data Source	Notes	Type
Average sea surface temperature	World Ocean Atlas [Locarnini et al., 2006]	Cumulative average from early 1900s	Cruise data
Average sea surface phosphorus	World Ocean Atlas [Garcia et al., 2006a]	Cumulative average from early 1900s	Cruise data
Average sea surface dissolved oxygen	World Ocean Atlas [Garcia et al., 2006b]	Cumulative average from early 1900s	Cruise data
Average sea surface salinity	World Ocean Atlas [Antonov et al., 2006]	Cumulative average from early 1900s	Cruise data
Average annual temperature variability	World Ocean Atlas [Locarnini et al., 2006]	Difference between warmest average month and coldest average month	Cruise data
Temperature anomaly- Degree Heating Weeks	NOAA Coral Reef Program [Eakin et al, 2009]	Average DHWs from 1985-2010	Satellite data
Average aragonite saturation state	GLODAP [Key et al., 2004], WOA [Antonov et al., 2006; Locarnini et al., 2006]	Calculated aragonite saturation state from 1985-2010	Satellite + cruise data
Annual storm frequency	NOAA Historic Hurricane Tracks	Includes all cyclonic storms within 110 km diameter cell	Satellite data + observations
Intense hurricane hits	NOAA Historic Hurricane Tracks	Category 4 and 5 hurricanes within 110 km diameter cell	Satellite data + observations

We considered three temperature metrics- mean temperature, annual temperature variability, and degree heating weeks, since temperature and temperature variability have been repeatedly associated with coral reef environments and stress events. Degree heating weeks (DHW) time series data for each point with coral reefs were collected from 1985-2010 [Eakin et al, 2009] and averaged. DHW are the cumulative sum of temperature anomalies greater than one degree Celsius above the warmest temperature in the mean monthly climatology. NOAA DHW were used, which are calculated twice weekly from Advanced Very High Resolution Radiometers on board NOAA's Polar-Orbiting Operational Environmental Satellites. Then grid points were aligned with the WOA data, corresponding to an approximate grid point resolution of 110 km x 110 km.

Aragonite saturation state (Ω-arag) was calculated from Global Data Analysis Project (GLODAP) dissolved inorganic carbon and alkalinity [Key et al., 2004], and WOA temperature and salinity [Antonov et al., 2006; Locarnini et al., 2006] using CO2SYS in MATLAB for the surface ocean at 1° latitude by 1° longitude resolution.

Cyclonic storm data were collected from the GIS-based NOAA historic hurricane track tool (http://www.csc.noaa.gov/hurricanes/). This stores information on cyclonic storms from 1982 to present, including tracks centered at the storm's eye, storm category, and storm name from a combination of satellite data and observations. Each location was queried with a 55km radius (to match 110km grid cells of 1 degree latitude by 1 degree longitude), for all months from January 1985-December 2010. The 55-km radius is also consistent with the 'buffer' from storm centers used in a previous meta-analysis [Gardner et al., 2005]. These dates were selected to align with the DHW data. For each location, the total number of cyclones that passed through the 110km diameter cell over 25 years was recorded to calculate annual storm frequency, as well as the number of hurricanes that reached category 4 or 5 on the Saffir-Simpson wind scale (sustained winds of 131-155 mph, and greater than 155 mph, respectively) while inside of that particular cell (intense hurricane hits). NOAA describes both of these categories with "catastrophic damage will occur." For reference, a category 3 hurricane has sustained winds of 111-130 mph and is described as "devastating damage will occur."

These data are representative of local oceanographic conditions in diverse coral reef regions of the Pacific. We recognize that smaller-scale physical oceanographic variations are important for coral reef habitats, which have very fine-scale structures, even within a single reef [Selig et al., 2010]. But our philosophy here is to focus on the regional scale structures that can serve to classify and categorize broad-brush groupings of coral habitats for which this resolution is appropriate.

Each data set was normalized to be unitless and have a mean of zero and standard deviation of one so that all variables were weighted equally in analyses [Lewis et al., 2008]. Coral reef locations were determined from ReefBase Geographic Information Systems maps (reefbase.org) and extrapolated to a 1° latitude by 1° longitude grid for a total of 305 cells. Barrier reefs or reefs near landmasses were not included in this analysis due to a paucity of oceanographic data available at these points as well as poorly resolved satellite land/sea correction resulting in less reliable satellite data. High latitude rocky reefs with solitary corals were also excluded. For each cell (1°x1°), each physical and chemical variable was extracted and stored.

A cluster analysis was performed on these coral reef cells using k-means clustering. K-means clustering is an iterative loop that determines clusters by cumulative root mean square distance between points, for a set number of clusters (k).

The maximum point to centroid (mean value of all variables for the cluster) distance was calculated for k=1-20 total clusters. The point-to-centroid distance is a measure of strength of the cluster analysis- a smaller point-to-centroid distance indicates more tightly confined clusters, or habitats. To minimize variance within habitats defined by our nine data metrics we used the k=7, which had minimum point-to-centroid distance, for final calculations. All calculations were performed in MATLAB Version 7.12.0, 2011 release.

To compare an independent measure of coral reef health with the cluster analysis habitat results, we chose percent coral cover as the comparative metric because of its wide availability and common use in previous studies to indicate the status of a given coral reef. Percent coral cover is also often associated with a number of biological variables such as macroalgal cover and herbivore abundance [Graham et al., 2008; Hoegh-Guldberg, 1999; Sandin et al., 2008]. These ecological data were collected from the World Atlas of Coral Reefs [Spalding et al., 2001], NOAA Coral Reef Ecosystem Division [Waddell and Clark, 2008], the Global Coral Reef Monitoring Network [Salvat, 2002; Wilkinson, 2008], and from recent observations obtained in field surveys. If multiple data points were available within a 1° latitude by 1° longitude cell, they were averaged. These particular data are island- or reef-wide averages obtained via multiple surveys and/or photo transects. To minimize discrepancies between collection methods, coral cover percentages were discretely binned into 10 categories. While this ecological dataset does not cover the entire set of coral reef locations used in the cluster analysis of physical habitats, it is extensive enough to provide a cursory insight into the relationship between coral habitats and percent coral cover. We recognize the potentially serious deficiencies in this dataset, including long-term trends due to non-physical oceanographic stressors (e.g., local human population changes, fishing, and pollution) and small scale variations in percent coral cover [Edmunds and Bruno, 1996]. This is not intended to act as a meta-analysis of percent coral cover data, but rather to serve as an initial ecological comparison with our analysis of physical oceanographic data.

2.4 Results

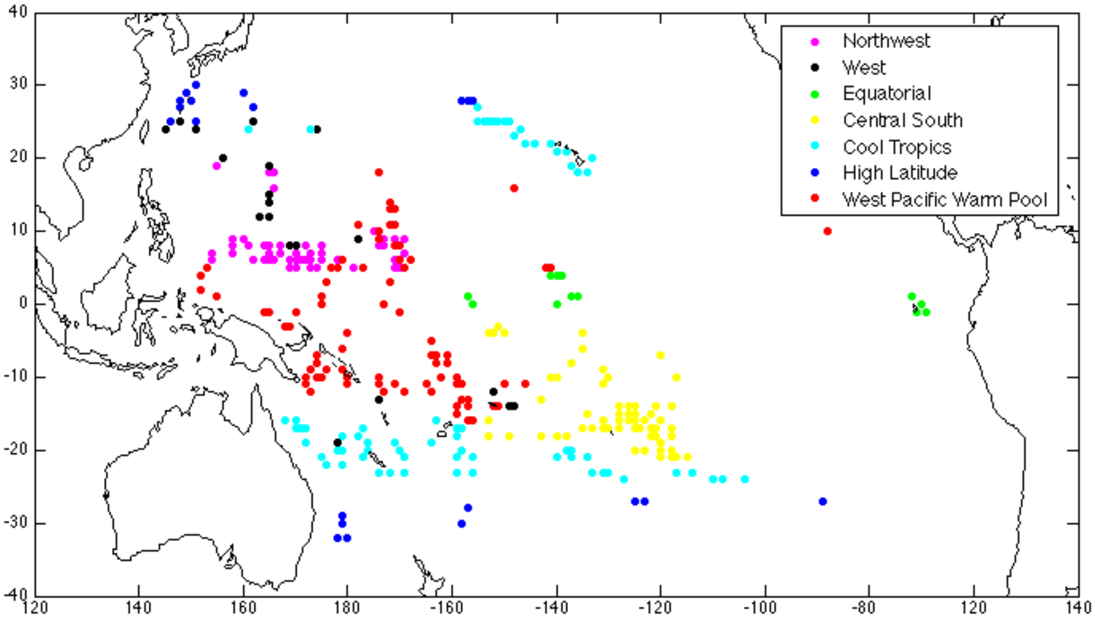


Figure 2.1: The seven coral habitats mapped spatially with each habitat as a different color.

The cluster analysis produced seven habitats based on nine variables (Figure 1). The average normalized values for each habitat are described in Table 1.2.

Table 2.2: (Opposite) Description of each habitat by centroid
Top: exact values in original units.
Bottom: desriptive values from cluster analysis result. Descriptive values were defined from normalized variables (zero mean, unit standard deviation) as ‘Very Low’ > -2, ‘Low’ = -2 to -0.5, ‘Average’= -0.5 to 0.5, ‘High’ 0.5 to 2, ‘Very High’ > 2. These give an indication of conditions in each cluster relative to all of the coral reef locations used in the analysis

Habitat	Annual Storm Frequency	Intense Hurricane Hits	Salinity	Phosphate	Seasonal Temp Range (C)	Oxygen	Ω-arag	DHW (C)	Mean Temp (C)
Northwest Pacific	0.62	0.00	34.23	0.13	0.91	4.54	3.95	0.19	28.90
West Pacific	0.61	1.11	34.67	0.12	2.84	4.60	3.91	0.31	27.74
Equatorial Pacific	0.00	0.00	34.86	0.55	1.84	4.63	3.59	1.62	26.31
Central South Pacific	0.04	0.00	35.84	0.29	1.78	4.63	4.15	0.17	27.63
Cool Tropics	0.14	0.00	35.29	0.14	3.51	4.76	3.85	0.27	25.50
High Latitude Reefs	0.28	0.00	35.14	0.12	5.92	4.93	3.60	0.46	23.37
West Pacific Warm Pool	0.13	0.00	34.60	0.20	1.10	4.55	3.87	0.22	28.70
Northwest Pacific	High	Average	Low	Low	Low	Low	Average	Average	High
West Pacific	High	Very High	Low	Low	Average	Average	Average	Average	Average
Equatorial Pacific	Low	Average	Average	Very High	Average	Average	Low	Very High	Low
Central South Pacific	Low	Average	High	High	Average	Average	High	Average	Average
Cool Tropics	Average	Average	Average	Average	High	High	Average	Average	Low
High Latitude Reefs	Average	Average	Average	Low	Very High	Very High	Low	High	Very Low
West Pacific Warm Pool	Average	Average	Low	Average	Low	Low	Average	Average	Average

The clusters were not uniform in size. The numbers of locations per cluster and number of locations with coral cover data per cluster are shown in Figure 2. Each habitat was characterized by a different combination of the nine oceanographic variables, as described here. All of the locations considered except two were classed as “no-worries” by [Kleypas et al., 1999b]. By considering several additional environmental variables, we have been able to show distinct geographic groupings of coral reef locations based on their physical environment. While latitude gives a rough approximation of oceanographic conditions, our results show that there is also a large degree of zonal variation.

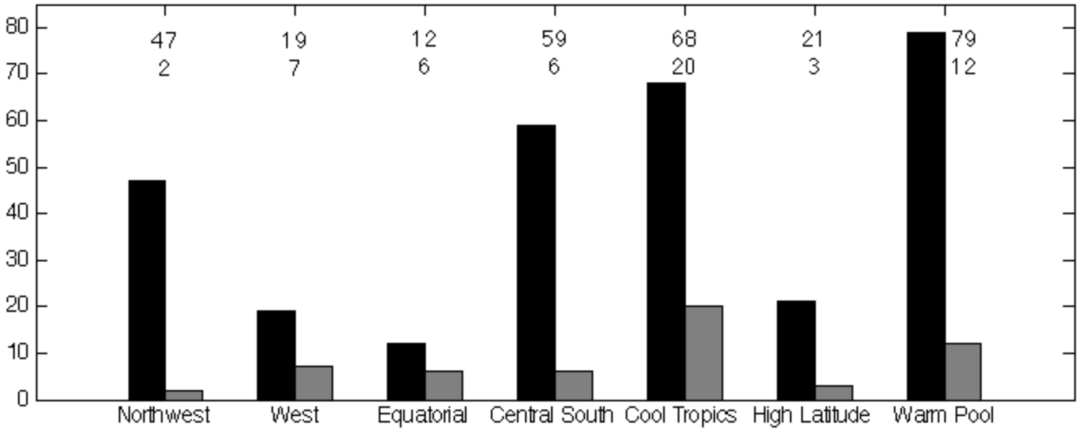


Figure 2.2: Number of points that contain coral reefs within each habitat (black bars) and number of points that contain percent coral cover data (gray bars). Labels are number number of points per habitat (top) and number of points with percent coral cover data per habitat (bottom).

Hurricane distribution was nonrandom with respect to both latitude and longitude. Annual storm frequency was 2-3 times greater in the northern hemisphere than the southern, and showed a linear decline from west to east (Figure 3). The difference between hemispheres is also reflected in a previous study of hurricane intensity [Emanuel, 2005], and increases from east to west is expected from SST patterns. One point in the eastern Pacific also experienced high storm frequency as a result of cyclones that were formed in the Caribbean traveling across Central America. No hurricanes occurred within 3° of the equator because of weak Coriolis force at low latitudes.

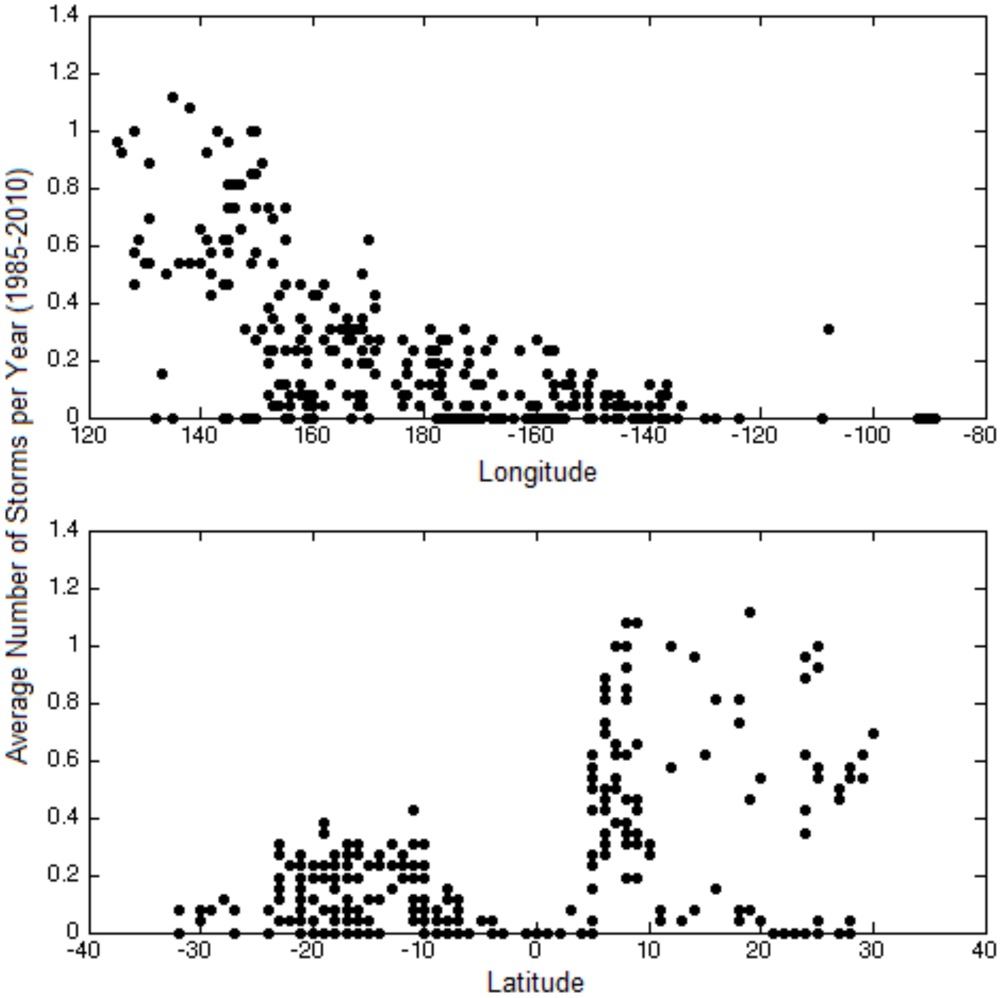


Figure 2.3: Distribution of cyclonic storms by longitude (top) and latitude (bottom). Average annual storm frequency was calculated for each data point from 1985-2010.

2.4.1 Northwest Pacific

The Northwest Pacific habitat is completely located between 5-20°N and 130-180°E (Figure 1) and includes most of the Federated States of Micronesia, notably Palau. It is characterized by the highest annual storm frequency and mean temperature of all habitats, and a low seasonal cycle and nutrients. The storms and mean temperature both differentiate this habitat from the West Pacific Warm Pool, which experiences slightly lower values of each. The mean temperature in the Northwest Pacific is 28.9°C and the seasonal cycle is less than a degree.

2.4.2 West Pacific

The West Pacific habitat is the most scattered geographically, from 120°E to 160°W and from 20°S to 25°N (Figure 1) and includes Guam and the Northern Marianas Islands. It is characterized by intense hurricane hits and high annual storm frequency. The only locations with intense hurricane hits in the past 25 years fall into this cluster. In addition to receiving intense storms, these locations have the second highest annual storm frequency (0.61 storms per year, versus 0.62 in the Northwest Pacific), so they receive both regular and severe disturbance.

2.4.3 Equatorial Pacific

The Equatorial Pacific habitat has the smallest by number of points (12), and includes the Galapagos Islands and other Central Pacific reefs, all within a few degrees of the equator. This habitat has the highest values of phosphorus by far and relatively low temperatures, which can be attributed to regular upwelling along the equator and eastern boundary. These reefs have experienced no hurricanes/cyclones in the past 25 years. Annual temperature variability is also average, although interannual temperature variability would likely be high due to El Nino Southern Oscillation cycles. [Wyrtki, 1975]. This habitat has the lowest values of Ω-arag, as well as the highest value of DHW, which may be a result of a weak seasonal cycle overlaid by strong interannual variability. El Nino (or warm) years would result in much higher DHW values in this region.

2.4.4 Central South Pacific

The Central South Pacific is located exclusively in the Southern Hemisphere, between 130-180°Wand includes French Polynesia and the Society Islands. It is characterized by high salinity, nutrients, and Ω-arag; low storm frequency; and otherwise average results. It is one of the larger habitats with 59 locations, and is tightly clustered geographically.

2.4.5 Cool Tropics

The Cool Tropics habitat has a strong seasonal cycle and high nutrient levels, low temperatures, and otherwise average results. This habitat includes reefs in the Cook Islands and New Caledonia in the Southern Hemisphere and the main Hawaiian Islands in the Northern Hemisphere. It is differentiated from the Central South Pacific by lower Ω-arag, temperature, and nutrient values.

2.4.6 High Latitude Reefs

This habitat encompasses the highest latitude region of all seven habitats, including reefs in the central and western subtropical Pacific. As a result, it is associated with the lowest temperatures and a strongest seasonal cycle of all of the habitats. This habitat is further characterized by high oxygen and DHW values. The higher DHW values may be a result of lower temperatures in the baseline climatology used to calculated DHW. This habitat includes part of the northwest Hawaiian Islands, reefs near southern Japan, and remote reefs in the south Pacific such as Lord Howe Island and Easter Island.

2.4.7 West Pacific Warm Pool

The Warm Pool Tropics habitat is the largest in number of points (79), and is characterized by a low seasonal cycle. It has low dissolved oxygen and salinity, and a mid-range value of DHW. It occurs between 20°S and 20°N, with most of the points grouped to the west. This habitat includes reefs of Papau New Guinea, the Soloman Islands.

2.4.8 Percent Coral Cover Comparison

Geographic distribution of percent coral cover is shown in Figure 2.4. A comparison of average coral cover between habitats shows different values for each habitat, although the sample size is very small and standard deviation large (Figure 2.5). The Northwest, Central South, and West Pacific Warm Pool habitats have the highest average coral cover, and the High Latitude reefs have the lowest average coral cover.

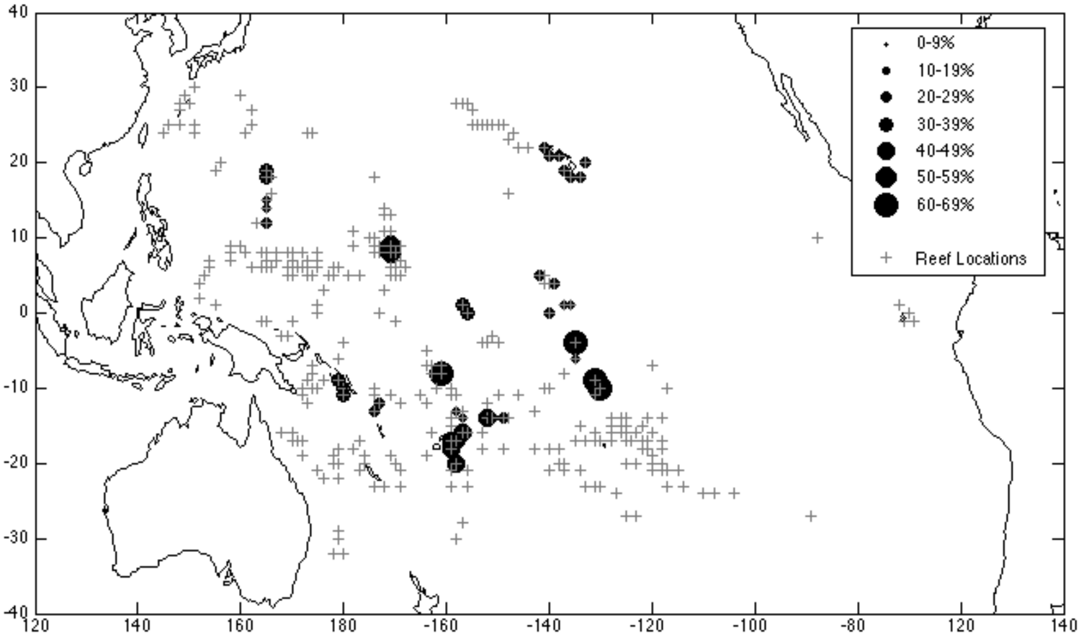


Figure 2.4: Spatial locations of percent coral cover data from low (small circles) to high (large circles). Each size marker represents a coral cover bin. Coral reef locations considered in this study are marked with gray crosses.

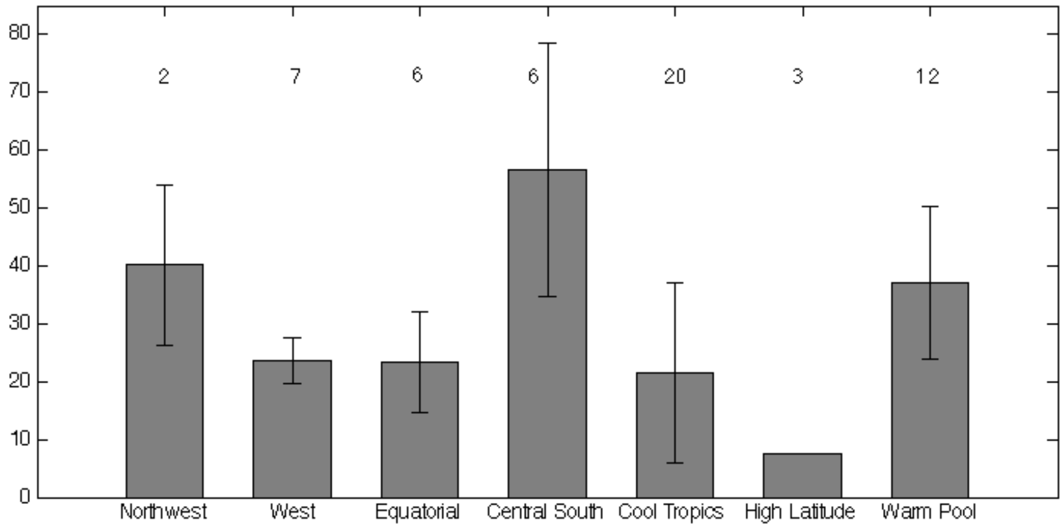


Figure 2.5: Average percent coral cover within each habitat (gray bars) with 2*standard deviation plotted as error bars.). Labels are number number of points with percent coral cover data per habitat.

2.4.9 Sensitivity Analysis

We tested the sensitivity of the cluster analysis in two ways. First, one of the physical variables or variable groups (i.e. all temperature metrics) was removed from the analysis and the cluster analysis was executed with six to nine variables. This process was repeated for each of the six primary variable groups. The clusters in each case (not shown) were very similar to the clusters for the nine variables analysed together. In comparing the individual results, the designation of locations to specific clusters was between 74% (storms excluded) and 93% (Ω-arag excluded) similar. Second, the cluster analyis was repeated using all nine variables at all open-ocean grid boxes in the tropical Pacific between 35N and 35S. Again, the structure of the top seven clusters was very similar to the results when including only the grid boxes where coral reefs are present indicating the robustness of our analysis.

Variance within habitat (or maximum deviation from habitat centroid) was not related to habitat stability when defining metrics are weighted or removed. The Northwest Pacific has the lowest variance within habitat, but also experienced a high rate of exchange with the West Pacific Warm Pool when variables were shuffled for stability analyses. The West Pacific and Equatorial Pacific are by far the most stable habitats, but they have average variance within habitat. The Cool Tropics and West Pacific Warm Pool have the highest variance within habitat.

2.5 Discussion

A cluster analysis of remote coral reef habitats in the Pacific Ocean based on physical and chemical oceanography reveals habitat differences expressed by latitudinal zonation as well as a coarse longitudinal zonation. Reef habitats tend to become differentiated from each other with distance north or south of the equator, as is the case for the distribution of ocean biomes. There is also east-west differentiation into three main groups: eastern, central, and western tropical Pacific habitats. This zonation suggests that the habitats are not just a function of latitudinal temperature gradients. Previous studies have found a strong latitudinal control on oceanic biomes or habitats [Lewis et al., 2008; Sarmiento et al., 2004]. Latitudinal control here seems to be strongly correlated to oceanographic variables that vary across the Pacific basin, in particular temperature variability on an annual and inter-annual timescale.

Our habitats also show strong similarities to known trends in biodiversity. First order approximations of biodiversity increase with decreasing latitude, and also increase towards the western tropical Pacific [Bellwood and Hughes, 2001; Gaston, 2000; Veron et al., 2009a]. These trends are particularly pronounced for coral reefs [Willig et al., 2003]. Although biodiversity was not included in our analyses, it is interesting to note that other studies have found patterns that appear to be related to our habitats, with the West Pacific Warm Pool and Northwest Pacific having the highest biodiversity and High Latitude Reefs having the lowest biodiversity.

The seven oceanographic habitats that were identified here were associated with various levels of coral cover. In particular, the higher latitude habitats Cool Tropics and High Latitude tend to show low levels of coral cover; and the Central South, Northwest, and West Pacific Warm Pool regions show high levels of coral cover. Tropical sites, in contrast, have some of the highest coral cover, although there is considerable variation within these habitats. The Northwest Pacific has the highest annual storm frequency and the second highest mean percent coral cover, but the West Pacific has much lower coral cover and all of the intense hurricane hits. DHWs are highest in the Equatorial Pacific, followed by High Latitude Reefs, both of which have relatively low coral cover. These observations provide some evidence for disturbance and stress in the physical environment affecting coral reef ecosystems. We postulate that the physical environment likely sets the ecological bounds for coral reef development. However, because of the large number of anthropogenic impacts occurring on local scales on reefs today it is difficult to know how much these natural and anthropogenic factors contribute to present day coral cover on reefs around the world.

The Northwest Pacific habitat and West Pacific Warm Pool displayed a relatively large amount of exchange of points during sensitivity tests. In the final result, much higher storm frequencies and mean SST as well as lower nutrient levels in the Northwest Pacific distinguish it from the West Pacific Warm Pool. The West Pacific habitat was extremely robust and was reproduced exactly in every combination of variables tested except when storm data were excluded. This habitat is dominated by the 'intense hurricane hits' metric, and all reefs that experienced a category 4 or 5 hurricane in the past 25 years are included in this habitat. The Equatorial Pacific habitat was also extremely robust, and was reproduced exactly with almost every combination of variables tested. In two tests, it lost three points from its western edge to the West Pacific Warm Pool. The Central South Pacific showed some fluctuation under stability tests, exchanging points with the Cool Tropics (from its southern edge) and West Pacific Warm Pool (from its northwestern corner). Similarly, the Cool Tropics experienced some exchange with the Central South Pacific as well as High Latitude Reefs.

By exploring different combinations of variables, we gained further insight into what was controlling the habitat distribution. Most importantly, the geographic pattern is reproducible using a wide range of oceanographic variables, and is stable to perturbations in weighting of variables. The habitats characterized by extremes (very high intense hurricane hits in the West Pacific, very high nutrients and DHWs in the Equatorial Pacific, very low temperatures in High Latitude Reefs) were the most robust to stability testing. The inclusion of nine physical and chemical oceanographic metrics allows us to better resolve the ‘buffer zones’ at the edges of habitats (i.e. between the Northwest Pacific and West Pacific Warm Pool) by considering as many factors as possible that could affect coral reef ecosystems.

Our results provide a first step in accounting for broad patterns in physical oceanographic parameters around the Pacific in areas where coral reefs exist. The geographic pattern of coral habitats found here provides an interesting setting for oceanographic studies within and between habitats using downscaling from models or finer resolution data products. In addition, these results alongside downscaled oceanographic studies can potentially be used in combination with local anthropogenic factors to examine how these different factors may affect the structure and development of coral reef communities. Our results will thereby strengthen ecological comparisons of coral reefs that range across large geographic areas, in that some of the variance in oceanography can be removed. For example, we found that the large, encompassing category of “no-worries reefs” in the Pacific from Kleypas et al., [1999b] actually includes a wide range of temperatures, ambient nutrient levels, and variability on annual and weekly scales.

This study of current climate conditions can also serve as a baseline for understanding coral reef survival capabilities in studies where climate conditions change under global warming scenarios. While coral reefs have already changed dramatically from human impacts, understanding their state and oceanographic habitat now allows us to explore the capacity for coral reefs to survive in future climate scenarios. Future work on this topic must determine what combinations of conditions will be conducive to coral reef survival in the future. For example, what physical environments are appropriate? Where is variability tolerable, and where is it not? How do direct anthropogenic stressors affect coral reef ecology in the different habitats? Our results begin to narrow the range of answers to these questions. Instead of saying ‘all coral reefs’ we can talk about warmer water reefs, cooler water reefs, places where there is a high degree of variability in temperature, and places where the environment is so stable that small perturbations may cause huge responses in the species present.

This study has discretized remote Pacific coral reefs into seven geographic habitats, each of which is characterized by a unique set of physical and chemical oceanographic conditions. These sets of oceanographic conditions define the physical environment, which sets the foundation for understanding ecological disturbance in the form of alteration to or perturbation of the physical environment.

2.6 Acknowledgement

Chapter 2, in full, is a reprint of the material as it appears in Journal of Geophysical Research Oceans 2012. Freeman LA, Miller AJ, Norris RD, Smith JE: Classification of remote Pacific coral reefs by physical oceanographic environment (1978-2012) 117(C2). The dissertation author was the primary investigator and author of this paper.

CHAPTER 3

Case Study I
Environmental Drivers of Community Structure in the Hawaiian Islands

3.1 Abstract:

In this chapter, meso-scale spatial ecological structure is assessed in the Hawaiian Islands. The island chain is situated within two distinct oceanographic regimes, and includes a series of marine reserves and protected areas of varying size and protection level. The impacts of both ocean habitat and marine reserve status on 42 ecological metrics are tested, as well as the effects of human population density and accessibility. I find that each island explains more variance in ecological metrics as a cohesive unit, such that the ecology of surrounding reefs not significantly influenced by the cardinal direction toward the open ocean that the reef is facing. Although oceanographic differences around an individual island do not result in significant differences in ecological structure, comparisons between islands find significant differences when islands are grouped by ocean habitat. This indicates that on a regional to mesoscale, oceanography has an impact on resulting community structure. Furthermore, the effect of marine reserves is assessed. Fewer distinctions are found than expected, however there are significant differences in rugosity between reserves and sites with no protection. Comparing the large Papahanamokuakea Marine National Monument with the remainder of the Hawaiian Islands yields further significant differences in fish and benthic invertebrate abundances.

3.2 Introduction:

The Hawaiian Islands are the most remote archipelago in the world, located in the tropical to subtropical central north Pacific. The islands are grouped as the predominantly inhabited main Hawaiian Islands (MHI) and the uninhabited Northwest Hawaiian Islands (NWHI) (Figure 3.1). The NWHI are fully contained within the Papahanaumokuakea Marine National Monument (PMNM) (established 2007), the largest marine protected area in the world (Figure 3.2). The main Hawaiian Islands range from completely uninhabited (e.g. Kahoolawe) to a permanent population of just under one million on Oahu. There are a number of smaller marine protected areas and fishing restricted areas around individual islands, but none that encompass complete islands or are as extensive as the PMNM.

The archipelago continues to undergo expansion by way of a tectonic hotspot in the mantle under the southeast end of the chain. The Big Island (Hawaii) is the youngest island and is still actively growing from the Kilauea vent. Further south, the Loihi seamount is a volcanically active structure and will eventually break the surface to add to the island chain. Traveling northwest through the island chain is akin to moving forwards in time. Each subsequent island is slightly more eroded, with lower elevation and an increase in dramatic topography created by rain erosion. In the far northwest, barely any land remains and what is above sea level consists of sand spits and low-lying atolls (e.g. Kure Atoll, Neva Shoals).

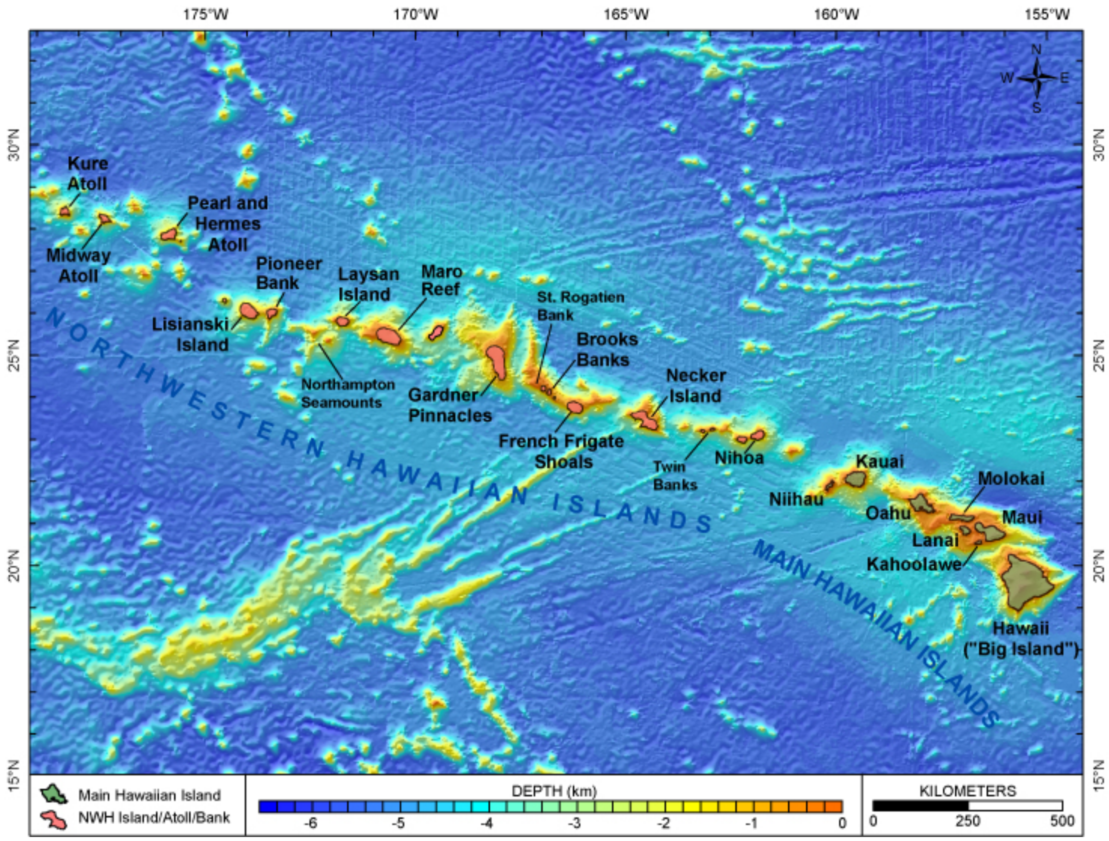


Figure 3.1: Bathymetric chart of the Hawaiian Islands. The color scale marks depth from shallow (yellow) to deep (blue). Islands are labelled by name and outlined in black. The Northwest Hawaiian Islands extend from Nihoa to Kure Atoll on the West side of the chart (marked in pink). The Main Hawaiian Islands are to the East, from Niihau to Hawaii (colored green). Credit: Pacific Islands Benthic Mapping Center (http://www.soest.hawaii.edu)

The Hawaiian Islands are situated in a prevailing westward current [Wyrtki 1974]. Large swells arrive most frequently from storms to the north (Alaska/Aleutian Islands) and impact the north-facing shores of the Hawaiian Islands [Snodgrass et al. 1966]. This creates a steady lee to the west, and somewhat to the south, of each of the islands. The underwater topography also changes from the young, southern islands to the older northern islands (personal observation, detailed below). All of the Hawaiian Islands host coral reef ecosystems around their perimeters.

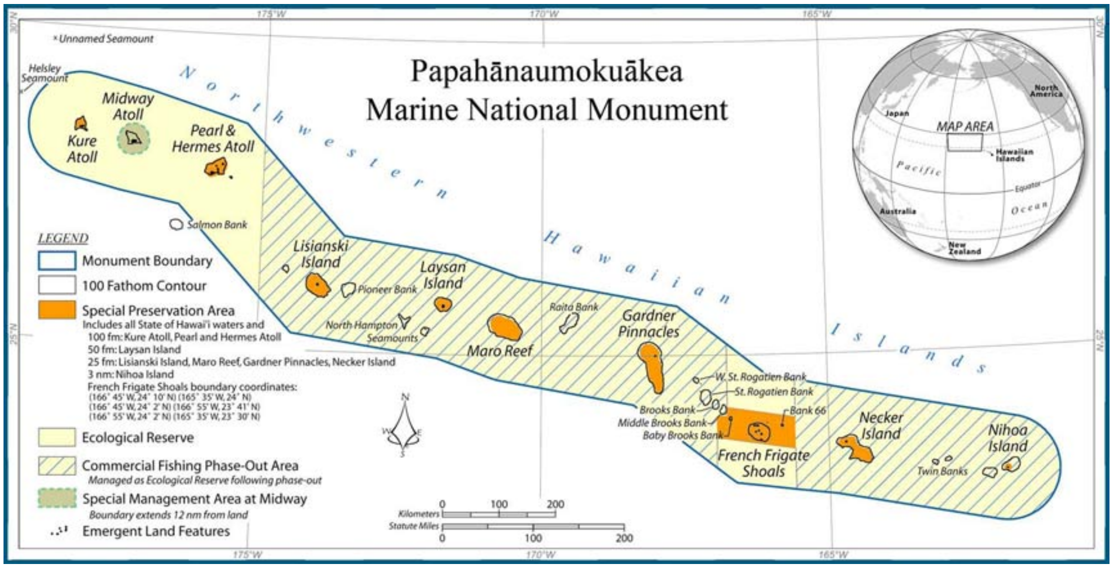


Figure 3.2: Map of the Papahanaumokuakea Marine National Monument encompassing the Northwest Hawaiian Islands, including special preservation areas. Credit: NOAA (www.noaa.gov)

3.2.1 Oceanographic Setting

In Chapter 2, I found that the NWHI and MHI were situated in two distinct oceanographic regimes (Figure 3.3). Three of the four NWHIs visited are in the High Latitude Reefs habitat, while the remainder of the sites considered, including all of the MHI, are in the Cool Tropics. Low temperatures, strong seasonal cycle, low Ω_{arag}, and high nutrient levels characterize the Cool Tropics. The High Latitude reefs are characterized by the same distinctive variables but are subject to more extreme values: even lower temperatures, stronger seasonal cycle, and particularly high thermal stress (degree heating weeks). In this chapter I test the ecological differences between these habitats, and within each habitat by comparing sites around individual islands.

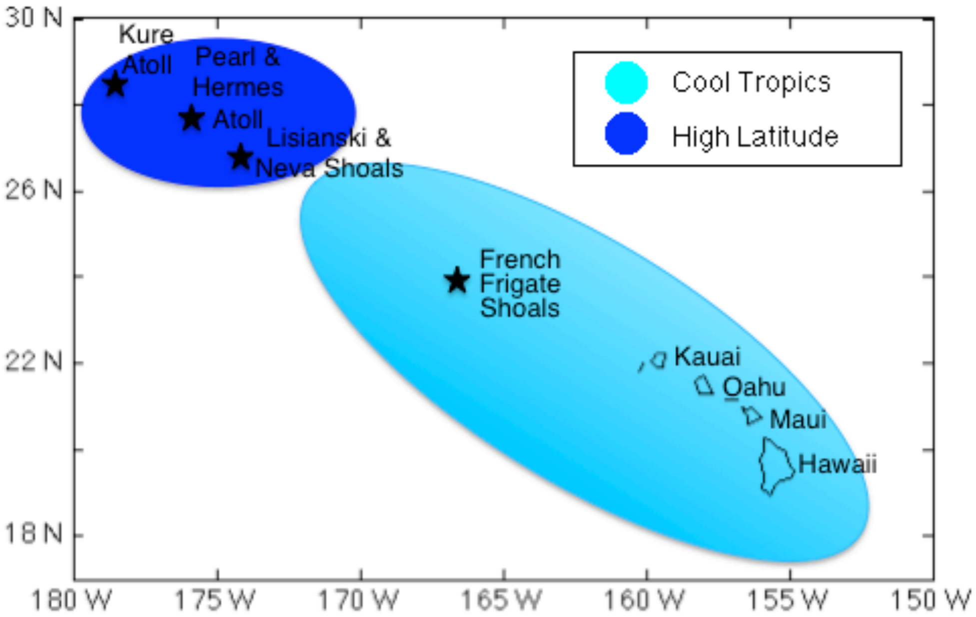


Figure 3.3: Chart of the Hawaiian Islands where ecological data was collected. The Northwest Hawaiian Islands are marked as stars, and the main Hawaiian Islands are outlined on the map. The habitats identified in Chapter 2 are identified by color. The Cool Tropics region in light blue, the High Latitude region in dark blue.

Many of the remote Pacific reefs considered in Chapter 2 are situated in a prevailing current (Figure 3.4) [Freeman et al. 2012]. The NWHI archipelago is located in the path of the North Equatorial Current, which travels east to west [Wyrtki 1974]. The current results in general characteristics that are common to most of these islands. The up-current (east) and pole-ward sides of the island tend to be exposed to greater kinetic energy and receive a greater quantity of large swells from storms in the high pacific latitudes [Snodgrass et al. 1966]. The down-current side produces an island wake, resulting in upwelling [Wolanski et al. 1984]. This leads to a general trend of cooler temperatures in the lee, which may afford some protection from coral bleaching [Riegl & Pillar 2003; West & Salm 2003].

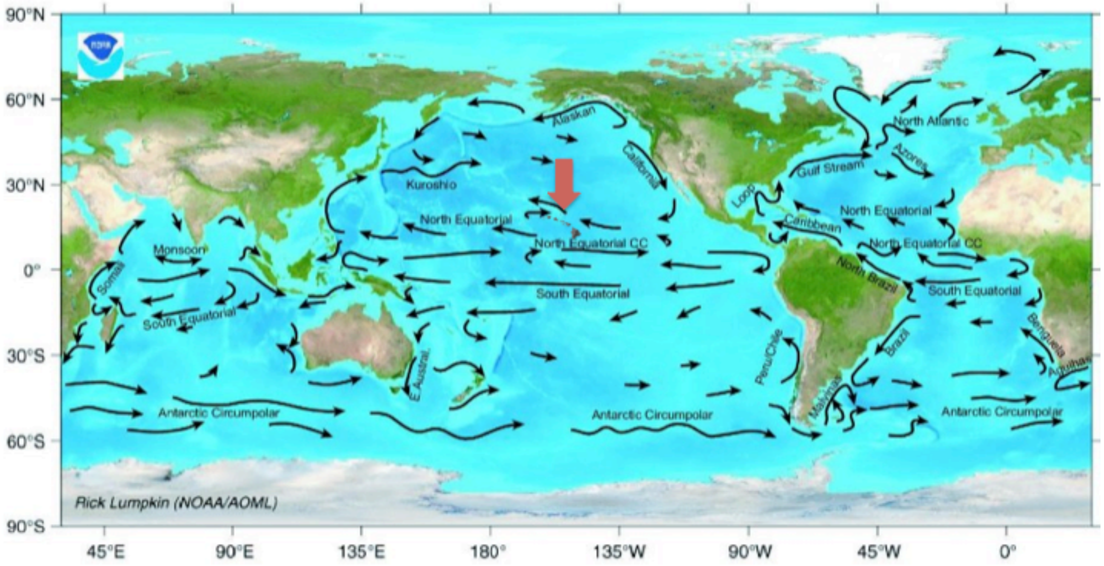


Figure 3.4: Chart of prevailing ocean currents of the world. Hawaii is marked with the red arrow (modified from NOAA, www.NOAA.gov).

3.2.2 Motivation

A field study was designed to test some basic generalizations about coral reef community structure in the Hawaiian Islands. This work was designed to scale down the basin-wide statistical analyses from Chapter 2 [Freeman et al. 2012] by assessing trends around and between islands. This case study was entirely based in the Hawaiian Islands, but the results may be applicable to other remote tropical islands when interpreting basin-wide or global studies such as Freeman et al. [2012] and [2013]. A range of ecological metrics were collected to test the following questions:

- Are there differences in community structure between the High Latitude Reefs and the Cool Tropics reefs? Can these be distinguished from differences in community strucutre between the NWHI and MHI?

- Is there a strong distinction between the exposed side of an island and the sheltered side? Does this grouping explain more variance than considering all sites around an individual island?
- Are there differences in community structure on reefs located with marine reserves versus those located outside of marine reserves?
- Are there differences in coral reef community structure associated with human accessibility, exposure to ocean energy, or human population density?

3.3 Methods

The same methods of data collection, described below, were employed in the MHI and the NWHI. In the NWHI, data were collected during NOAA Remote Areas Monitoring Program (RAMP) Cruise HA-12-04 on the R/V Hi'ialakai. Operations were shore-based on the four inhabited main Hawaiian Islands included in this study - Kauai, Oahu, Maui, and Hawaii (the Big Island).

Only one site was visited per island in the NWHI due to time constraints and cruise scheduling with the exception of Kure Atoll, where data were collected at two sites. Sites were selected based on prevailing weather conditions and proximity to the station site chosen by the captain of the R/V Hi'ialakai. For each of the MHIs, four sites were selected to estimate the around-island variability and to investigate the differences between exposed and sheltered sides of islands. Sites were selected based upon ease of accessibility from shore, safety, weather conditions, and advice from knowledgeable locals. Only three sites were surveyed on Kauai due to accessibility constraints, and three of the sites on the Big Island were on the western side due to time and weather constraints (Figure 3.5). At each site, photo mosaics of reef structure, rugosity measurements, time-lapse photo series, and stationary point counts of fish were collected. Field data were collected concurrently with Scripps graduate student Simon E. Freeman, who was additionally collecting acoustic recordings of the reef environment.

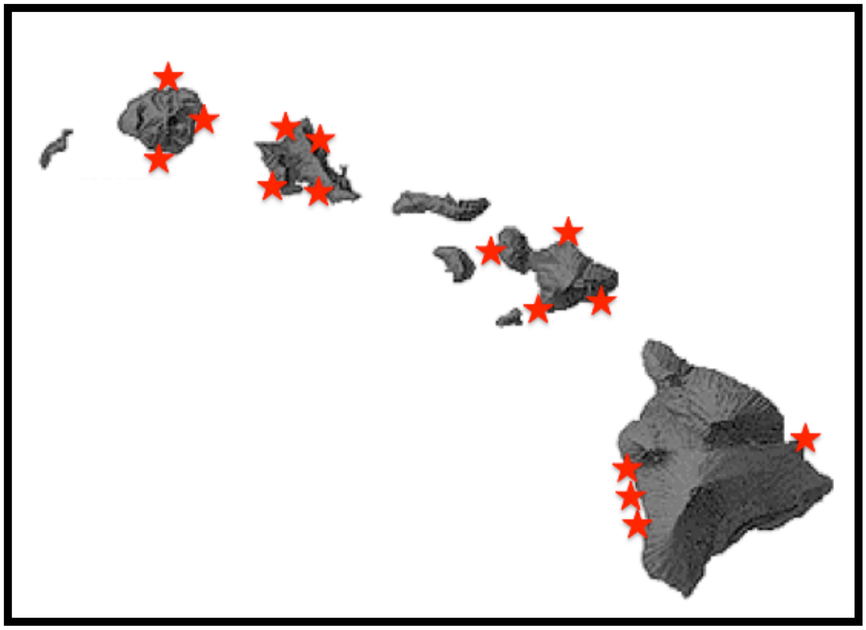


Figure 3.5: Map of the main Hawaiian Islands with the location of data collection sites marked as red stars.

3.3.1 Data Collection

Photo mosaic images of each field site were collected by swimming at a uniform depth (approximately five meters above the reef) and taking a series of overlapping digital photographs, which were subsequently stitched together using Hugin open-source photo mosaic software.

Rugosity measurements were collected along a 10-meter transect, marked as a 10 m tape stretched horizontally above the bottom. A fine-link chain was then draped over benthic contours alongside the transect tape and the length of the chain was then recorded. Two rugosity measurements were collected at each site, from which a mean and standard deviation were calculated.

Time Lapse Photo (TLP) data were collected using Canon D10 underwater cameras programmed using the open-source software package CHDK (www.chdk.wikia.com). Cameras were programmed to take one image every five minutes, using flash photography if required. Cameras were mounted on a polyvinyl chloride (PVC) pipe frame and positioned above the substrate facing downward, so that the field of view encompassed an area of coral reef substrate of approximately one square meter area. In order to circumvent use of the autofocus light (which may elicit a behavioral response from some benthic organisms), cameras were pre-focused manually. The distance between the lens and the substrate at the center of the field of view was measured using a tape measure after the camera had been mounted. Each camera was subsequently programmed *in situ*, setting focal distance to this value. Cameras were always deployed over live coral substrate, or as large an area of live coral substrate as was available. Four cameras were deployed at each site. TLP series that were short (less than 30 photos) or out of focus were discarded. Of the remaining TLP series, two were randomly selected and analysed per site. From each TLP series, animals were identified by eye, frame by frame. Counts of the photographed organisms were divided into the following functional groups: sea urchins (*Echinoida* and *Cidaroida*), crabs (*Brachyura*), hermit crabs (*Paguroidea*), brittle stars (*Ophiuroidea*), starfish (*Asteroidea*), sea cucumbers (*Holothuroidea*), fish (*Osteichthyes*), worms (*Annelida* and *Polychaeta*), eels (*Muraenidae*), and molluscs. Functional groups were selected based on the ability of the human examiners to identify organisms in the photographs. All photographs were analyzed to provide both time series information as well as overlying community structure at each site. Example data from Kahekili, Maui is shown in Figure 3.6.

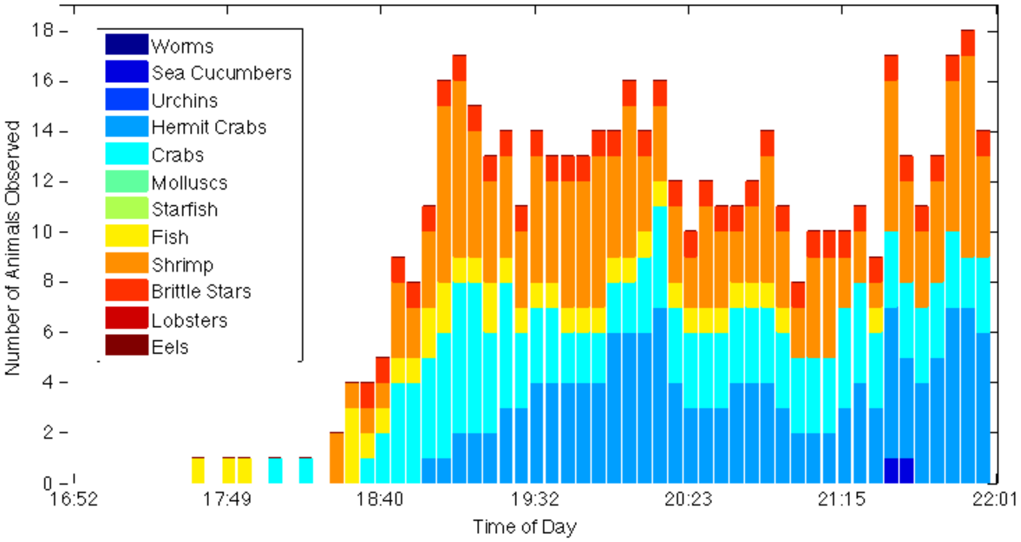


Figure 3.6: Example time series of animals recorded in time-lapse photographs from Kahekili, Maui. The horizontal axis shows local (HI) time. Each color indicates a different organism type, stacked to show the total number of animals counted per photograph. Note that not all functional groups were observed at this site (worms and eels). Sunset occurred at 18:36 local time at this site on the day these data were collected.

Stationary Point Count (SPC) methods were based on NOAA Coral Reef Ecosystem Division (CRED) protocols (www.noaa.gov). All surveys were conducted at 10 meters depth. Fish assemblages in shallower water (1-5 meters) have been found to be the same as those at greater depth (10-15 meters) [Friedlander et al. 2003]. One diver remained in a stationary position 10 meters away from TLP cameras and transect equipment, which were simultaneously being deployed by the second diver. All fish longer than 25 centimeters total length that entered a 20-meter radius of the SPC diver were recorded during a timed five-minute count. Care was taken to avoid over-counting large transient or schooling species. Fish were recorded as belonging to the following species or groups: triggerfish (*Balistidae*), surgeonfish (*Acanthuridae*), parrotfish (*Scaridae*), drummer (*Kyphosidae*), Yellow tang (*Zebrasoma flavescens*), squirrelfish (*Holocentrinae*), wrasse (*Labridae*), Ulua/giant trevally (*Caranx ignobilis*), snapper (*Lutjanidae*), trumpetfish (*Aulostomus spp.*), Galapagos shark (*Carcharhinus galapagensis*), pufferfish (*Tetraodontidae*), Omilu/Bluefin trevally (*Caranx melampygus*), White tip reef shark (*Triaenodon obesus*), Roi/Peacock grouper (*Cephalopholis argus*), scorpionfish (*Scorpaenidae*), and lizardfish (*Synodontidae*). Two replicate counts were conducted at each site, from which a mean and standard deviation of each functional group was calculated for subsequent analyses.

3.3.2 Data Processing

Species richness and diversity were calculated from both the TLP and the SPC data. These two datasets were treated separately due to the different data collection methods required for each. Species richness was calculated as the total number of groups present at a site. Diversity was calculated as the Shannon-Wiener Index, shown in Equation 3.1:

$$D = \sum_{1}^{i} p_i * \ln(p_i) \qquad 3.1$$

Where *D* represents diversity, *i* the number of groups considered (12 for the TLPs, 19 for the SPCs), and p_i represents the proportion of the total number of individuals that constitute a particular group. Shannon-Wiener diversity accounts for the entropy of the ecosystem by considering the distribution of each ecological group and the evenness of the overall species distribution, instead of merely whether or not the group is present (as in species richness).

In addition, the mean number of organisms recorded per frame, per site in the TLP data were used as an ecological metric. The total number of herbivores, predators, and large oceanic predators observed per site from the SPC data were also grouped as a separate metric. This resulted in a total of 42 ecological metrics.

Time stamps from TLP data and the GPS coordinates from each deployment site were used to calculate when sunset occurred during TLP camera deployment, and to group the data separately depending on whether photographs were taken during the day or at night. Individual and total animal counts during day and night-time periods were compared in separate analyses between all islands, between only the NWHI, between only the MHI, and between each of the ocean habitats.

To test the variability around and between islands, the 19 field sites were grouped in seven ways, detailed in Table 3.1. For divisions into two groups, a two-sample t-test was performed to test for statistical differences in the means of the ecological metrics between the two groups. For division by island (eight total), an analysis of variance (ANOVA) was performed to test for differences in the means between islands. Results were considered statistically significant if the test statistic p was less than 0.05, giving a result with 95% confidence.

For multivariate analysis, only the predominant ecological metrics were considered. For TLP data, these included animals that had an average mean occurrence (across all time series) greater than 0.7. This group included brittle stars, urchins, hermit crabs, and crabs. For SPC data, fish groups were considered predominant if the mean occurrence of fish per site across all sites was greater than 6.0. This group included triggerfish, surgeonfish, and all predatory fish. In addition, the sum of all organism counts from TLP data, and richness from both SPC and TLP data, were included. Two multivariate analyses were conducted on the resulting dataset- multivariate analysis of variance (MANOVA) and principle components analysis (PCA).

Table 3.1: Sites were separated by seven metrics for statistical comparison. A description of each group and the number of sites in each group is shown.

Grouping Scheme	**Description (# of sites)**
Accessibility	Entry within 0.5 km of public vehicle parking (9); further than 0.5 km from public vehicle parking (10)
Exposure	Exposed: north and east sides of islands (8); Not exposed: south and west sides of islands (11)
Island	French Frigate Shoals (1); Hawaii (4); Kauai (3); Kure (2); Lisianski (1); Maui (4); Oahu (3); Pearl & Hermes (1)
Marine Reserve	Any marine protected status (8); No legal protection (11)
NWHI/MHI	NWHI (5); MHI (14)
Ocean Habitat	Cool Tropics (15); High Latitude Reefs (4)
Population Density	Low population density: less than fifty people per square mile (10); High population density: greater than 50 people per square mile (9); data for nearest square mile of land from U.S. Census Bureau 2010

3.4 Results

3.4.1 Personal Observations, South to North:

Hawaii (the Big Island) slopes away rapidly to deep water close to shore and reefs are limited to relatively narrow regions near shore, presumably due to a limited habitable area within the desirable depth window. Much of the coral structure is below the surface water layer that contains terrestrial runoff, and the water clarity over the reefs is superior to that of the other MHI. The reefs have high degrees of coral cover and structural complexity. Fish are more prevalent than the other MHI, although there remain relatively few predators. Herbivores are visible in schools of 10-100 individuals, including yellow tang (*Zebrasoma flavescens*), convict tang (*Acanthurus triostegus*), and other surgeonfishes (other *Acanthurus* sp.). Reefs tend to be fairly continuous with few sand patches between coral covered regions from about 5-20 meters depth.

Maui exhibits a more gradual slope in comparison to the Big Island, and the reefs extend right up to the shoreline. Shore dives do not reach depths greater than 15 meters because shore gradient is lower. The corals nearest the beach are almost all dead- smothered with sediment, trodden on by tourists, and regularly bathed in runoff. They are overgrown with a variety of macroalgae. Further offshore, however, the live coral cover is higher. There are more sandy areas here than on the Big Island, and the reef seems patchier. The coral does not appear as healthy as that around the Big Island, although better than Oahu or Kauai. There are more fish, and a few schools of herbivores were observed in protected areas.

Oahu shores were of a yet more gradual slope, dotted with patchier reef structure. Shore dives are shallow here as well, averaging 10 meters depth. The reefs are in better shape than expected, despite the large urban area (Honolulu and Pearl City) on this island. Reefs are more often described as patch reefs than continuous, with large expanses of sand in between. We observed greater numbers of fish than in the NWHI, but the fish are all small and rarely seen in cohesive schools. There is a clear difference between the exposed side and the lee sites here, that didn't seem as pronounced on Maui or the Big Island. Exposed sites are murky with high wave energy. The reefs are sturdier with less coral and low diversity. Despite this, large numbers of shrimp and brittle stars were visible on dives.

Kauai is much more eroded above water and we found very patchy reefs with extremely limited coral cover near shore. There is much more algae and rubble than the other MHI. Visibility is notably poorer compared to all of the other islands. The reefs are more topographically dramatic, especially at Tunnels Beach. Tunnels Beach is one of the few places in the MHI where we observed reefs to exist in a vertical, wall-like setting arrangement, built atop volcanic rock that had eroded in an unusual manner. There are relatively few fish here compared to other sites and most are small. This is the only island where sharks were observed by divers (white tip reef sharks) in the caves at Tunnels Beach on the north shore.

French Frigate Shoals contains a single pinnacle of basalt – all that remains from what was once a large island (La Perouse Pinnacle). This is the northernmost basaltic outcrop in the Hawaiian archipelago. Two dive sites here, one near the pinnacle and one on the outer shoals of the reef, revealed abundant predatory fish, mainly giant trevally *Caranx ignobilis* ('Ulua' in Hawaiian) and green jobfish *Aprion virescens* ('Uku' in Hawaiian). Steep underwater topography exists near the pinnacle, with long spurs of reef and narrow sand channels between them. Coral cover was higher near the pinnacle and low on the outer shoals, presumably due to wave action and erosion (the pinnacle is entirely within the atoll).

Pearl and Hermes Atoll also exhibited relatively low coral cover and high numbers of predatory fish, including Ulua and the Galapagos shark (*Carcharhinus galapagensis*). The underwater topography was more rugose within the lagoon, with patch reefs rising from 20 meters to 2 meters depth. Visibility was poor for the NWHI (15 meters) within the lagoon. Visibility was better near the pinnacles, which were remnants of the outer wall of an atoll. There exist a number of sandbars around the edge of the atoll that are fringed with a few scrubby plants and trees.

Lisianski and Neva Shoals contained surprisingly high coral cover compared to the other NWHI, and seem quite different overall, lacking a fringing reef. The benthic ecology team on board the Hi'ialakai could not give us a strong reason for this high cover, but mentioned that it has been a consistent pattern as long as they had been surveying here. Walls of coral rise up from sandy patches and channels. The number of predatory fish is still very high, although not as high as other islands. The density of reef fish and herbivores is higher than the other NWHI. Near the small patches of outcropping rock at the center of Neva Shoals, water clarity is reduced as well as the number of predatory fish. However, a rare monk seal was spotted here.

Kure Atoll is the highest latitude coral reef in the world. Small fringing islands of sand are the only remains of a once tall volcanic island. The coral reefs on the outside of the atoll are well-defined, large spur and groove formations. Spurs rise ~10 meters higher than the sandy bottom and are up to ~100 meters wide, with up to ~30-meter wide sand channels between them. Coral cover is not extremely high but the reef appears healthy overall with few dead areas, and there are high numbers of predatory fish. Less common subtropical fishes were regularly sighted here including the Hawaiian morwong (*Goniisitus vittatus*).

3.4.2 Statistical Analyses

Of the seven groupings, the largest numbers of significant differences were found when data sets were grouped by island (14 occurrences of $p < 0.05$), ocean habitat (9 occurrences of $p < 0.05$), and NWHI/MHI (8 occurrences of $p < 0.05$). These differences are displayed in Figure 3.7 for the two ocean habitats.

Ocean Habitat. Data from sites in the Cool Tropics indicated a higher number of urchins and hermit crabs from the TLP counts, as well as a higher number of triggerfish. The High Latitude Reef data indicated a greater abundance of unicornfish, parrotfish, drummer, wrasse, and sharks than the Cool Tropics Reefs. The NWHI/MHI and ocean habitat ecological comparisons are quite similar. The only site that is unique between these two groupings is French Frigate Shoals, which is administratively included in the NWHI but is identified as belonging to the Cool Tropics group in terms of its oceanographic setting. Both divisions result in significant differences in urchins, hermit crabs, unicornfish, drummer, wrasse, Galapagos shark, and all sharks. The NWHI are further differentiated by generally higher numbers of Ulua (Giant trevally).

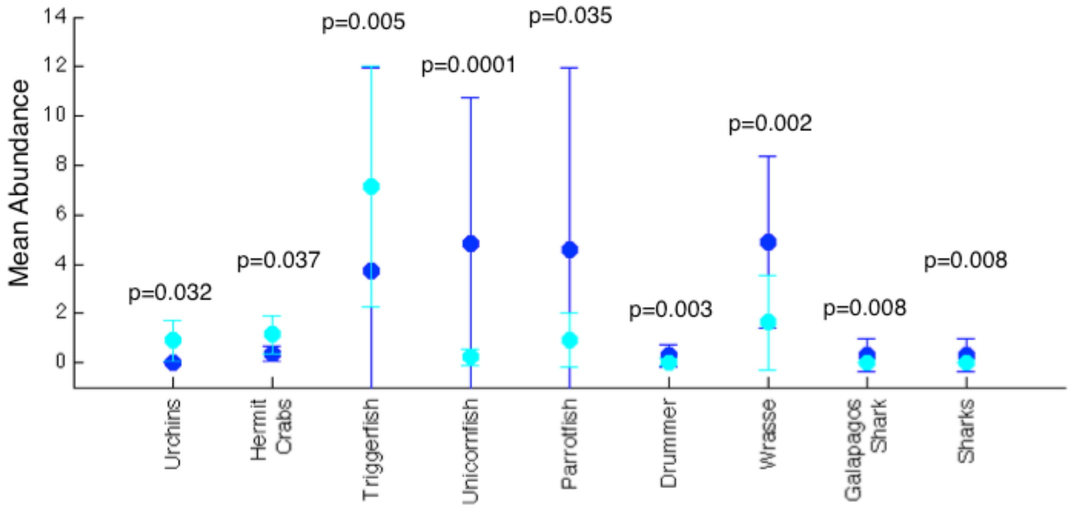


Figure 3.7: Comparison of ecological metrics between the Cool Tropics habitat (light blue) and the High Latitude Reefs habitat (dark blue). Mean abundance is indicated with solid circles, and error bars represent ± 2σ. P-values from two sample t-tests are marked above each respective metric.

Multivariate techniques considering only animals that were abundant were successful in differentiating between the Cool Tropics and the High Latitude Reefs based on ecological metrics only, as shown in Figure 3.8. Of particular importance in differentiating these variables were triggerfish, surgeonfish, predatory fishes, the total number of organisms counted in the TLP data, SPC-derived richness, and brittle stars. The habitats are differentiated along the first canonical variable axis from MANOVA (Figure 3.8A), and the second principle component axis (Figure 3.8B).

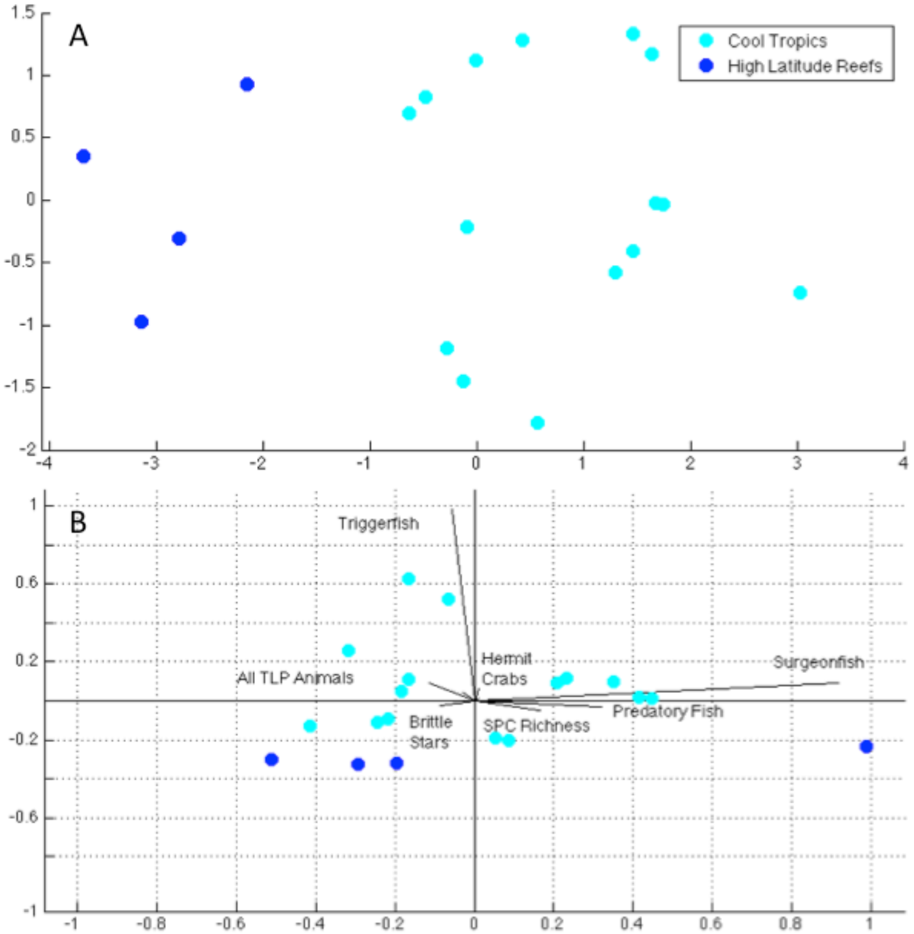


Figure 3.8: Results of multivariate analysis of variance (A) and principle components analysis (B) using only abundant ecological metrics. Dark blue circles indicate High Latitude sites and light blue circles indicate Cool Tropics sites. A: MANOVA canonical variables, calculated as linear combinations of original ecological variables to maximize differentiation between groups. The first canonical variable is along the x-axis, and the second along the y-axis. B: principle components calculated from original ecological variables to best explain variation amongst all sites. The first principle component is along the x-axis (50% of variance), and the second (25% of variance) along the y-axis. The original ecological variables are plotted as black lines and labeled in black text.

Marine Reserves. A comparison of rugosity between sites located within marine reserves and located outside of marine reserves resulted in a significant difference irrespective of whether the PMNM sites were included (p=0.008) or not (p=0.003) (Figure 3.9). In this study, none of the other metrics tested showed significant difference between sites located within marine reserves and sites located outside of marine reserves. When considering a different grouping where small reserves are excluded and the PMNM sites are compared to all non-PMNM sites, significant differences were found in the number of sea urchins and hermit crabs from TLPs (p=0.013; p=0.016 respectively) as well as unicornfish (p=0.001), drummer (p=0.013), wrasse (p=0.021), Ulua (p=0.022), and sharks (p=0.022).

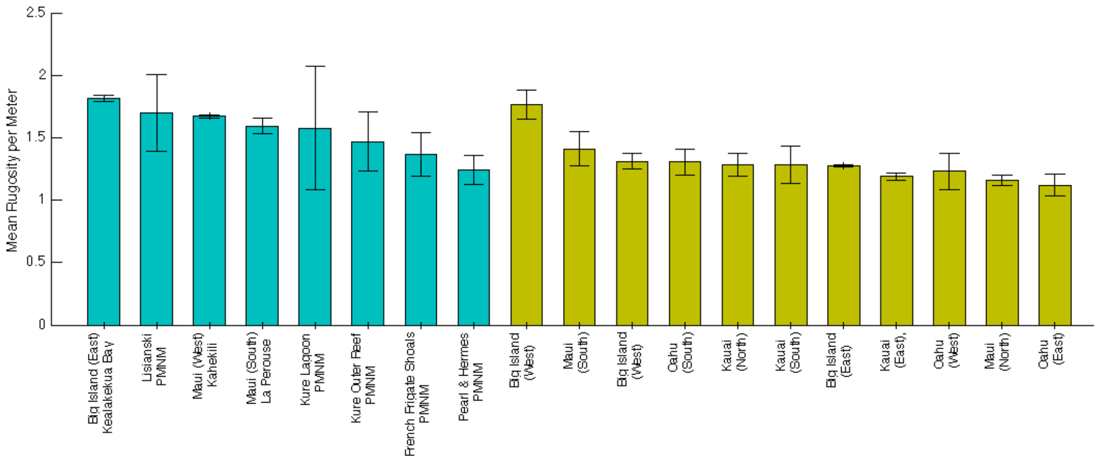


Figure 3.9: Mean rugosity per meter of each site with error bars indicating ± 2σ. Blue bars represent marine reserves and yellow bars represent areas with no legal protection. Labels indicate the island name, marine reserve name if applicable, and the compass orientation of each site around the island.

Accessibility. Data collected from accessible reefs showed significantly fewer predatory fish than less accessible reefs in both the case when the PMNM sites were included and when they were not ($p=0.014$; $p=0.020$, respectively). No further significant differences were found in herbivorous fish, diversity, or invertebrates from TLPs.

Exposure. Comparison of the TLP data and SPC from exposed (windward) reefs against not exposed (leeward) reefs yielded no significant differences. When only the MHI were considered, a significant difference was found in rugosity ($p=0.043$).

Population Density. Regions of high human population density returned lower richness and diversity of benthic organisms from TLP data when considering all 19 sites ($p=0.004$; $p=0.015$, respectively) and additionally when restricting the analysis to just the 14 sites in the MHI ($p=0.019$; $p=0.041$, respectively). No significant differences were found in SPC data or rugosity from this grouping.

Day vs. Night. Division of TLP data sets by day and night indicated significant differences in the abundance of hermit crabs ($p=3.7\times10^{-5}$), crabs ($p=0.021$), shrimp ($p=6.57\times10^{-5}$), brittle stars ($p=4.87\times10^{-4}$), and total number of animals recorded by TLP ($p=1.67\times10^{-5}$) (Figure 3.10). For each of these metrics, the overall mean was greater at nighttime. This is consistent with previous studies employing TLP on coral reefs [Freeman et al. 2013b].

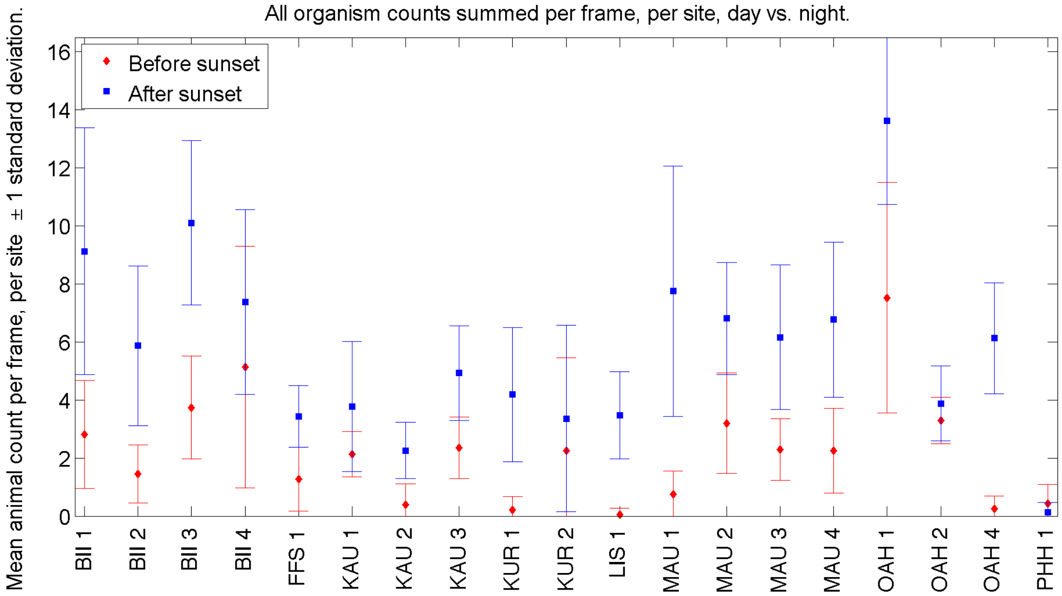


Figure 3.10: Mean total number of animals recorded per photograph from time lapse cameras, divided by daytime (red diamonds) and nighttime (blue circles), by site. Error bars represent ± 2σ.

3.5 Discussion

This study focused on comparisons between sites and islands in order to find general trends in community structure between distinct ocean habitats, marine reserve status, and geographic variables with ecological metrics. The strongest differences were found between all eight islands individually, and between the two ocean habitats.

When considering accessibility to a site, I expected to see an impact on food fish from recreational fishing activities. A significant difference was found in the total number of predatory fish with lower number of predatory species counted in sites with high levels of accessibility compared to site more distant from access roads. This difference was not reflected in counts of individual predators (e.g. snappers), indicating that different sites had unique community structure regardless of accessibility to humans. However, the overall lower numbers of predatory fish near more accessible sites is likely a result of human impacts. Fishing pressure tends to be applied higher on the food chain [Pauly et al. 1998], supporting the idea that this difference is a result of fishing pressure.

When diversity and richness calculated from the TLP data were compared with human population density on the adjacent coastline, a significant difference in diversity and richness was found between regions that are densely populated, and those that are not. This is another metric that can indicate the level of human impact that, in this case, resulted in reduced benthic community complexity. This is a less obvious chain of events than fishing impacting the number of predators at more accessible sites, since most of the animals in the TLP are invertebrates. A variety of human impacts could be responsible for less diverse benthic communities near more densely populated areas including runoff, heavy use by swimmers and snorkelers eliciting an avoidance response by animals, fishing and collection of invertebrates for food, and effects on the coral itself resulting in less healthy reef habitat for these animals to occupy.

Surprisingly, exposure to prevailing currents and swells were not factors in any of the significant differences obtained from the ecological metrics tested here. These metrics may need to be resolved on a smaller scale, as previous studies have found significant differences between fish populations at sites directly exposed to incoming waves compared to those with some kind of shelter [Friedlander et al 2003]. In this present study, individual islands explained more variance in the ecological metrics considered than did the compass position of the field site around an island, across the archipelago. This result is of particular interest when considering large-scale oceanographic studies such as in Chapters 2 and 4. The data here support treating islands as individual entities, as opposed to treating the exposed and lee sides separately.

3.5.1 Comparison of Reefs in Two Distinct Oceanographic Regimes

This field study was designed specifically to test the impact of ocean habitat regime on coral reef community structure. I found that the High Latitude Reefs, with lower temperatures and larger seasonal cycle, contained significantly more fish than the Cool Tropics Reefs as documented in SPC data. The most notable fish found in the High Latitude Reefs were the physically larger functional groups such as sharks and wrasse (Figure 3.7). The Cool Tropics Reefs, which are characterized by more moderate conditions, contained significantly greater numbers of benthic invertebrates including urchins and hermit crabs, as well as triggerfish. One factor driving the higher numbers of urchins and hermit crab in the Cool Tropics Reefs may be a higher percent coral cover, as these animals tend to be associated with coral substrate (personal observation). A previous study concluded that within the NWHI, coral abundance and diversity were highest in the mid-NWHI (included in the Cool Tropics Habitat, e.g. French Frigate Shoals) and declines to the north and west, towards the High Latitude Reefs habitat [Maragos et al. 2002].

Of the metrics tested here, nine out of 42 returned significant differences between oceanographic regimes. This response in nearly 25% of the variables suggests that the oceanographic regime greatly influences many aspects of ecological state. This is further reflected in the differentiation of the two groups in multivariate analysis techniques (Figure 3.8). While the MANOVA canonical variables are calculated to cluster the sites as much as possible based on the original ecological variables, the PCA variables are calculated to account for as much variance as possible. The first principle component explains 50% of the variance from the input ecological variables (abundant animals only), while the second, which partitions the two habitats, explains an additional 25% of variance. The original ecological variables are also marked, revealing that triggerfish and surgeonfish are particularly important in structuring the principle component axes. The variables most closely aligned with the y-axis (second principle component) are responsible for more of the differences between the two ocean habitats. These include brittle stars, SPC richness, all TLP animals, surgeonfish, and predatory fish. The wide range of ecological metrics delineating the two ocean habitats is a strong indication that the fundamental community structure and ecology are different between the two physico-chemical regimes.

One reason for this significant difference may be the protected status of all of the High Latitude Reefs as part of the PMNM. However, I postulate that the ocean habitat was structuring the ecosystem before the monument was established in 2007, and continues to do so today. A previous large-scale study conducted before the region became a protected area found that fish biomass was 260% greater at sites in the NWHI compared to the MHI and that the numbers of fish were significantly different [Friedlander and DeMartini 2002]. Personal observations indicate that the environments in the High Latitude Reefs were distinct to those of the Cool Tropics. High Latitude Reefs contained less live coral cover and consequently less small-scale structure. Previous monitoring studies conducted in 2002 support this claim, with percent coral cover trending at 10-20% in the PMNM and 15-55% in the MHI. Lisianski had exceptionally high coral cover (50%), as did Kaneohe Bay on Oahu (67%) [Friedlander et al. 2005a; 2005b]. Large, erosion-derived topography predominated the underwater environment, with bedrock and limestone in different stages of spur-and-groove erosion. At the most northerly sampling site, Kure Atoll, sand channels 20 meters wide (grooves) were observed, with walls of reef rising abruptly 5-10 meters to a relatively flat rocky area before descending again into another sand channel (spur).

I suggest that the documented differences in fish population structure and density and invertebrate activity are at least in part explained by the unique oceanographic conditions affecting the High Latitude Reefs, as compared to the Cool Tropics. This result is consistent with the implications of the work in Chapter 2, indicating that there are in fact certain ecosystem qualities that are differentiated by oceanographic environments. This finding strongly supports the consideration of oceanographic physico-chemical variables when conducting ecological studies, and for management decisions such as the selection of marine reserve areas.

3.5.2 The Importance of Marine Reserves

Of the 42 ecological variables tested in this study, only rugosity regularly returned a significant difference between sites with some level of protection (marine reserves) against those with no legal protection. This result is surprising given the inclusion of the PMNM in this study. It is well documented that the NWHI reefs are less impacted by people than those in the MHI, even prior to establishment of the PMNM in 2007 [e.g. Maragos et al 2002; Friedlander *et al*. 2003]. This includes observations of greater numbers of large fish [Friedlander *et al*. 2003] and the Hawaiian Monk Seal, which is rarely seen in the MHI [Baker *et al*. 2011]. Even so, based on these data, marine reserves do not appear to create statistically significant differences in traditional measures such as diversity..

When all marine reserves were included in statistical tests, only rugosity returned a significant difference between the two groups (marine reserve vs. non-reserve). There were no significant differences associated with mobile organisms. This finding was the case both when the NWHI were included in analyses, and when only the MHI were considered. Rugosity is an important ecological metric as it is indicative of the physical reef structure, the majority of which is created by reef-building corals. Reefs that contain more topological complexity have been found to contain higher diversity and healthier coral [Risk 1972; Dustan et al. 2013].

The result that reserves within the MHI do not create significant statistical differences in the large number of ecological metrics considered here, when considered against nearby unprotected areas should be viewed with caution. The ecological metrics obtained through TLP may not be indicative of the ecological benefits afforded by protection. Marine reserves are implemented primarily to restore species that are targeted by humans for consumption (fishes, lobster, etc.). Populations of small benthic organisms may only be indirectly affected by this protection and may be influenced more significantly by other, unknown factors.

My personal observation suggested large differences in ecology between the NWHI and the MHI. Although the MHI yielded more fish in the SPC data collections, much larger individual fish were observed in the NWHI. Furthermore, animals in the NWHI exhibited extraordinary behavior. Large fish were unafraid of people in the monument, actively approaching divers and even head-butting scientific equipment. Comparatively, in the MHI, fish were observed to flee as soon as a diver entered the water, presumably from experience with spearfishers. In addition to the behavior of fish, the larger invertebrates were observed to be more curious and willing to explore scientific equipment and interact with SCUBA divers in the PMNM. While this study did not document behavior specifically, this observation speaks heavily to the importance of the level of protection provided by the marine monument.

CHAPTER 4

Coral Reef Habitat Response to Climate Change Scenarios

4.1 Abstract

Coral reef ecosystems are threatened by both climate change and direct anthropogenic stress. Climate change will alter the physico-chemical environment that reefs currently occupy, leaving only limited regions that are conducive to reef habitation. Identifying these regions early may aid conservation efforts and inform decisions to transplant particular coral species or groups. Here a species distribution model (Maxent) is used to describe habitat suitable for coral reef growth. Two climate change scenarios (RCP4.5, RCP8.5) from the National Center for Atmospheric Research's Community Earth System Model were used with Maxent to determine environmental suitability for corals (order Scleractinia). Environmental input variables best at representing the limits of suitable reef growth regions were isolated using a principal component analysis. Climate-driven changes in suitable habitat depend strongly on the unique region of reefs used to train Maxent. Increased global habitat loss was predicted in both climate projections through the 21st century. A maximum habitat loss of 43% by 2100 was predicted in RCP4.5 and 82% in RCP8.5. When the model is trained solely with environmental data from the Caribbean/Atlantic, 83% of global habitat was lost by 2100 for RCP4.5 and 88% was lost for RCP8.5. Similarly, global runs trained only with Pacific Ocean reefs estimated that 60% of suitable habitat would be lost by 2100 in RCP4.5 and 90% in RCP8.5. When Maxent was

trained solely with Indian Ocean reefs, suitable habitat worldwide *increased* by 38% in RCP4.5 by 2100 and 28% in RCP8.5 by 2050. Global habitat loss by 2100 was just 10% for RCP8.5. This projection suggests that shallow tropical sites in the Indian Ocean basin experience conditions today that are most similar to future projections of worldwide conditions. Indian Ocean reefs may thus be ideal candidate regions from which to select the best strands of coral for potential re-seeding efforts.

4.2 Introduction:

Anthropogenic climate change will alter many physical and chemical characteristics that comprise the niches of marine species and ecosystem habitats. Changes in these physico-chemical conditions are already leading to shifts in the habitat ranges of some marine species [Cheung et al. 2009], and extinction rates of marine species are expected to increase [Pereira et al 2010; Cahill et al. 2012]. The environmental conditions in which many ecosystems have evolved are shifting geographically. Consequently, suitable habitat spaces for these ecosystems are being ‘re-mapped’ in accordance with changes in multiple environmental variables. Projecting the geographic distribution of these future marine habitat areas is made difficult by our incomplete knowledge of not only the physico-chemical limits of marine habitats, but the biological and ecological limits of the species that occupy these habitats (e.g., the role of species interactions in defining ecosystems). Habitat niche models, which predict suitable habitat envelopes for a given species or group of organisms, are a good first estimate of habitat requirements. Habitat niche models can thus be used to estimate the future geographic range of appropriate habitat areas in climate change scenarios.

As climate change alters oceanographic conditions, the geographic range of ocean habitat suitable for the growth of coral reef ecosystems is shifting. Corals of the order Scleractinia provide the foundation of shallow-water coral reef ecosystems. Scleractinia corals secrete calcium carbonate skeletons, which accumulate as reef structures that in turn support highly biodiverse communities. All shallow-water, tropical coral reefs are defined by the same broad ecological functional groups, but they develop across a wide array of ocean environments [Freeman et al. 2012]. The mean environmental conditions in which reefs are found differ across the three tropical ocean basins (Caribbean/Atlantic, Pacific, and Indian), and there is further variation within each basin [Freeman et al. 2012]. While individual coral colonies are acclimatized to the conditions of their own unique location, each region will experience a different combination of environmental shifts associated with climate change.

Increasing sea surface temperatures and extreme temperature excursions are considered a major threat to coral reef ecosystems primarily because they have been shown to be the major factor behind the recent global increase in coral bleaching [Glynn 1993; Brown 1997]. Ocean acidification has also been shown to affect coral colonies in multiple ways, including reducing the ability of coral polyps to secrete calcium carbonate skeletons, and reducing the integrity of the reef structure [Kleypas & Yates 2009]. The geographical limits of shallow-water coral reef ecosystems are also defined by salinity, light availability as photosynthetically active radiation (PAR), water current speed, [Freeman et al. 2012; Kleypas et al. 1999b], and other variables that are more difficult to quantify such as species interactions and connectivity.

This article considers the geographical change in physico-chemical environments appropriate for coral reef ecosystems, as projected by the National Climate and Atmospheric Research (NCAR) center's Community Earth System Model Version 1 (CESM1) in a suite of climate change scenarios. Suitable reef habitat was defined using a niche model, Maxent [Phillips et al. 2006], through analysis of the environmental envelope in which coral reefs exist in the present-day. In combining model outputs and suitable environmental parameters as defined by Maxent, projections are made regarding how these physico-chemical changes may influence the spatial distribution of suitable habitat. The environmental variables projected by CESM1 include key limiting variables to reef development. The results yield a range of possible future states regarding the world-wide spatial distribution of coral reef ecosystems as they experience climate change. Combining CESM1 and Maxent, two state-of-the-art tools, provides a projection of coral reef ecosystem survivability in up-to-date climate change scenarios. While a number of caveats are raised due to the use of species distribution models (SDMs) and similar tools in projecting future habitats [Dawson et al. 2011; Dobrowski et al. 2011], these projections provide some insight toward actions that could help guide coral reef ecosystem preservation. For example, resources may be better utilized by focusing conservation efforts on those areas where suitable reef habitats are likely to persist under future climate conditions.

4.3 Materials and Methods

Potential coral reef habitat was modeled using Maxent, a maximum entropy niche model that performs well with presence-only data for species or communities [Phillips et al. 2006]. Maxent is based on deterministic algorithms that converge to the optimum (maximum entropy) probability distribution of habitat suitability across a spatial domain. Environmental inputs for the model were based on climate simulation outputs for the present day from CESM1. Present-day coral reef distributions, obtained from ReefBase (www.reefbase.org), were used to train Maxent.

4.3.1 Climate model data

CESM1 is a global atmosphere-ocean, fully coupled climate model that includes global carbon cycling. CESM1 is built on the Community Climate System Model version 4 (CCSM4), with a nominal horizontal resolution of 1° by 1° which is enhanced in the tropics and at high latitudes [Gent et al. 2011]. The ocean component of the global carbon cycle includes the Biogeochemical Element Cycle (BEC) model of Moore *et al.* [Moore et al. 2004], which includes four nutrients (N, P, Si, Fe), three phytoplankton functional types (diatoms, pico/nano-phytoplankton, and diazotrophs), and one zooplankton class. The model determines the complete suite of carbonate system components (pH, pCO_2, HCO_3^-, CO_3^{2-}, and alkalinity), which are then used to calculate calcium carbonate (aragonite) saturation state [Long et al. 2013].

Model data were extracted from the CESM1 BEC 20th century run (1985-2005) and two 21st Century scenario runs described by unique representative carbon pathways (RCPs): RCP4.5 (2005-2100) and RCP8.5 (2005-2100). The scenarios yield differences of approximately 2°C in mean global air temperature. Ocean data were retrieved only from the surface layer (the upper 10 m), as most shallow-water coral growth occurs in the upper littoral zone (shallower than 30 m). The absolute increase in mean sea surface temperature for the domain considered is 0.73° C for RCP4.5 and 2.10° C for RCP8.5. The variables extracted from CESM1 included sea surface temperature, sea surface salinity, phosphate concentration at the sea surface (PO4), average light availability in the surface layer as PAR, surface horizontal current velocities, and carbonate system parameters. Since concentrations of the nutrients nitrate, phosphate, and silicate are strongly correlated in seawater [Redfield 1934], only phosphate was retained.

Monthly output from the CESM1 biogeochemistry model simulations of the 20th century (for training Maxent), and the two 21st century simulations RCP4.5 and RCP8.5, were interpolated to a grid with 1° by 1° resolution. The monthly data were averaged over 20-year time periods, from 1985-2005 for the 20th century model and as overlapping time periods in the 21st century runs (2011-2030, 2021-2040, etc.) until 2100. As the 21st century runs begin at year 2005, data were also collected for the ten-year time period 2006-2015 to calculate an average for 2010. These files were converted to Matlab® structure files for processing in Matlab® (R2011a). This process is described in more detail below in Section 4.3.3.

4.3.2 Biogeographic data

Coral-reef ecosystems presently exist in limited regions of the tropical and subtropical oceans. Data regarding the specific locations of these ecosystems are available from ReefBase (www.reefbase.org). ReefBase locations are provided by the Millennium Coral Reef Mapping Project. These spatial data were interpolated to the same 1° by 1° resolution grid as the CESM1 data. Ocean basins were divided by geographic boundaries into the Indian, Pacific, and Caribbean/Atlantic basins. These three sub-regions allow for separate application of the habitat niche model through training it for one particular subset of reefs restricted to the basin in which they reside, as described in section 4.3.4. Coral-reef ecosystems also exist in the Red Sea and Persian Gulf. The unique oceanographic conditions of these two regions would require their treatment as separate sub-regions, none of which contain a sufficient number reef locations once interpolated to a 1° by 1°grid to adequately train the niche model. Consequently these regions are not included in this analysis.

4.3.3 Determination of environmental variables

Surface current speeds were calculated from the horizontal velocity components of the CESM1 data. Aragonite saturation state (Ω_{arag}) was calculated as the ratio of carbonate ion concentration and carbonate ion concentration at $\Omega_{arag} = 1$, from the CESM1 carbon-system components. The mean, maximum, minimum, and annual range for current speed, Ω_{arag}, sea surface temperature, sea surface salinity, sea surface phosphate concentration, and surface PAR were obtained for each of the 20-

year time periods. Averaging across a 20-year time period provided an estimate of the climatological state from CESM1. All variables are normalized prior to subsequent analyses.

From temperature (SST), further calculations were performed to estimate cumulative thermal stress (CTS), as shown in (1). CTS is similar to the degree heating week measure (e.g. [Mumby et al. 2004]), and is calculated as the temporal accumulation of the excess monthly SST when SST exceeded the mean monthly maximum (MMM) plus two standard deviations of mean monthly maximum for each grid cell [Teneva et al. 2012]. Using two standard deviations (as opposed to one degree Celsius, used to calculate degree heating weeks) is more effective for the broad geographic area considered as well as for monthly data (versus weekly). Equation (4.1) describes the method by which cumulative thermal stress was estimated:

$$CTS(x,y,t) = SST(x,y,t) - [MMM(x,y) + 2\sigma_{MMM}] \qquad (4.1)$$

where x represents latitude, y represents longitude, t represents time, SST represents sea surface temperature, and σ_{MMM} represents the standard deviation of the MMM. MMM data were calculated from the 1985-2005 20th century run, and CTS was then calculated and summed over each 20-year simulation period. These data are not a direct analog to degree heating weeks, but rather represent the overall thermal stress for each 20-year time period considered in this study.

To reduce aliasing between variables and to improve the performance of Maxent, highly correlated variables were eliminated using principle component analysis (PCA) for three time periods in the 21st century (2011-2030, 2041-2060, and 2081-2100). Each of these runs yielded two dominant (25-element) structure functions that combined explain at least 60% of the total variance among the spatial locations, and each generated similar structure functions that revealed correlations among the variables when plotted along perpendicular axes (Figure 4.1). Six groups of highly correlated variables consistently arose in the PCA for each time period and scenario. Appendix 1 shows that similar results prevail when computing Spearman rank correlations among variables directly. From each group of correlated variables, only one was chosen for use in final calculations based on the following two criteria: the known importance of the variable to coral-reef ecosystem habitat state, and whether the variable was likely to change appreciably in future climate scenarios. The resulting list of variables included CTS, phosphate maximum, current speed maximum, salinity minimum, PAR minimum, and Ω_{arag} minimum.

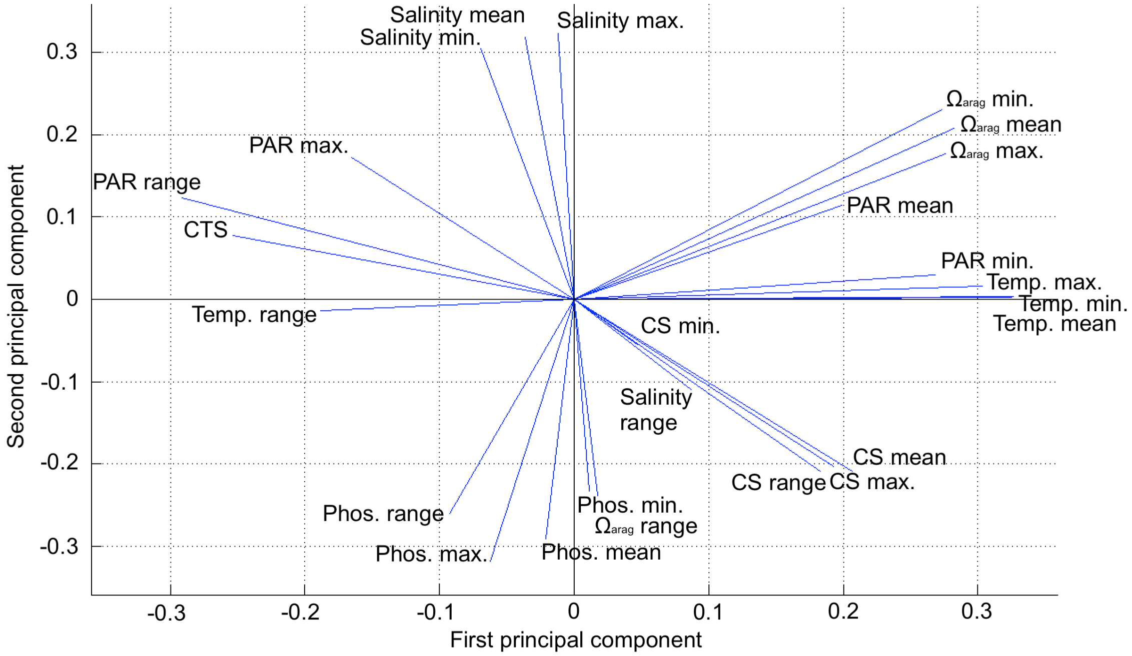


Figure 4.1: The 25 environmental variables initially considered in this study as projected into principle component space. This projection shows the correlation between variables, as equivalent to the cosine of the angle between vectors. Tightly clustered vectors are used as groups from which final variables were selected to minimize aliasing in subsequent analyses. Each vector group is detailed in Appendix I.

CTS: (strongly correlated with PAR annual range) provides an indication of the duration and magnitude of temperature excursions that exceed the tolerance of coral organisms. Temperature stress is strongly correlated with coral bleaching [Mumby et al. 2004], which often leads to partial or complete mortality of individual coral colonies. CTS is expected to increase in most reef locations as the effects of climate change intensify.

Phosphate maximum: (strongly correlated with Ω_{arag} annual range; and PO4 minimum, annual range, and mean) is also considered representative of nitrate and silicate levels in this study. Nutrient enrichment is often associated with coral-reef ecosystem degradation as it can lead to a shift in community structure towards one dominated by fleshy macroalgae [McManus & Polsenberg 2004]. Climate change may cause a shift in nutrient patterns in the future through changes in circulation and increased ocean stratification.

Current speed maximum: (strongly correlated with PAR maximum, annual range of salinity; current speed minimum, mean and annual range) is an indication of the hydrodynamic energy in the surrounding environment. Currents are important to coral-reef ecosystems because they provide a well-oxygenated environment that enhances food availability and provides flushing of reef waters. High current speeds have been correlated with reduced heat stress and thus less coral bleaching and mortality in several previous studies [Riegl & Pillar 2003; Woesik 2001; McClanahan et al. 2005].

Salinity minimum: (strongly correlated with maximum and mean salinity). Most reef building coral organisms are intolerant of salinities less than 25 parts per thousand (ppt), [Coles & Jokiel 1992], and no coral reefs are found where the minimum monthly salinity is less than 23 ppt [Kleypas et al. 1999b]. Climate-related changes in rainfall patterns could affect salinity regimes in the future, particularly in coastal regions.

Ω_{arag} minimum: (strongly correlated with mean PAR; Ω_{arag} mean and maximum) is a measure of the degree of aragonite saturation in seawater. Both the skeletal growth rate in individual coral colonies and the rate of increase in the quantity of reef-building framework have been correlated with Ω_{arag} [Langdon et al. 2000]. Because ocean acidification is causing significant decreases in Ω_{arag} , regions of high Ω_{arag} are contracting in area, mostly equatorward [Guinotte et al. 2003; Hoegh-Guldberg et al. 2007; Silverman et al. 2009]. Once atmospheric CO_2 levels double in comparison to preindustrial levels (estimated occur at approximately 2050 in RCP 8.5), the combined effects of coral bleaching and decreased Ω_{arag} will decrease net calcification on reefs to the point that most will shift from net reef-building to net dissolution [Hoegh-Guldberg et al. 2007].

PAR minimum: (strongly correlated with temperature mean, maximum, annual range, and minimum) represents the amount of radiation available to organisms for photosynthesis. As coral polyps house photosynthesizing symbiotic dinoflagellates, PAR is critical for their survival. Minimum PAR levels can be limiting to suitable reef habitat area, particularly at high latitudes where persistently low PAR can limit coral structures to very shallow regions [Kleypas et al. 1999b]. Climate change may affect the distribution and opaqueness of clouds [Marsh & Svensmark 2000], which in turn could affect PAR in reef habitats.

4.3.4 Bioclimatic envelope modeling

Maxent is a maximum entropy niche model that uses environmental variables (also termed “layers”) combined with species presence data to determine the likelihood of suitable habitat for that species at each grid cell within a geographic domain [Phillips et al. 2006; Phillips & Dudik 2008]. Maxent has been successfully used to identify suitable habitats for endangered species (e.g. [Kumar & Stohlgren 2009]), to map potential habitats for cold water coral reefs (e.g. [Tittensor et al. 2009; Davies & Guinotte 2011; Yesson et al. 2012]), and to understand modern environmental limits to shallow-water coral reef development in the tropics [Bridge et al. 2012; Couce et al. 2012]. Couce *et al.* [2012] determined that Maxent performed well in projections of the present-day distribution of shallow-water coral reefs. Their results showed that temperature-related variables were the most important in accurately modeling present-day reef distribution, followed by Ω_{arag}, nutrients, and light [Couce et al. 2012]. Here, climate model projections of a similar suite of variables are used as layers in the Maxent model. These extend the use of Maxent from considering only present-day spatial distributions of coral reefs to exploring how the envelope of suitable coral reef habitat (the “bioclimatic envelope” following the terminology of [Araujo & Peterson 2012]) might change in the future. The data ‘jackknifing’ analysis in Maxent confirmed our PCA-based choice of input variables as the most relevant to predicting the suitability of a habitat for coral reef presence.

Maxent version 3.3.3 (http://www.cs.princeton.edu/~schapire/maxent/) was first trained using the worldwide distribution of coral reefs and the six selected environmental parameters from the CESM1 model output for the time period 1985-2005. The model was trained using 75% of reef locations, selected randomly, and testing of model performance was implemented by predicting the remaining 25% of reef locations. For the first case considering all reefs, 894 locations were used for training and 298 additional locations were used for testing. For the Indian Ocean case, 146 sites were used for training and 48 for testing; for the Pacific Ocean case, 569 sites were used for training and 189 for testing; and for the Caribbean case 135 locations were used for training and 45 additional sites were used for testing. For each of the 72 sets of Maxent runs, the mean AUC score (an indicator of model performance) was greater than 0.8 with the 'Clamping' function enabled.

To project how the spatial distribution of coral reef habitat may change in the future, Maxent was run with the 21st Century CESM1 output for the overlapping 20-year time periods in both RCP scenarios. Projections were first run based on training with the global distribution of coral reefs. Projections were also run based on training restricted to three separate coral reef domains corresponding to the Caribbean/Atlantic, Pacific, and Indian Ocean basins. For these three cases, the Maxent model was trained using a subset of coral reef distribution that only included regions where corals are found within each ocean basin. These basin-specific projections were run to examine how the suitable environmental area in which coral reefs specific to each domain reside would shift geographically both within and outside each domain during the specified climate change scenarios. Predictions outside of the 'home' domain enabled

Maxent to estimate where coral reef habitat, as represented in each basin, would theoretically exist within other ocean basins.

These projections of suitable habitat areas for coral reef growth in the future do not take into account bathymetry. That is, suitable habitat illustrates regions where the phsyico-chemical conditions are adequate for coral reef growth, but in reality reef growth within these habitats will be restricted to water depths of approximately 30 m or less.

4.4 Results

Compared with Maxent's prediction of the 1985-2005 distribution of reefs, projected coral-reef habitat declined with time in both the RCP4.5 and RCP8.5 climate scenarios (Figure 4.2). Percent change in habitat is calculated as the summation of habitat suitability from the RCP scenarios divided by the summation of habitat suitability in the training run. By the year 2100, the area of suitable habitat over the global domain was reduced by 43% in the RCP4.5 scenario, and by 82% in the RCP8.5 scenario (Figure 4.2).

When Maxent was trained separately for each ocean region using the basin-specific physico-chemical preferences associated with the presence of coral reefs, the resulting projections of suitable habitat area for both the Pacific and Caribbean/Atlantic reefs were similar to when the global distribution of reefs was used (Figure 4.2). The envelope of Pacific coral reef habitat was reduced globally by 90% by 2100 in the RCP8.5 scenario, and the global envelope of habitat suitable for

Caribbean/Atlantic coral reefs was reduced by 89%. However, when Maxent was trained with the spatial distribution and physico-chemical data for Indian Ocean reefs, the global envelope of suitable habitat area for Indian Ocean coral reefs increased by 38% in RCP4.5 by 2100 and decreased by only 10% in RCP8.5 by 2100 (Figure 4.2).

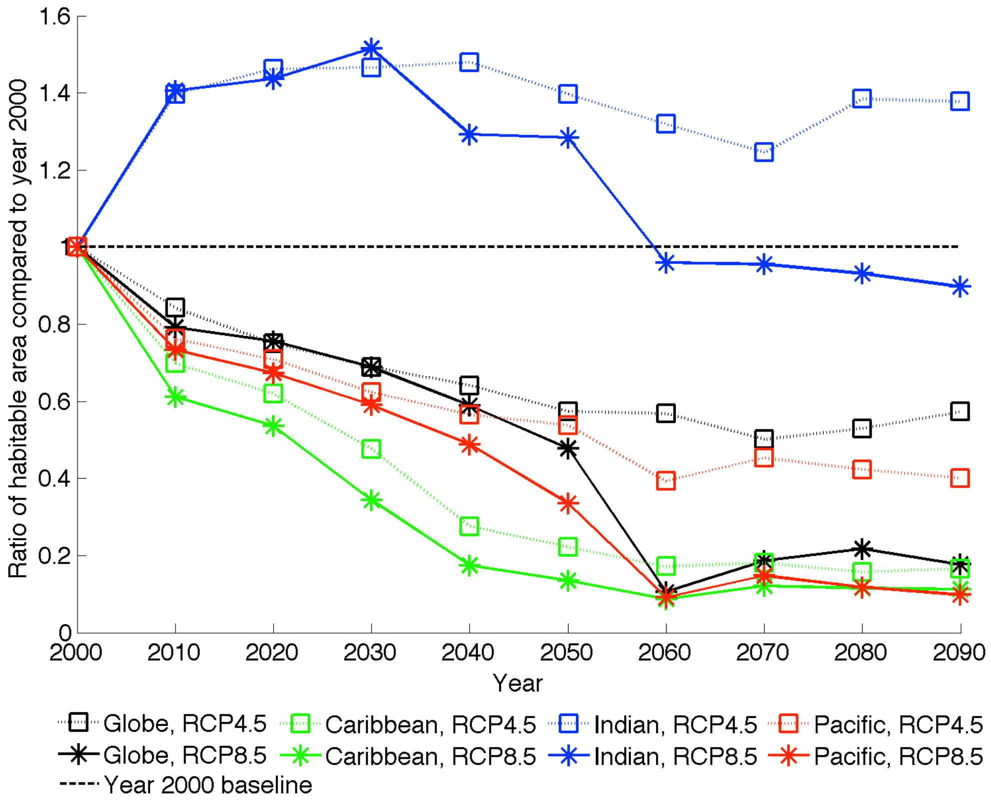


Figure 4.2: A time series showing the estimated change in habitable area over time, as compared to what was available in the 20th century. Average habitat suitability worldwide was calculated from NCAR CESM1 data for the year 2000, then for future climate projections. Global model runs considering all reefs are marked in black, runs considering only Caribbean reefs to train Maxent are marked in green, runs considering only Indian reefs to train Maxent in blue, and runs using only Pacific reefs in red. The less extreme RCP4.5 projection is indicated by squares and dotted lines, while the more extreme RCP8.5 is indicated by stars and solid lines. No change from 20th century habitable area (2000) is represented by the dashed black line.

The global runs, as well as those considering only Indian reefs and only Pacific reefs, all experience a precipitous drop in percent of suitable habitat from 2050 to 2060 in the RCP8.5 scenario only. This is mainly a result of a dramatic change in Ω_{arag} minimum in the climatological variables calculated from CESM1 (20 year averages) from the 2050 mean to 2060 mean. The average for the entire study area is 2.48 in 2050, 1.87 in 2060, and recovers to 2.15 in 2070. Suitable habitat in the Caribbean/Atlantic had already decreased by over 70% in 2050 and does not show the same drop.

Spatial distributions of the relationship between physico-chemical variables and the existence of present-day of coral reefs indicate marked differences in the "habitat space" occupied by reefs from different basins. In addition, model projections suggest markedly different basin-specific shifts in those habitats (Figures 4.3-4.6). Based on the six environmental parameters used here, very little habitable space for Caribbean/Atlantic coral reefs exists today outside of their present geographic domain (Figure 4.4). These models estimate that the possibility of habitat expansion in the case of Caribbean/Atlantic corals is almost eliminated by the middle of this century, even in the RCP4.5 scenario.

Under both climate change scenarios, the region of suitable habitat for Pacific reefs is reduced in a relatively uniform manner across all ocean regions. Apart from the Pacific, some suitable habitat was identified in both the Indian and the Atlantic Oceans but not in the Caribbean (Figure 4.5). Regions of suitable habitat were identified for Indian Ocean reefs in both the Pacific and Atlantic Oceans but not in the

Caribbean (Figure 4.6). Under both climate-change scenarios, the area of suitable habitat for Indian Ocean reefs increases in the Pacific Ocean and to a lesser degree in the Atlantic. Patterns of habitat suitability shown in Figures 4.3-4.6 and the trends shown in Figure 4.2 were persistent through many iterations of Maxent using various model parameters and settings. In addition, results remained stable when the combination of input variables used to train Maxent were changed to assess the sensitivity of the model.

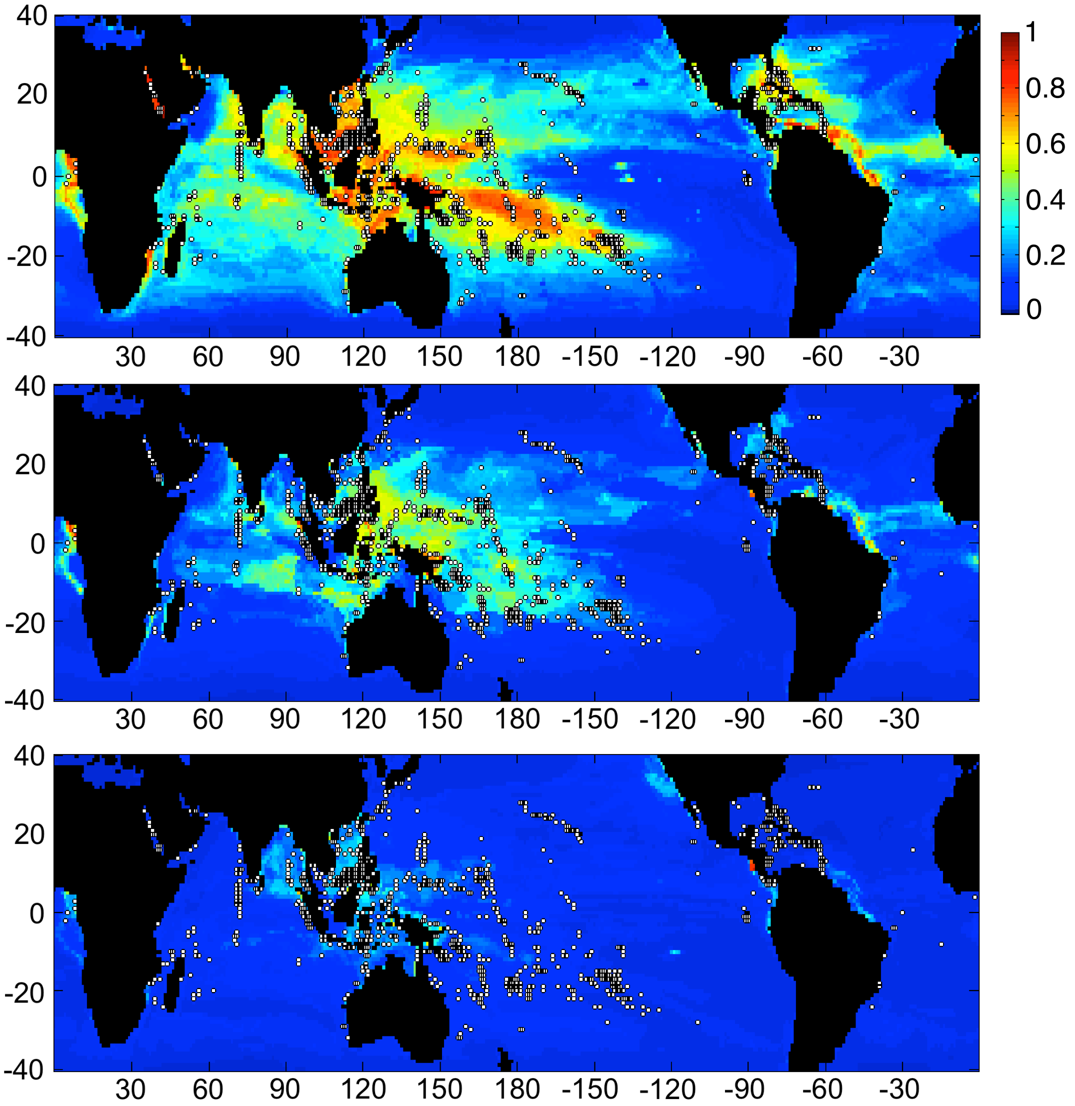


Figure 4.3: Three charts showing habitat suitability estimates when Maxent was trained using the current location of coral reefs worldwide (white dots), and based on CESM1 model output for the RCP8.5 scenario. Color scale indicates the probability that conditions are suitable for reefs: red = high probability, green = average probability (typical conditions for present-day reefs), blue = low probability. Horizontal axes indicates longitude, while vertical axes indicate latitude from 40° north to 40° south. Charts from top to bottom present results from the training run from 2000, estimates for 2050, and estimates from 2100, respectively. The 2100 RCP4.5 projection is similar to the 2050 RCP8.5 projection shown here.

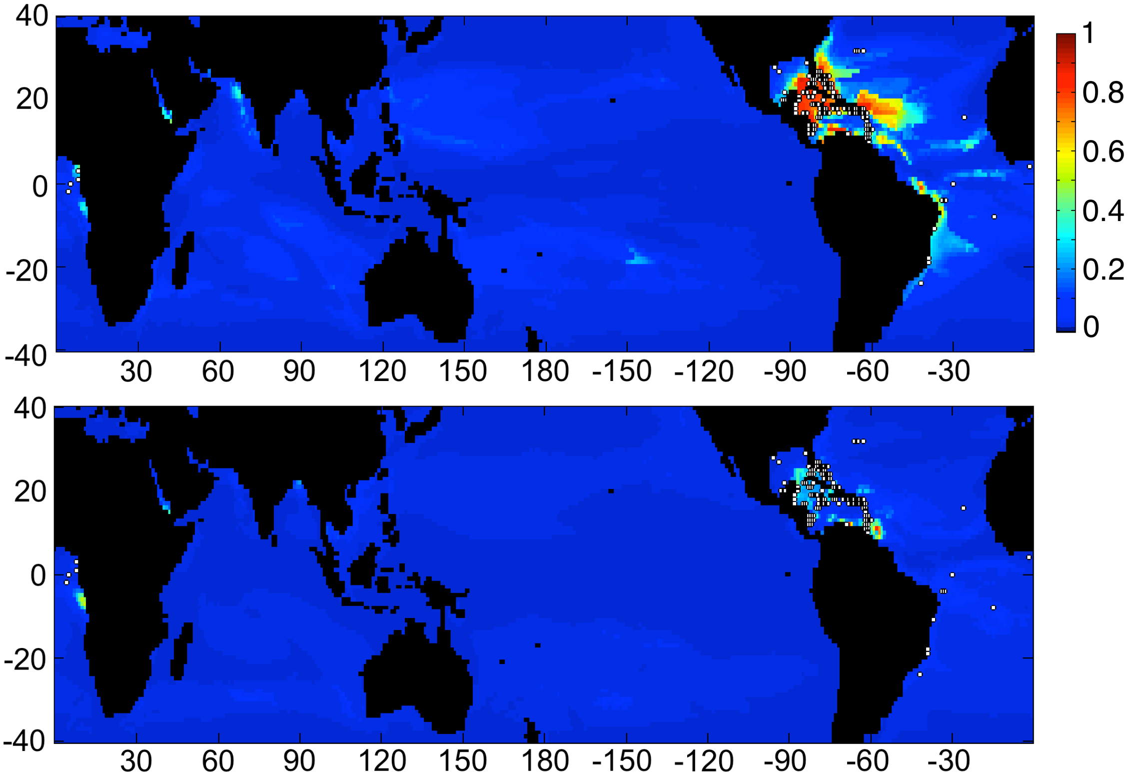


Figure 4.4: Two charts showing habitat suitability estimates when Maxent was trained using the current location of reefs within the Caribbean (white dots), and based on CESM1 model output for the RCP4.5 scenario. Charts from top to bottom present results from training based on current climate CESM1 data from 1985-2005, and estimates for conditions in 2050, respectively. Color scale and axes are identical to Figure 4.3. Note that present habitat suitable for Caribbean/Atlantic reefs is shown globally. These are model results and do not consider the ability of specific corals to migrate between basins, as no coral species are shared between the Caribbean and the Indo-Pacific. Estimates for 2100 conditions, as well as those for RCP8.5 for 2050 and later revealed almost no suitable habitat for Caribbean reefs anywhere on earth.

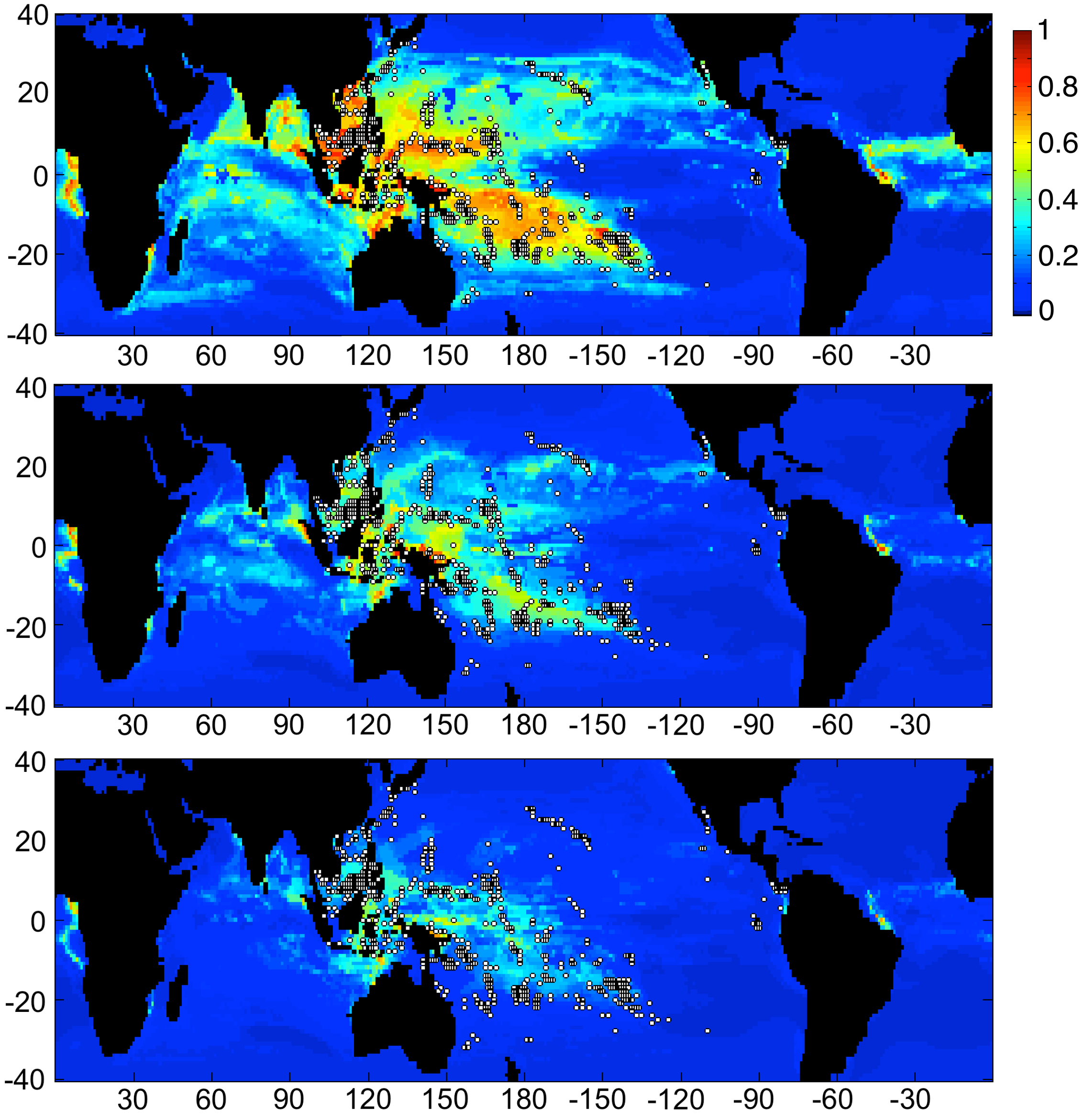


Figure 4.5: Three charts showing habitat suitability estimates when Maxent was trained using the current locations of Pacific Ocean coral reefs (white dots), and based on CESM1 model output for 2050. Color scale and axes are identical to Figure 4.3. Charts from top to bottom present results from training based on current climate CESM1 data from 1985-2005, 2050 conditions in RCP4.5, and 2050 conditions in RCP8.5, respectively. 2100 conditions in RCP4.5 are very similar to 2050 conditions for RCP8.5.

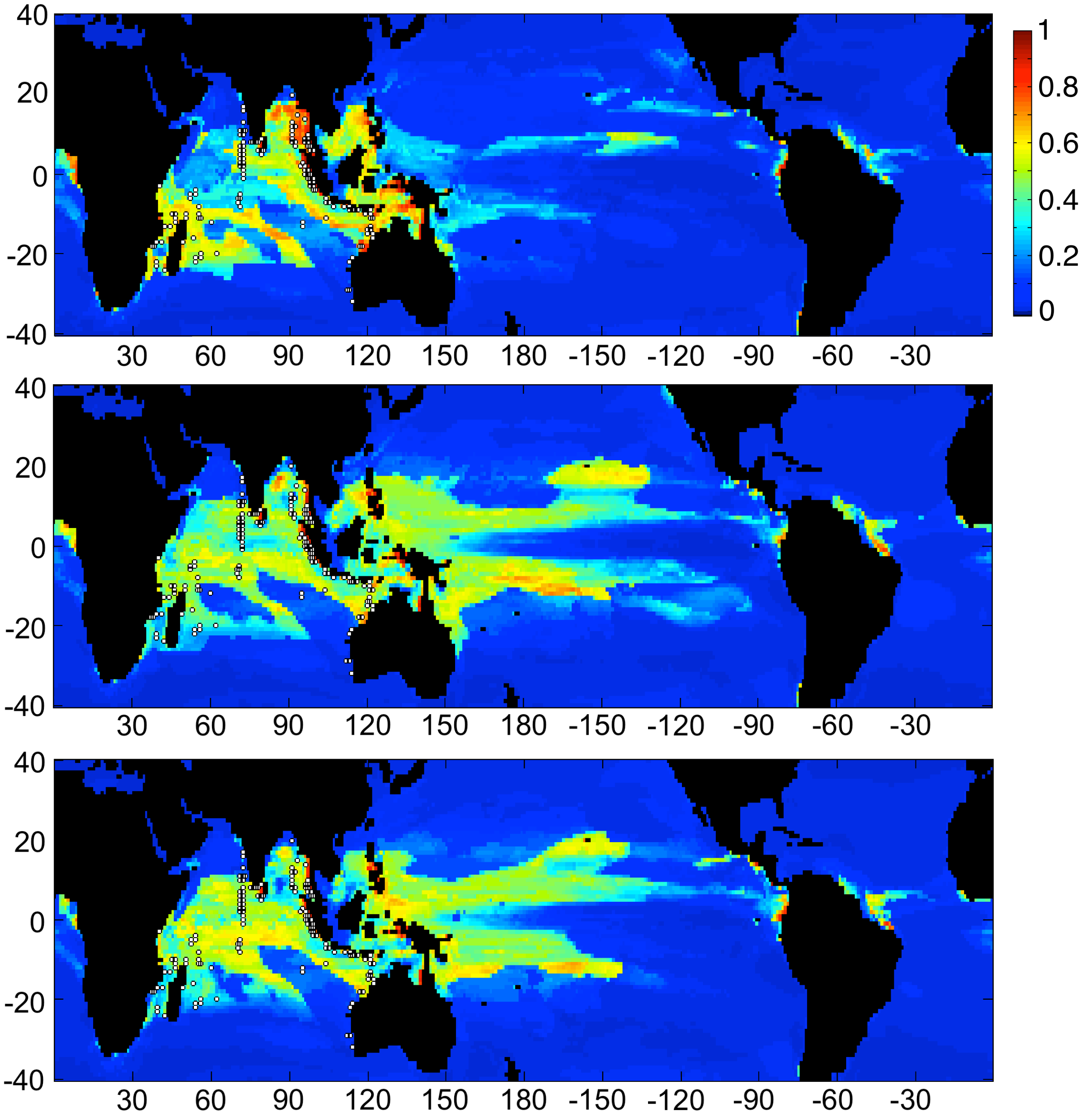


Figure 4.6: Three charts showing habitat suitability estimates when Maxent was trained using the current locations of Indian Ocean coral reefs (white dots), and based on CESM1 model output for 2050. Color scale and axes are identical to Figure 4.3. Charts from top to bottom present results from training based on current climate CESM1 data from 1985-2005, 2050 conditions in RCP4.5, and 2050 conditions in RCP8.5, respectively.

Under both climate change scenarios, the region of suitable habitat for Pacific reefs is reduced in a relatively uniform manner across all ocean regions. Apart from the Pacific, some suitable habitat was identified in both the Indian and the Atlantic Oceans but not in the Caribbean (Figure 4.5). Regions of suitable habitat were identified for Indian Ocean reefs in both the Pacific and Atlantic Oceans but not in the Caribbean (Figure 4.6). Under both climate-change scenarios, the area of suitable habitat for Indian Ocean reefs increases in the Pacific Ocean and to a lesser degree in the Atlantic. Patterns of habitat suitability shown in Figures 4.3-4.6 and the trends shown in Figure 4.2 were persistent through many iterations of Maxent using various model parameters and settings. In addition, results remained stable when the combination of input variables used to train Maxent were changed to assess the sensitivity of the model.

4.5 Discussion

These bioclimate modeling results indicate that climate change and ocean acidification will impact the distribution of suitable coral reef habitat in the future, for both the RCP4.5 and the RCP8.5 scenarios. Globally the envelope of oceanographic conditions favorable to coral reef development will decrease by 43% and 82% by the year 2100 for the RCP4.5 and RCP8.5 scenarios, respectively. The decreases in actual reef habitat will further depend, in part, on the existence of shallow substrate within the envelope.

The global runs also identify where potential new coral habitats may emerge in the future. For example, rising sea surface temperatures are expected to shift the suitable habitat envelope poleward in both hemispheres, and some coral species have indeed begun to colonize at higher latitudes [Precht & Aronson 2004; Yamano et al. 2011]. The results presented here, however, do not suggest a significant shift of coral reef habitat into new regions (Figure 4.3), indicating that other variables limit this expansion. Rather, the bioclimatic envelope suitable for coral reefs is predicted here to decline in all regions indicating that other variables may limit this expansion. Light availability (PAR) and Ω_{arag} have both been shown to limit coral reef development at high latitudes [Kleypas et al. 1999b; Guinotte et al. 2003] and declining Ω_{arag} has been associated with a decreased ability of coral communities to construct coral reefs [Guinotte et al. 2003; Silverman et al. 2007]. One previous study found Ω_{arag} to shift habitat to 'marginal' by the mid- to late-21st century, but those results also indicate that regions of habitat within the margins of present-day coral reef habitation persist for at least the next 100 years [Guinotte et al. 2003].

The bioclimatic envelopes amenable to coral reef growth are defined slightly differently for each ocean basin. The changes in the projected envelopes of suitable habitat for Pacific Ocean reefs are similar to those for the global projections, while those for Indian Ocean reefs are maintained across many regions, in spite of the significant changes in modeled ocean conditions throughout the 21st century. The projected envelopes of suitable habitat for Caribbean/Atlantic reefs, however, nearly disappear under both climate change scenarios. This striking difference for

Caribbean/Atlantic reefs remained robust across multiple iterations using Maxent, and persisted even when removing each of the six variables individually from training. Thus the susceptibility of Caribbean/Atlantic reefs to future conditions does not appear to be an artifact of a single variable skewing the results. The modeled vulnerability of reefs in this region may simply reflect the smaller number of reef locations in the Caribbean/Atlantic used to train Maxent, which may narrow the range of environmental conditions presently experienced by reefs across the domain. The difference may also be due to the unique physico-chemical environment of the Caribbean. Regardless of the cause, these projections suggest very different fates for coral reefs that presently exist in the three major ocean basins.

In both the global and basin-scale projections, certain regions stand out for their retention of suitable reef habitat under future climate scenarios through the year 2050 and beyond. These include mostly equatorial regions in the northern Indian Ocean, the Coral Triangle region, French Polynesia, and the northeast Brazilian shelf east of the Amazon River. These regions are where the CESM1 projections estimate suitable temperatures, Ω_{arag}, light, nutrients and current speeds. Among these variables, projected temperature and Ω_{arag} change markedly in the future, so that Maxent's projection of future reef habitat strongly reflects the net effect of 1) a poleward shift of suitable habitat due to increasing temperature, and 2) a shift of suitable habitat toward the equator due to decreasing Ω_{arag}.

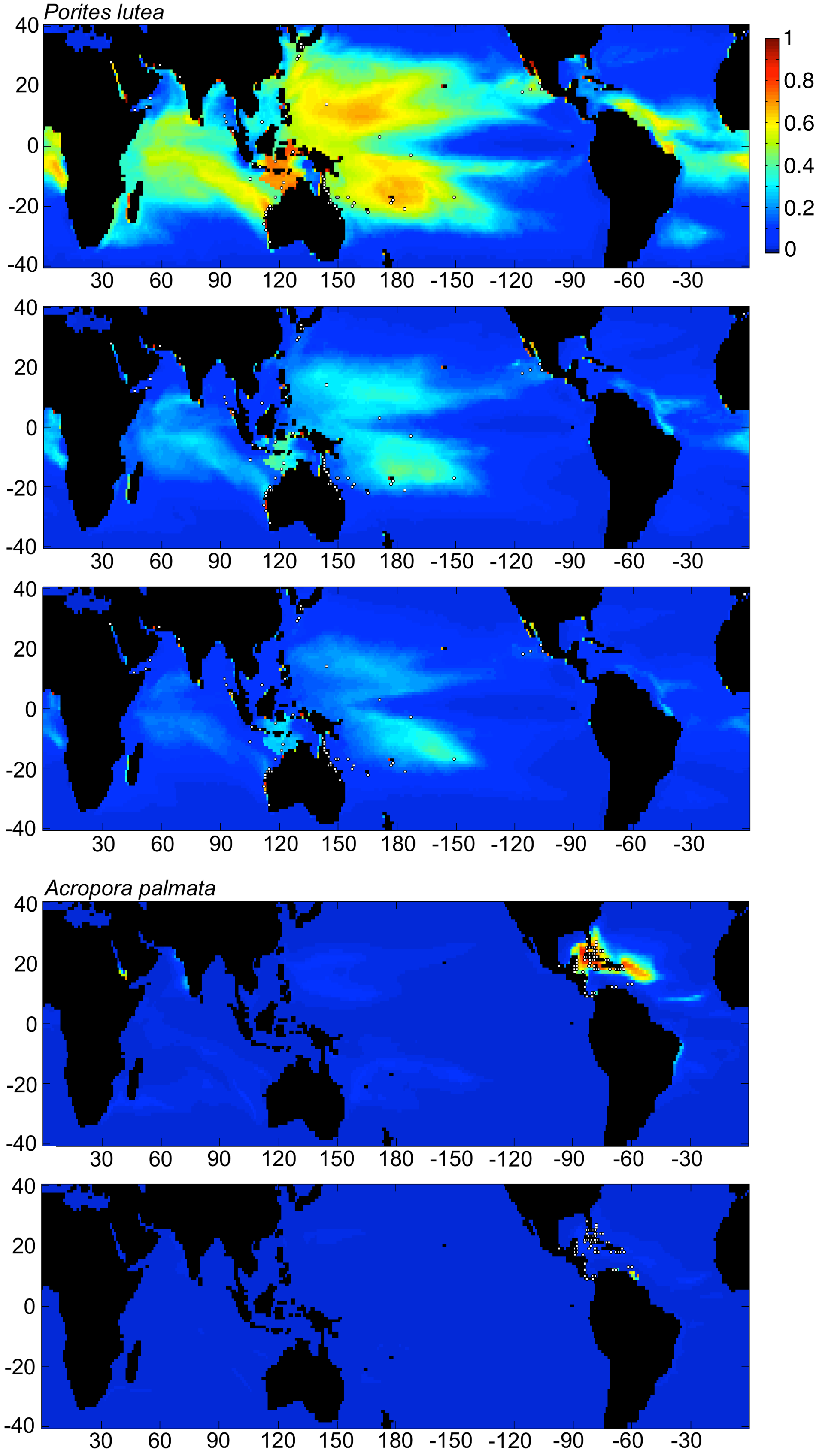
Our work is in line with previous predictions of coral reef decline in the 21st century. One previous study argues that coral reefs will face serious decline unless atmospheric CO_2 is limited to 350 ppm [Veron et al. 2009b]. Another study based solely on sea surface temperatures in global climate models indicated that approximately two-thirds of coral reefs worldwide faced degradation by the end of the 21st century under the RCP4.5 scenario [Frieler et al. 2012]. Our results which consider temperature as well as salinity, nutrient levels, current speeds, light availability, and Ω_{arag} similarly predict a loss of at least 43% of habitable area worldwide under the RCP4.5 scenario.

The results also indicate which basins presently include reef habitats that are “best conditioned” to spread to new regions. Present-day coral reefs in the Indian Ocean basin experience conditions that are most similar to future climate projections in the Indian as well as the Pacific and Atlantic Oceans (Figure 4.6). Another previous study found that Arabian and Persian Gulf reefs are amongst the most heat-adapted in the world, and argue for assisted migration of these corals to the Indo-Pacific [Riegl et al. 2011]. The shifting of suitable habitat space for a number of species has led some to consider species translocations or “managed relocations” - by introducing these species into new regions with suitable conditions - in order to conserve them [Richardson et al. 2009; Schwartz et al. 2012; Hellmann 2013]. A more synoptic motive for translocation, and much less studied, is to introduce a substitute for a foundation species, such as a dominant reef-building coral, with the goal of restoring or maintaining ecosystem function [Kreyling 2011; Schwartz et al. 2012]. The topic is justly controversial [Ricciardi & Simberloff 2009] but managed relocations and introductions may become more acceptable in cases where climate change severely limits more traditional conservation strategies [Hellmann 2013]. Should a major reef-building species decline due to factors associated with climate change, it may be advantageous to introduce an alternate reef-building species that is more suited to the new environment to maintain reef functionality. What would be the impact, for example, of introducing a species of reef-building coral endemic to the Indian Ocean to Caribbean reefs that have already seen the decline of several major reef building species [Sinclair et al. 2010], and which appear to be particularly vulnerable to climate related physico-chemical changes?

Answering the question above would require considerable further research, including a more comprehensive niche-based approach that addresses individual species and their biotic as well physical-chemical environments. Maxent and other niche distribution software packages are typically used for species distributions, although Maxent has been used in the larger sense for coral-reef ecosystem distributions [Bridge et al. 2012; Couce et al. 2012], as has been done here. The ‘niche’ used in this study is the bioclimatic envelope that spatially correlates with net reef growth, rather than individual species. As a result, this envelope includes a composite of all niches that include reef-building species of coral. Under the effects of climate change, the spatial distribution of each coral species will shift individually in response to changes in their individual environmental niches. These shifts may be geographically different when compared with the composite of all reef-building species. However, some of the major reef-building coral species are widespread within their ocean basins, such as *Porites lutea* in the Pacific and *Acropora palmata* in the

Caribbean/Atlantic. The responses of these two species alone were tested using Maxent, and the results were similar to the composite reef results. The main difference in both tests was a more constricted range, presumably as a result of the smaller number of locations used for model training, resulting in a more restricted suitable habitat envelope. While projections of suitable habitat area for *A. palmata* showed that suitable regions essentially disappeared in the future, there is some indication that hypothetically suitable habitat for *P. lutea* could persist in some portions of the Caribbean/Atlantic in addition to the Pacific and Indian basins through most of this century (Figure 4.7).

Figure 4.7: Two sets of charts showing habitat suitability estimates when Maxent was trained with the current locations of two coral species, *Porites lutea* (top) and *Acropora palmata* (bottom). Color scale and axes are identical to Figure 4.3. The charts for *Porites lutea* are based on CESM1 model climatology for the years 2000, 2050, and 2090 from RCP4.5. The charts for *Acropora palmata* are based on CESM1 model climatology for the years 2000 and 2050 only from RCP4.5.


Porites lutea
Acropora palmata
40
20
0
-20
-40
30
60
90
120
150
180
-150
-120
-90
-60
-30
1
0.8
0.6
0.4
0.2
0

These results should be viewed with some caution because recent reviews have questioned the validity of using SDMs to project changes in habitats across time [Sinclair et al. 2010; Dobrowski et al. 2011]. In addition, the results presented here are based on the projections of a single earth system model. However, these projections are at least qualitatively useful in demonstrating the nature of the shifts in bioclimatic envelopes for coral reef ecosystems.

The results describe how the spatial distribution of certain oceanographic environments strongly associated with reef development could shift while others experience less change. Continued investigation using a greater number of ensemble members and additional coupled climate models (as their results become available) are required to create models that are statistically more robust. Furthermore, these results do not consider the current ecological state of any coral-reef ecosystems, direct anthropogenic stressors such as pollution or fishing, the influence of invasive species, or molecular and ecological resilience of particular corals or coral-reef communities.

In summary, this study suggests that the response of shallow tropical coral reefs to increased CO_2 forcing is neither linear nor strictly latitudinal when considering a suite of representative variables known to influence coral ecology. Coral-reef ecosystems in different regions may respond in unique ways to the same forcing, and results suggest particular regions can be more suitable or less – an effect that remains consistent despite perturbations to model parameters. When individual basins are considered, conditions in which shallow-water coral-reef ecosystems presently exist in the Indian Ocean are shown to be most similar to future projections of global, tropical, physico-chemical ocean conditions. Coral reefs in this region may be most suited for persistence worldwide in future climate states.

4.6 Acknowledgment

Chapter 4, in full, is a reprint of the material as it has been submitted to PLoS-ONE 2013. Freeman LA, Kleypas JA, Miller AJ: Coral Reef Habitat Response to Climate Change Scenarios. The dissertation author was the primary investigator and author of this paper.

4.7 Appendix

Groups of Variables from PCAs with selected variable in bold

PAR range
CTS

Phos range
Phos max
Phos mean
Phos min
Ω_{arag} range

CVM max
CVM min
CVM mean
CVM range
Salinity range
PAR max

Salinity min
Salinity max
Salinity mean

Ω_{arag} min
Ω_{arag} mean
Ω_{arag} max
PAR mean

PAR min
Temp mean
Temp min
Temp max
Temp range

Correlation Matrix of Selected Variables (ρ correlation)

	CTS	**CVM maximum**	**Ω_{arag} minimum**	**Salinity minimum**	**PAR minimum**	**PO4 maximum**
CTS	1	-0.42	-0.49	0.26	-0.45	0.16
CVM maximum	-0.42	1	0.32	-0.32	0.35	0.13
Ω_{arag} minimum	-0.49	0.32	1	0.27	0.30	-0.38
Salinity minimum	0.26	-0.32	0.27	1	-0.04	-0.07
PAR min	-0.45	0.35	0.30	-0.04	1	-0.12
PO4 maximum	0.16	0.13	-0.38	-0.07	-0.12	1

CHAPTER 5

Case Study II
A Framework for Testing Regional Oceanographic Changes in French Polynesia

5.1 Abstract

A regional ocean model is developed to assess regional oceanographic changes within larger model frameworks (i.e. AOGCMs). The model is implemented for a domain including the islands of Mo'orea and Tahiti in French Polynesia. Initial results show regular eddy shedding to the south and southwest off of both islands, periodically creating a potential pathway from Tahiti to Mo'orea. Eddies are never shed to the north or east, and there is no possible oceanographic connection from Mo'orea to Tahiti. Furthermore, a persistent wake with cool, upwelled water is present to the southwest of both islands.

5.2 Introduction

The large-scale effects of physical environment on coral reef ecosystem existence and state has been thoroughly discussed in Chapters 2-4. However, the impacts of changes in the regional physical oceanographic environment around coral reefs are much less studied. Given that coral reefs actually live in a wide range of oceanographic environments [Freeman et al. 2012], more subtle effects of the physical circulation may be profoundly important in the controlling the distribution and habitat quality of coral reefs on a regional scale. For example, the patterns of ocean circulation around islands contribute to vertical and lateral nutrient fluxes that drive primary production near reefs [Pedlosky et al. 1997; Leichter et al. 1996; Leichter et al. 2003] . Furthermore, mean and eddying currents affect the way coral larvae are dispersed during mass spawning events [Harrison et al. 1984].

5.2.1 Mo'orea Long Term Ecological Response Site

The coral reef ecosystem of the island of Mo'orea, French Polynesia has been the subject of intensive study as part of the Mo'orea Coral Reef Long Term Ecological Research project (MCR-LTER), a component of NSF's Long-Term Ecological Research Program. Mo'orea is roughly 10 km west of larger Tahiti in French Polynesia in the tropical South Pacific. Mo'orea is a steep sided volcanic island, triangularly shaped, and approximately 60 km in circumference. Its fringing reef extends roughly 500 m off the coast and supports coral communities from the surface to at least 60 m depth. This island pair sits in the westward flowing limb of the South Pacific Subtropical Gyre in the South Equatorial Current. A major research effort of the MCR and other coral reef ecological studies has resulted in extensive observations of the biological populations affecting this coral reef ecosystem [Berumen & Pratchett 2006; Trapon et al. 2011]. As part of the MCR and related field studies, an extensive oceanographic effort has resulted in the collection of multi-year time series of a wide range of physical oceanographic observations around Mo'orea, including sampling the flow patterns from the reef crest to roughly 15m depth. Local-scale physical forcing, such as cross-reef transport driven by surface waves, has been shown to influence biological processes. Hench et al. [2008] quantified the effects of the surface gravity waves on lagoon circulation on the north shore of Mo’orea. The resulting flow in the lagoons modulates a number of ecological processes, including coral recruitment [Edmunds et al. 2010] and fish settlement behavior. The largest waves are typically forced by winter North Pacific storms during austral summer, so this is a good example of how a remote forcing of a physical oceanographic process can control important ecological processes in coral reef ecosystems.

These MCR observations also point to the effects of large-scale physical oceanographic and atmospheric processes, such as mesoscale eddies and storms, on the coral reef ecosystems of the island. But a limitation of the in situ oceanographic observations around Mo’orea to date is that they are collected near the island. This is due to the remoteness of the island, which limits participation of large research vessels, and the very great water depths near the island, which limits deployment of moored instrumentation. These factors have constrained the ability to connect important nearshore physical and ecological processes to regional and basin-scale oceanographic processes. Here, a numerical modeling approach is presented to make these links and to provide insights into which large-scale transport processes are most important in controlling the physical environment around the island.

5.2.2 Importance of a Regional Case Study

Islands like Mo’orea are generally ignored in global climate models (GCMs) because of their small size and insufficient model resolution. However, they influence upwelling, mesoscale eddy transports, and other local oceanographic conditions that are important to coral reef ecosystems. High-resolution ocean models that better simulate these small scale processes, combined with locally observed physical oceanographic data, broad-scale remotely sensed data, and locally observed ecological variables, will provide a more detailed understanding of the physical-biological interactions involved in reef ecosystems. Our model can give first insights to larval connectivity and nutrient patterns between Mo'orea, Tahiti, and more distant island groups upstream and downstream. This approach can also be combined with IPCC GCM forecast models and used to improve our ability to anticipate the future state of the coral reef ecosystem.

5.2.3 The Regional Ocean Model (ROMS)

The ocean model is the Regional Ocean Modeling System (ROMS), a state-of-the-art, free-surface, hydrostatic primitive equation ocean circulation model developed at UCLA and Rutgers University. ROMS is a terrain-following, finite difference (Arakawa C-grid) model with the following advanced features: extensive restructuring for sustained performance on parallel-computing platforms (MPI); high-order, weakly dissipative algorithms for tracer advection; a unified treatment of surface and bottom boundary layers, based on the [Large et al. 1994] and Styles and Glenn (bottom boundary layer) algorithms; and an integrated set of procedures for data assimilation (e.g., optimal interpolation and adjoint-based methods). Numerical details can be found in [Haidvogel et al. 2000; Moore et al. 2004; Shchepetkin and McWilliams 2005; Haidvogel et al. 2008].

5.3 Methods

A 20-year climatological run of the ROMS model in a 2,000 km^2 domain including the islands of Tahiti and Mo'orea was conducted. Model resolution was 3 km, and model time step was five minutes. Outputs were stored every six hours. The first two years were considered spin-up time and not included in analysis. The region including the islands of Tahiti and Mo'orea has steep changes in topography, and much of the topographic structure near the coast is poorly measured. A smoothed version of ETOPO2 was constructed with adequate horizontal resolution to reduce pressure gradient errors to acceptably small levels. The model was run with 42 vertical levels. The lateral boundary conditions (BC) for this ROMS run are monthly-mean forcing determined from the NCEP reanalysis products. Winds and fresh-water fluxes are specified. Heat fluxes are computed by using a bulk formulation where ocean model SST is included with observed air temperatures, humidity, wind speed and short wave radiation.

5.4 Results

Preliminary analysis showed consistent eddy shedding to south and west off of both islands. Eddies were never observed to the north or east. This is summarized from the mean sea surface height anomaly (zeta) (Figure 5.1), calculated from root mean square. The regions of large sea surface height anomaly are the regions with the most eddy activity, found to the south-southwest of each island, with larger eddies pinching off of Tahiti than Mo'orea. Although the main pathway does not travel from

Tahiti to Mo'orea (Figure 5.1), eddies create a periodic pathway from Tahiti to Mo'orea that could potentially transport larvae, nutrients, or cool water. Examining sea surface temperatures from the model shows that there is a minimal seasonal cycle (Figure 5.2). A southwest-facing wake is present from both islands year-round (Figure 5.2).

This model is run at 3km resolution from 100 km resolution forcing. This downscaling (from NCEP) causes several edge effects, which were not entirely absorbed by the implemented sponge layer. A static eddy formed and remained in the northwest corner of the domain, part of which is visible in Figure 5.1. This is a model edge effect, not a realistic representation of the circulation in this region.

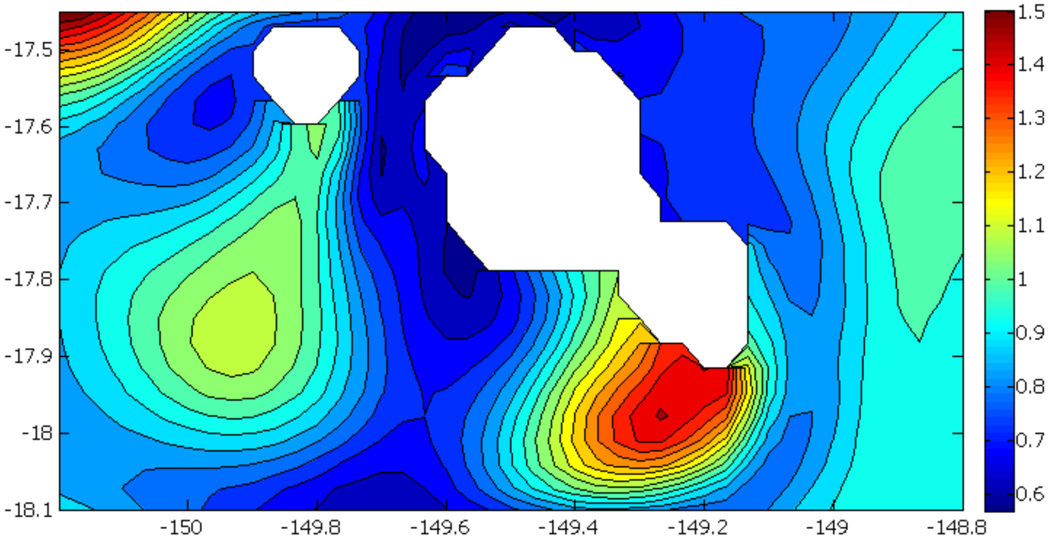
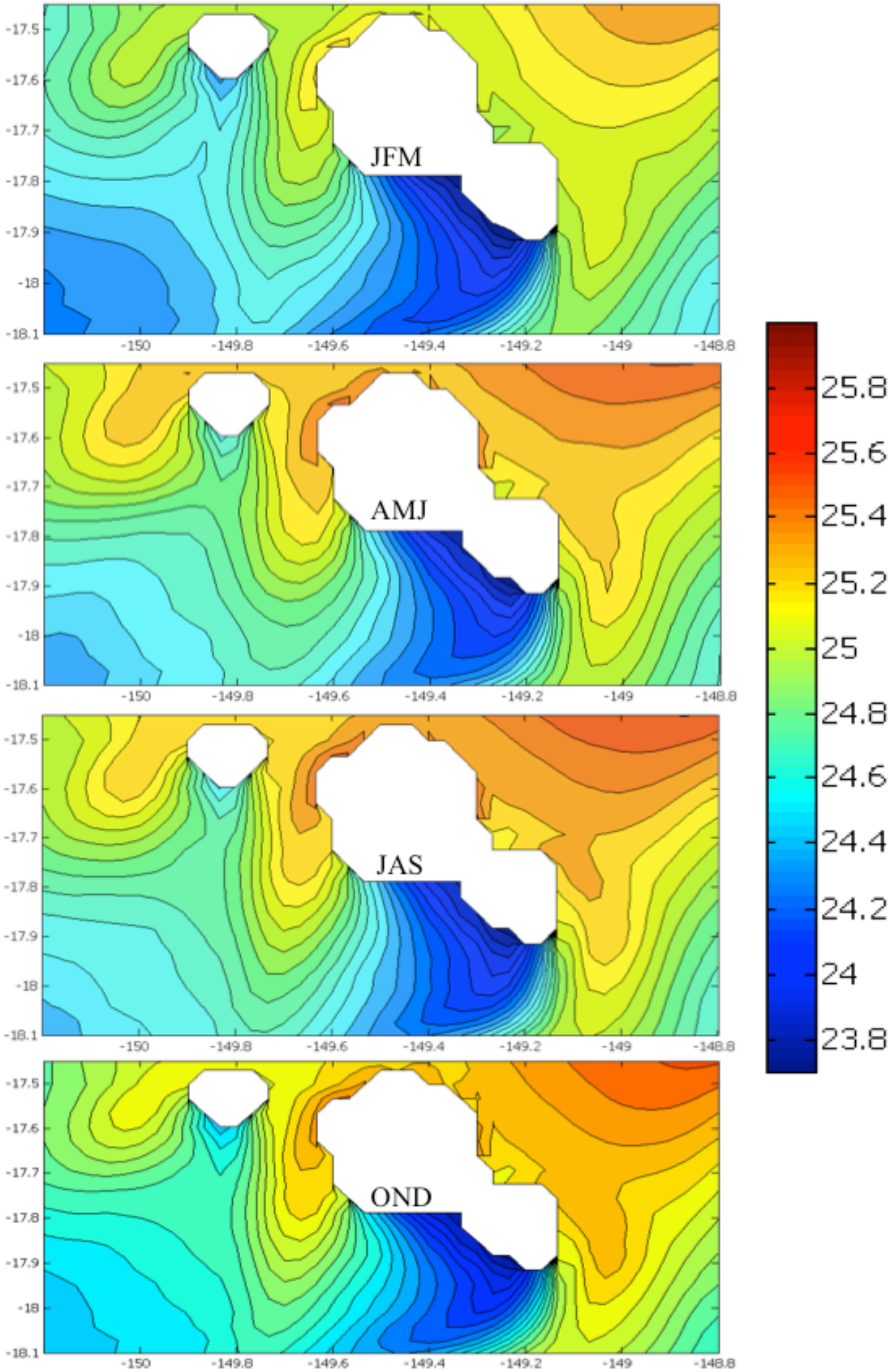


Figure 5.1: Average root-mean-square of sea surface height anomaly (zeta) over the central model domain. Warmer colors indicate regions of high eddy activity. Each island clearly produces an eddy field to the south-southwest.

Figure 5.2: Average sea surface temperature by season over the central model domain. From top to bottom: January-February-March; April-May-June; July-August-September; October-November-December. Cool temperatures indicate upwelling to the southwest of both islands, consistent year round.


JFM
AMJ
JAS
OND
-17.5
-17.6
-17.7
-17.8
-17.9
-18
-18.1
-150
-149.8
-149.6
-149.4
-149.2
-149
-148.8
25.8
25.6
25.4
25.2
25
24.8
24.6
24.4
24.2
24
23.8

5.5 Future Work

To address how the circulation around Mo'orea will change under IPCC projected global warming scenarios, I will run the same ROMS model with atmospheric forcing derived from future climate states for both emissions scenarios considered in Chapter 4 from CESM1. It is likely that higher upper-ocean temperatures will occur under these conditions, and changes in ocean circulation may also occur. Circulation changes could exacerbate or ameliorate the thermal effects. They could also change local productivity due to nutrient flux changes and alter patterns of coral larval transport, affecting population distributions. These impacts need to be considered within the context of other effects of greenhouse-gas induced global warming, including decreasing ocean pH from increased CO_2 concentration (acidification), direct effects of ocean warming [Hoegh-Guldberg et al. 2007; Doney et al. 2009] and increasing wave heights due to changing wind patterns [Bromirski et al. 2005]. Addressing these climate change issues will give us a better perspective of how to manage and protect coral environments, not just locally at Mo'orea but at other tropical islands as well.

CHAPTER 6

Concluding Remarks

The work described in this dissertation addresses the impact of climate change on the physico-chemical environment of coral reefs. First, we sought to understand the variability and classification of reef habitat, and then determined the specific effects of climate change on those physical and chemical variables that define coral reef habitat. Finally, two case studies were considered. The first case study in the Hawaiian Islands compares aspects of coral reef ecology in two distinct oceanographic regimes and also tests the impact of marine reserves on reef ecology. The second case study in French Polynesia seeks to better understand the oceanographic variability around individual islands with a regional ocean model.

We showed that the warm, tropical oceans that corals inhabit can be divided into distinct oceanographic regimes based on physical and chemical variables. The results of Chapters 2 and 3 strongly indicate that this classification is further reflected in certain measures of coral reef ecology including percent coral cover (2), fish abundance (3), benthic invertebrate abundance (3) and abundance of oceanic predators (sharks) (3). Multivariate analyses of several ecological metrics showed clear partitioning of the two ocean habitats considered in Case Study I in the Hawaiian Islands (3).

Connectivity is often assumed to be a critical factor in coral reef recovery from disturbance, as is investigated in Chapter 5 for the islands of Tahiti and Mo'orea. Connectivity allows coral larvae from an undisturbed reef to re-colonize a region where a significant coral mortality has occurred. A long-term study documented the recovery of the Scott reef system in Western Australia after the 1998 bleaching event [Gilmour et al. 2013]. This reef is extremely isolated, located over 250 km from other coral reefs, and experienced little recruitment for six years following the bleaching. However, by ten years post-bleaching, coral cover and recruitment levels had reached pre-bleaching levels. This remarkable recovery is attributed at least in part to a healthy herbivore population that prevented algae from out-competing coral for space.

The resilience of coral reefs in the Caribbean is extremely low compared to coral reefs in the Indo-Pacific. The Caribbean is unique in several regards, including faster macroalgae growth, lower species diversity, loss of major herbivores, and loss of acroporid/fast growing corals [Roff & Mumby 2012]. This previous study suggests that for Indo-Pacific reefs to experience the type of phase shifts seen on Caribbean reefs, significant degradation would first have to occur. In addition, the two oceans are very different in their physical oceanography, variability on ecological time scales, and their productivity. The differences in oceanography and ecology between the Indo-Pacific and Caribbean are well documented and have been for some time [Roff & Mumby 2012]. Recently, further differentiation has been documented within each of these basins based on physico-chemical environment in the Pacific Ocean [Freeman et al. 2012] and the Caribbean Sea [Chollett et al. 2012].

It is virtually impossible to disentangle the effects of all of the stressors shown in Table 1.1 on coral reef ecosystem state and community structure. Human impacts have influenced reefs for hundreds of years. Reefs that are more severely impacted by humans are more susceptible to climate change [Pandolfi et al. 2012]. It is not intended for the work presented here to account for all of the stressors that effect coral reefs, but rather to better explain the range of physico-chemical environments that coral reefs occupy in present climate conditions and provide estimates of how those environments change in future climate conditions. Given that not all coral reefs can be managed as full marine protected areas, this information provides further insight toward guiding the selection of protected areas and management efforts to minimize the contribution of climate change to reef stress as much as possible.

Projections of total reef loss by the end of the 21st century due to ocean acidification are likely extreme scenarios. Corals have been shown to calcify at much lower aragonite saturation states than the present ocean, in particular healthy corals that are not stressed or food-limited [Pandolfi et al. 2012]. Local management of fisheries and pollution may be able to delay net erosion from ocean acidification by at least 10 years [Kennedy et al. 2013]. Marine reserves are almost certainly critical for the conservation of species and ecosystems. However, we found that the effects of physical environment may be a stronger indication of many measures of coral reef ecology. This is an important consideration when planning future marine reserves and managing existing reserves and parks. A reserve in a favorable physical environment may be far more productive than a reserve in a convenient location.

Another way to look at the results presented in this dissertation is to consider it a call for a blanket null hypothesis in comparative coral reef studies: all of the variation between different reefs considered can be explained by differences in physico-chemical environmental variables. This is a critical first-step consideration that is often overlooked in comparative ecological studies. While it is unlikely for all ecological variation to be explained by the physico-chemical environment, there will almost certainly be underlying structure imparted to the ecosystem by oceanographic habitat. First assessing these differences will result in stronger ecological comparisons, and effective means of scaling ecological variables.

In planning future management, however, one must consider climate change impacts. The effects of climate change on the physical and chemical environment that coral reefs inhabit was modeled, and certain areas are predicted to experience less change by the end of the 21st century. These regions are identified in Figure 6.1 as conservation priorities. Furthermore, certain regions experience conditions today that are very similar to those modeled worldwide in the late 21st century. These regions are identified in Figure 6.2 as ideal locations from which to choose genetic strains of coral for assisted migrations to other regions of the world.

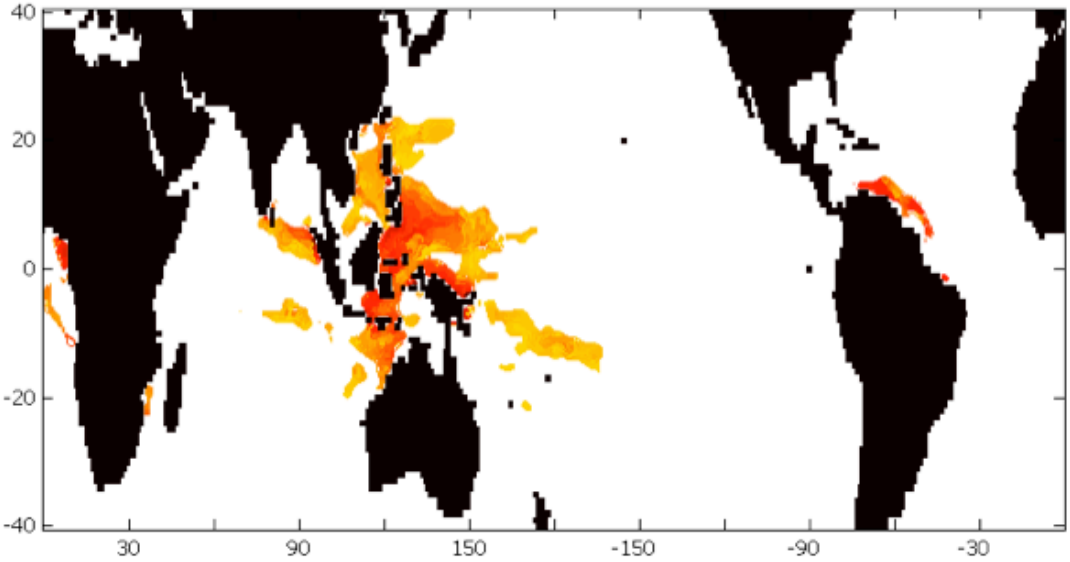


Figure 6.1: Regions that experience more suitable physico-chemical habitat in 2100. Suitability calculated from a suite of Maxent model runs, trained with all reefs worldwide, forced by 20-year climatological variables from 2080-2100 in both RCP4.5 and RCP8.5.

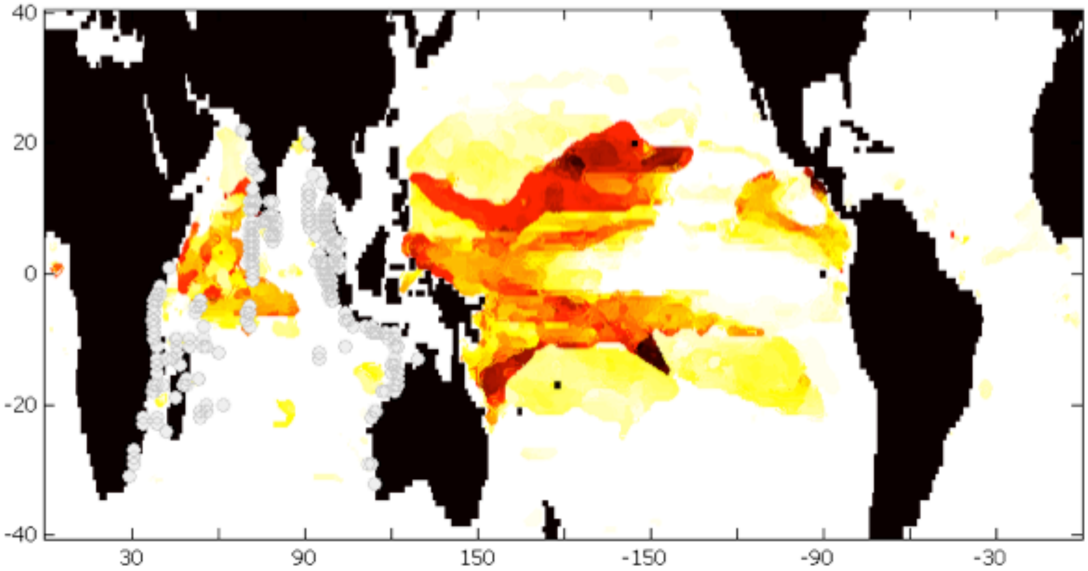


Figure 6.2: Locations of reefs (gray circles) used to train the Maxent model when an increase in habitat suitability was found worldwide (color scale; all colored regions showed an increase in habitat suitability by 2100, darker colors are more suitable) in 2100. Differences calculated from a suite of Maxent model runs, trained with only Indian Ocean reefs, forced by 20-year climatological variables from 1985-2005 and 2080-2100 in RCP4.5.

Thus there are three critical considerations discussed in this dissertation to consider in planning management of coral reef ecosystems.

1- The present physico-chemical habitat and types of reefs that are characteristic of that habitat;
2- The expected shifts of physical and chemical variables critical to corals in the particular region of interest under climate change conditions, and
3- The ability for transplanted coral species to survive in the predicted conditions a given area will experience in the late 21st century.

In addition to these considerations of the physico-chemical environment, managers should of course further consider the stressors that are not contained in these models (Table 1.1) on a case-by-case basis.

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