FACTORS INFLUENCING BENTHIC DISTRIBUTIONAL PATTERNS IN A

NEAR-PRISTINE CORAL REEF ECOSYSTEM: PEARL AND HERMES ATOLL

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ABSTRACT

Many factors, both biotic and abiotic, act to structure coral reef communities. I examined potential determinants of coral reef community structure in a near-pristine system, Pearl and Hermes Atoll (PHA). I measured percent cover of benthic organisms along with herbivorous fish density and biomass, urchin density, nutrient availability, and wave exposure at PHA.. It was determined that wave exposure and herbivory (fish and urchins) largely explain distributional patterns observed in benthic communities. For instance, when all benthic functional groups were combined in a multivariate analysis, herbivorous fish density combined with wave exposure was identified as having the highest significant correlation with benthic community composition at PHA.. Nutrient availability, based on algal tissue nutrient content, however, did not correlate with percent cover of benthic organisms. My results suggest that wave exposure along with top-down mechanisms have primacy over bottom-up mechanisms in an ecosystem free from direct anthropogenic impacts, including fishing.

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CHAPTER 1

LITERATURE REVIEW

Coral reefs and their threats

Coral reefs are found in clear, warm, and oligotrophic water and represent some of the world's most diverse marine habitats (Odum and Odum 1955; Connell 1978; Huston 1985; Lalli and Parsons 1993; Dawes 1998). These biotic reefs occur pantropically and are comprised of diverse assemblages of corals, algae, invertebrates, fish, and microbial organisms (Sale 1991; Lalli and Parsons 1997).

Coral reefs are increasingly at risk from anthropogenic activity. For instance, overfishing and pollution are two direct impacts that have occurred throughout human history (Jackson et al. 2001; Pandolfi et al. 2003; Birkeland 2004). In addition, humans have indirectly impacted the environment through global climate change (Watson et al. 2001). In the Pacific, there has been an increased occurrence of El Niño events that lead to elevated sea surface temperatures (SST) and increased tropical storm activity (Timmermann et al. 1999; Guinotte et al. 2003; Hughes et al. 2003). Such elevated SST's have been implicated in mass mortality bleaching events that threaten reefs world-wide (Stone et al. 1999; Aeby et al. 2003; Hughes et al. 2003).

Chronic degradation through impacts such as over-fishing impedes the ability of coral reefs to recover from acute large-scale disturbances such as bleaching or hurricanes, therefore decreasing the resilience of the ecosystem (Hughes 1994; Hughes et al. 2003). The combination of chronic and acute disturbances has pushed some reefs beyond a threshold into an alternative state, from coral dominated to algal dominated (Hughes

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1994; McClanahan et al. 1999; Bellwood et al. 2004; Folke et al. 2004). The two main chronic stressors that are implicated in causing these phase-shifts are over-fishing and coastal eutrophication—top-down and bottom-up respectively (Hughes 1994; Jackson et al. 2001; Hughes et al. 2003; Pandolfi et al. 2003).

Eutrophication is thought to exacerbate phase-shifts from coral domination to algal domination by relaxing nutrient limitations to algae, all of which are likely to grow faster than corals (Smith et al. 2001; Szmant 2001; LaPointe et al. 2004). Many coastal areas are heavily impacted by eutrophication (Ryther and Dunstan 1971; Carpenter et al. 1998; Howarth et al. 2000; Koop et al. 2001; Lapointe et al. 2004). An example of the effect of eutrophication was demonstrated by the overgrowth of corals in Kane'ohe Bay, Hawai`i by the green alga *Dictyosphaeria cavernosa* (Forsskål) Børgesen in the 1970's (Hunter and Evans 1995; Larned 1998; Stimson et al. 2001). Treated sewage input decreased the nitrogen and phosphorus limitation of *D. cavernosa* and enabled it to out-compete and overgrow coral (Pastorak and Bilyard 1985; Hunter and Evans 1995; Stimson et al. 1996; Larned 1998; Stimson et al. 2001). After the sewage outflow was removed from Kane'ohe Bay, *D. cavernosa* populations significantly reduced in certain areas (Hunter and Evans 1995), while remaining persistently high in other areas of the bay (Stimson et al. 2001). The lack of herbivore grazing pressure has been implicated in causing certain areas to remain to have high levels of *D. cavernosa* (Stimson et al. 2001). However, at the time of the initial study, very little data was collected on the effect grazing on *D. cavernosa* in Kane'ohe Bay by herbivores, which limits our ability to fully test whether eutrophication was the cause of the initial algal overgrowth (Stimson et al. 2001).

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Phase shifts of coral dominated reefs to algal dominated reefs have also been blamed on over-fishing (Hughes 1994). Most coral reefs throughout the world have been fished for many centuries (Jackson et al. 2001; Pandolfi et al. 2003; 2005). In recent years with an increase in population and technological advances, fishing has become less sustainable and it is feared that many reefs are chronically over-fished (Jackson 2001; Birkeland 2004; Pandolfi et al. 2005). There are fewer large predatory fish, which subsequently increases fishing pressures on smaller herbivorous fish (Hughes 1994; Pandolfi et al. 2003). Once released from the pressure of herbivory, naturally occurring populations of algae on tropical reefs are expected to grow more prolifically (Hughes 1994; Smith et al. 2001). For instance in Discovery Bay, Jamaica; fishing for many centuries led to the proliferation of urchins as they were released of competition for food and predation pressures; however when a disease caused a mass mortality of urchins, algae overgrew a once coral dominated reef thus shifting it from coral to algal dominated (Hughes 1994).

Another threat to coral reefs is the introduction of non-indigenous, invasive species. When algal species are introduced to eutrophic coastal waters where their native grazers are lacking these plants often out compete and ultimately displace other naturally occurring reef organisms (Russell 1992; Smith et al. 2002). *Hypnea musciformis* (Wulfen) J.V. Lamouroux is an example of a non-indigenous, invasive alga in Hawai`i that not only displaces natural species, but can create large blooms that have been tied to at least $20 million/yr loss from declines in tourism and tax revenues on the island of Maui (Russell 1992; Smith et al. 2002; Cesar and van Beukering 2004). Similarly, *Caulerpa taxifolia* (M. Vahl) C. Agardh is an example of a non-indigenous species that

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has invaded coasts of six countries in the Mediterranean and turned a diverse biota into monospecific, homogenized benthic habitats (Jousson et al. 1998; Meinesz et al. 2001). A large effort to understand and control invasive marine algae is underway in many areas around the world (Jousson et al. 1998; Meinesz et al. 2001; Smith et al. 2002; Anderson 2005).

These various threats have lead to a decline in reef health worldwide (Pandolfi et al. 2003; 2005). This has lead to increased interest in research examining factors are important in regulating communities on coral reefs.

Community ecology

Ecologists have long sought to understand what determines the distribution and patterns of organisms observed within a community (Hutchinson 1959; Hairston et al. 1960; Connell 1978; Menge and Sutherland 1987; Menge 1992). Both biotic forces (e.g. competition and trophic level interactions) and abiotic forces (e.g. disturbance) are themes used to explain community regulation (Connell 1978; Menge and Sutherland 1987; Menge 1992; Power 1992). Within a given ecosystem, there are many possible factors that are acting in concert to structure a biological community. These interactions are highly complex which make pinpointing the dominant determining force responsible for structuring a particular community an extremely difficult and often confounding task. Despite these obvious complexities, many scientists argue that there is one dominant determining force (e.g. disturbance or trophic interactions) that is responsible for structuring communities within an ecosystem (Hairston et al. 1960; Hughes 1994). With evidence for many different factors affecting community structure, a more likely scenario

is one in which different factors are determinate depending on a number and range of variables such as location and time of year (Hunter and Price 1992). Thus, heterogeneity occurs on a number of levels (Hunter and Price 1992).

There are a number of theories in coral reef ecology that have been introduced to describe biological variability within a system. Biotic theories used to explain community structuring in coral reefs include competition for space, predation, trophic interactions, and recruitment limitations (Jones 1990; McCook et al. 2001). Abiotic forces thought to structure coral reef communities are disturbance regimes as well as geomorphic structure (i.e. zoning and rugosity) (Connell 1978; Hixon and Beets 1993; Friedlander and Parrish 1998). While it is necessary to recognize the complexity of a system and to realize there are many potential factors affecting coral reef communities, the scope of many projects prevents different theories from being analyzed in concert. For the purpose of this study, I will focus on the effect of geomorphic zoning and trophic interactions on coral reef communities. In the following paragraphs I will look in more detail at some of these existing theories.

Coral reefs: *geomorphic regions, exposure, and disturbance*

Most introductory texts dealing with coral reef biology have historically segregated single reef systems into simple zones based on the following geomorphic features (Dawes 1998; Lalli and Parsons 1997; Nybakken 1988; Sumich 1988): Ocean facing reefs are referred to as reef slopes or buttresses, sublittoral, and fore reef zones, while lagoon facing reefs inside the reef crest are alternatively called reef flats, littoral zones, or back reefs. Reefs within the lagoon are sometimes termed moat reefs, lagoon

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reefs, or patch reefs. Although terminology of these regions is interchangeable and varies

among sources, these geomorphic zones are commonly used by reef biologists to

circumscribe distinct habitat types because each experiences environmental conditions

unique from the others (Odum and Odum 1955; Morton and Challis 1969; Womersley

and Bailey 1969).

Hydrodynamic energy of these environments is also quite distinct: ocean facing

reefs are typically highly dynamic environments, experiencing high wave and surge

energy, as well as great depth ranges which effect light and temperature (Sumich 1988).

Back reefs and lagoon reefs are more sheltered from high wave energy and experience

higher irradiance because of shallow depths. However, back reefs are continually flushed

and sometimes experience high surge due to the proximity to the reef crest, whereas

lagoon reefs represent calmer environments with low water circulation and potentially

higher water temperatures (Hoeke et al. 2006). The varying levels of wave exposure sets

up a disturbance gradient across the different reef regions: fore reef regions have high to

intermediate levels of disturbance, back reefs have intermediate to low levels of

disturbance, and patch reefs have low disturbance. Disturbance is ecologically defined as

a mechanism which acts to prevent a system from reaching equilibrium by causing

destruction of organisms within the system (Connell 1978). Disturbance from wave

exposure has been attributed as one of the dominant factors affecting species diversity

and community structure in marine ecosystems (Connell 1978; Littler and Littler 1984;

Huston 1985; Kilar and McLachlan 1989; Hixon and Brostoff 1996; Connell et al. 1997).

The intermediate disturbance hypothesis states that highest species diversity should be

present at an intermediate level of disturbance; high levels of disturbance limit the

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number species because of the extreme nature of the environment, and low levels of disturbance allow for competitive exclusion to occur (Connell 1978).

Because each geomorphic region experiences similar disturbance regimes, it seems logical that biological benthic communities would be similar within a particular geomorphic region or disturbance regime and differ between regions. Chapter two of my thesis will address this question. It is thought however, that subtle variations in a suite of physical or biotic factors such as turbidity and herbivory may cause there to be variation within these geomorphic regions creating smaller microcosms which support unique biological benthic communities (Littler and Littler 1984; Huston 1985; Hixon and Brostoff 1996; Connell et al. 1997). For example at French Frigate Shoals in the Northwestern Hawai`ian Islands, reefs within the lagoon region were found to be more biologically variable than those in fore and back reef areas (Vroom et al. 2005). In order to understand which factors are most influential in structuring spatial patterns on reefs, a fundamental understanding of how benthic biological communities are organized in each geomorphic region is essential.

Trophic interactions

Scientists who study trophic interactions have been divided into two camps: those who believe that top-down forces are dominant in structuring coral reef communities (Hughes 1994), and those who feel that bottom-up forces are dominant (LaPointe et al. 2004). In reality both forces act in concert. In order to understand what is meant by top-down vs. bottom-up, one must recall the early description of food chains. Primary producers create the base or "bottom" of the food chain, followed by herbivores that

graze on the primary producers, and ending with predators at the "top" that eat the herbivores. A system that has bottom-up control is one in which resources that effect the primary producers are responsible for structuring the biological community. An example of bottom-up control was discussed earlier with the example of the alga *Dictyosphaeria cavernosa* in which excess nutrients (resources) caused a shift from coral dominated to algal dominated (Pastorak and Bilyard 1985; Hunter and Evans 1995). On the other hand, a system that is controlled by top-down mechanisms is one in which organisms in higher trophic levels (predators or herbivores) are responsible for structuring a biological community. The mass mortality of herbivorous urchins in Jamaica that resulted in algal overgrowth is evidence for top-down control in a coral reef ecosystem (Hughes 1994). Therefore, both top-down forces (change in herbivore abundance) and bottom-up forces (change in nutrient availability) have been shown to be important to coral reef ecology.

The debate of top-down vs. bottom-up factors is a long standing argument in ecology. One of the most noted early papers on the topic (Hairston et al. 1960) has come to be known as the "world is green" hypothesis. According to Hairston et al. (1960), the world is green because predators (including parasites) control populations of herbivores. This was the first time top-down control was argued. Since then, evidence has gathered in favor of top-down mechanisms (e.g., Hughes 1994). However logical arguments can be made for primary producers having a dominant role as well. The importance of primary producers was simply stated by Hunter and Price (1992) who wrote, "removal of higher trophic levels leaves lower levels present (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all." There is also evidence for

bottom-up control especially in resource limited ecosystems (e.g., Pastorak and Bilyard 1985; Hunter and Evans 1995).

Increasingly, ecologists are realizing that trophic interactions are complex and that neither top-down or bottom-up forces are acting solely, but perhaps in concert. This leaves a tangled web of species interactions that have caused some scientists to conclude that no generalities on trophic interactions are possible (Polis and Strong 1996). However, Hairston and Hairston (1997) argue that generalities can and have been made and the best way to test the importance of trophic structure is through experiments.

Coral reef ecology has not been immune to the debate over top-down vs. bottom up structuring of communities. In fact the situation discussed above at Discovery Bay in Jamaica has been hotly debated by the marine research community. In 1994, Hughes described a phase-shift from a coral dominated to an algal dominated reef. According to his report, the crash of herbivorous urchin populations was the cause the algal overgrowth; however, LaPointe (1997) argued that eutrophication was the main cause for the phase-shift at Discovery Bay, and concluded that the two processes (loss of herbivory and eutrophication) had an additive effect and that both processes were causal in the shift to a macroalgal dominated reef. Hughes (1999) responded by discrediting the data and data interpretation of LaPointe (1997) and claimed that loss of herbivores (top-down) were the sole reason for the change in the coral reef community. LaPointe (1999) defended his data and claimed that both top-down and bottom-up processes were important. Aronson and Precht (2000) re-examined the situation at Discovery Bay and concluded that there was no evidence for bottom-up causal factors, therefore supporting the original hypothesis set forth by Hughes (1994). Because the outcome of this debate

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affected policy used to restore and manage this area, the debate was extremely heated. While it is interesting to note that there are seven scientists in support of the top-down mechanism and only one in support of the bottom-up mechanism, it seems likely that the truth of the situation lies somewhere near the middle. Prolonged eutrophication and overfishing may have caused increased stress at this reef, making the urchin die off the proverbial straw that broke the camels back.

In an attempt to resolve differences between the top-down vs. bottom-up models, Littler and Littler (1984) published the Relative Dominance Paradigm (RDP). In this paradigm, the growth of the algal functional groups is linked to four stable states of a coastal reef. Interactions of nutrients and herbivore pressures are considered in structuring coral and algal communities (Fig. 1.1). For example, with low nutrients and high grazing pressure (characteristic of typical pristine reefs), corals were predicted to dominate. The Relative Dominance Paradigm provided testable hypotheses for the interaction of biological causal factors influencing phase shifts for the first time.

The RDP was experimentally tested in coral reef ecosystems by Smith et al. (2001). Ceramic tiles were used which were controlled for herbivory using cages, and supplied with extra nutrients using fertilizer sticks. The results of this experiment largely supported the RDP. The additive effect of herbivore removal and nutrients caused tiles to have the greatest biomass of algae, supporting the theory that trophic level interactions are important in shaping tropical reef communities. Two studies however found that nutrient enrichment alone had very little effect on algal abundance (Koope et al. 2001; Thacker et al. 2001). While Koope et al. (2001) found that increasing nutrients did not cause the reef to change from coral to algal dominated communities, they did find that

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nutrients negatively affected coral reproduction. These results suggest that the effect of nutrient enrichment varies between areas because of historical ambient nutrient concentrations. Also, differences in results may be explained by differences in experimental design.

While the RDP provides insight into coral reef community regulation, it only focuses on trophic interaction. As mentioned above, it is clear that other factors are also important in shaping and regulating community composition. It is difficult to even separate the various factors. Even on the most general level – abiotic vs. biotic, there is confusion. Often an abiotic factor will affect biotic factors. For instance, in a high disturbance regime, certain species may have a competitive advantage, thus linking disturbance and competition. Also, reef morphology provides refuges for prey species, thus linking the abiotic reef morphology to predation as well as competition for space (Hixon and Beets 1993; Friedlander and Parrish 1998). Therefore results from studies looking myopically at a single factor or a limited number of factors or even a single site, must be cautiously interpreted. However, there is still a great value in trying to decipher these complexities and subsequently applying them to experimentally driven hypotheses in unmanipulated field settings. Thus, one of the goals of this study is to examine the possible control of top-down (herbivory) and bottom-up (nutrients) factors on a coral reef benthic biological community focusing on the benthic algae.

Role of algae on coral reefs

While algae can be a nuisance and a sign of reef degradation, they are also a fundamental part of healthy and functioning reef ecosystems (Odum and Odum 1955).

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Algae are very diverse with over 25,000 species of marine algae (combined Rhodophyta, Chlorophyta, and Phaeophyta) occurring worldwide of an estimated total of 145,000 algal species (Andersen 1992; Huisman 2000; Guiry et al. 2005). They provide food and habitat for herbivorous fish and invertebrates as well as produce sand (e.g. the green alga *Halimeda*) and reef structure (e.g. crustose coralline red algae) (Adey and Vassar 1975; Carpenter 1986; Hixon and Brostoff 1996; Harney et al. 2000; Russ 2003). Algae are not only a diverse part of the coral reef ecosystem but often are naturally abundant as well (Womersley and Bailey 1965; Vroom et al. 2005; 2006).

In order to study benthic community dynamics in reef systems, algae have often been split into functional groups instead of being studied at a species level (Littler et al. 1983; Steneck and Dethier 1994). Functional group designations are an attempt to simplify extremely complex multi-species systems in order to look at large scale interactions. Functional group designation is now commonly used throughout ecological research in terrestrial, aquatic, and marine ecosystems. Crustose coralline red algae (of the red algal order Corallinales), turf algae and macroalgae from several distinct evolutionary lineages are the three functional forms commonly used in algal ecology (e.g. Smith et al. 2001; Costa et al. 2002; Vroom et al. 2005). Typically, each of these three functional groups occurs throughout coral reef habitats in varying abundances (Odum and Odum 1955; Costa et al. 2002; Vroom et al. 2006). These three functional forms of algae are also used by marine ecologists to categorize and simplify phase shifts from coral to algal domination (McCook et al. 2001; Smith et. al. 2001; Thacker et al 2001).

Crustose coralline red algae, fleshy macroalgae, and turf algae each play an integral role in the coral reef ecosystem. The importance of crustose coralline red algae

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was apparent in early studies of coral reefs (MacCaughley 1918; Galtsoff 1933; Odum and Odum 1955; Womersley and Bailey 1965), where it was documented that they are responsible for cementing the reef together, sand production, reef accretion, and providing settlement substrate for corals (Womersley and Bailey 1965; Adey and Vassar 1975; Harney et al. 2000; Harrington et al. 2004). With accretion rates determined to be between 1- 5.2 mm/ year, crustose corallines are large contributors to coral reef structure (Adey and Vassar 1975). Crustose corallines often dominate the reef crest in part because of their ability to withstand constant high wave energy and because of wave induced shelter from herbivory (Womersley and Bailey 1965; Adey and Vassar 1975).

While many scientists associate macroalgae with degraded coral reefs, macroalgae can be a naturally abundant and diverse part of tropical reefs (Vroom et al. 2005; 2006). Macroalgae provide food for herbivorous fish and invertebrates and shelter for many small organisms (Hughes et al. 1994). Certain species such as those from the calcified genus *Halimeda* produce sand upon breakdown (Harney et al. 2000). Harney et al. (2000) found *Halimeda* spp. to produce up to 32% of sand in Kailua Bay, Hawai`i.

Algal turf communities are also an abundant and diverse group. A recent study found a total of 102 species of turf at two sites in Hawai`i (Stuercke and McDermid 2004). Turf algae are productive and often cover the majority of the benthic substrate in coral reef communities (Odum and Odum 1955; Costa et al. 2002; Russ 2003; Vroom et al. 2005). Because of their high productivity abundance and presumed palatability, turf algae are an important food source for herbivorous organisms (Hixon and Brostoff 1996; Russ 2003).

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Contrary to what many people believe, recent evidence shows that when combined, algal functional groups often dominate the benthos in many coral reefs throughout the Pacific (Jokiel et al. 2004; Vroom et al. 2006). CRAMP studies have documented average coral cover in the State of Hawai`i at 20.3 % (Jokiel et al 2004). Swains Island in the South Pacific Ocean, an island with minimal anthropogenic activity, had one of the highest coral covers of all the reefs surveyed by NOAA cruises in 2004, with an average of 32.69% live coral (Vroom et al. 2006). The remaining benthic cover at Swains as well as Hawai`i consists of algal functional groups. It is believed that in past years field biologists simply overlooked algae because of a focus on corals.

Coral reef algae: requirements and limitations

Marine algae are photosynthetic organisms that are generally surrounded by seawater. In order to grow effectively, a number of physical, chemical, and biological factors are required (Dawes 1998). Physical factors that effect algal growth include light, temperature, water motion, waves, tides and currents (Santelices 1977; Kilar and McLachlan 1986, 1989; Lobban and Harrison 1997; Dawes 1998). Light is the essential ingredient in photosynthesis (Taiz and Zeiger 1991). With increasing depth, light exponentially decreases (Falkowski and Raven 1997; Dawes 1998), yet algae have evolved shade pigments that are capable of using these low light conditions. Temperature affects all levels of biological organization from the molecular level to community level and is thought to effect seasonality in certain species of algae (Diaz-Pulido and Garzón-Ferreira 2002). Water motion is important for reducing boundary layers that surround algal tissues (Dawes 1998; Hurd 2000). The boundary layer is a thin

layer of water (μm- mm thickness) directly adjacent to the plant. Because, gases such as CO_2 dissolve 10,000 times slower in water than in air, in order for seaweeds to receive the required gases and nutrients, water movement and subsequent disruption of the boundary layer is essential (Dawes 1998; Larned 1998; Hurd 2000). Waves, tides and currents can potentially decrease the boundary layer, making gases and nutrients more readily available; however, they also create disturbance. Extremely high wave energy and currents can limit growth of frondose forms of algae because they may be ripped from the substrate. Similar environmental conditions may favor encrusting forms of algae (Kilar and McLachlan 1986; 1989). Changes in tides may expose intertidal species to the air which leads to desiccation (Lobban and Harrison 1997). This suite of physical factors is highly dynamic, varying in both space and time on a coral reef.

Biological factors that affect algal success include tissue morphology, reproductive strategies, and interactions with other organisms (symbiosis, competition, and predation) (Dawes 1998; Larned 1998; Russ 2003; Santelices 2004). In order to overcome some of the physical factors in the field, some algae have evolved morphologies with high surface area to volume ratio (filamentous algae) other algal species have morphologies that enable them to envelope nutrients (Larned 1998; Santelices 2004), while other species are able to asexually reproduce via fragmentation, which takes advantage of high wave disturbance regimes and allows these species to be highly mobile and successful (Kilar and McLachlan 1986; Smith et al. 2002). There are also a number of interactions among other organisms that affect the success of an alga. As discussed above, herbivory has been shown to play a large role in algal distribution and abundance (e.g., Hughes 1994; Smith et al. 2001; Russ 2003). In addition,

competition for space, light, and nutrients as well as symbiosis with nitrogen-fixing cyanobacteria play a role in the success of algae (McCook et al. 2001; Lobban and Harrison 1997; Dawes 1998).

Due to the concern that excessive nutrients contribute to phase shifts in coral reefs; I have chosen to focus some of my research on the role of nutrients in structuring coral reef communities. Therefore, nitrogen and phosphorous assimilation, and limitation in marine algae will be discussed in detail below.

Two essential nutrients for algal growth and metabolism are nitrogen and phosphorus (Taiz and Zeiger 1991; Lobban and Harrison 1997). Nitrogen (Ammonia (NH_4^+), Nitrate (NO_3^-), and Nitrite NO_2^-) is a major macronutrient essential for plant growth and the formation of pigments and enzymes for photosynthesis, amino acids and cell proteins (Taiz and Zeiger 1991; Lobban and Harrison 1997). Nitrogen is readily taken up by cells where it is either stored in vacuoles or involved in a number of enzymatic processes that result in amino acid synthesis (Taiz and Zeiger 1991; Lobban and Harrison 1997). Phosphorus is essential for the formation of high energy molecules such as ATP. Phosphorus enters algal cells generally as inorganic phosphate (PO_4^{3-}); however, some organic phosphorus compounds can be utilized (Taiz and Zeiger 1991; Lobban and Harrison 1997).

Algal growth on most coral reefs has been shown to be limited by nitrogen and/or phosphorus (LaPointe et al. 1987; Larned 1998; Smith et al. 2001; Stimson et al. 2001; Fong et al. 2003; Lapointe et al. 2004) with a few exceptions (e.g., Thacker et al. 2001; Koope et al. 2001). It has been shown that in reefs with high carbonate sands, phosphorous is more limiting than nitrogen because of an equilibrium with fluoroapatite

(LaPointe et al. 1987; 1992; Howarth et al. 2000). However, other studies have found nitrogen to limiting over phosphorus in coral reefs (Smith et al. 2001; Larned 1998). Therefore, nutrient limitation is largely dependent on the location, history of the algal community, environmental factors and the physiology of the species of interest (LaPointe et al. 1987; Larned 1998; Fong et al. 2003).

Nitrogen and phosphorus enter the marine ecosystem by many pathways, both natural and anthropogenic (Ryther and Dunstan 1971; Zimmerman and Kermer 1984;Vitousek et al. 1997; Carpenter et al. 1998; Howarth et al. 2000; Diaz-Pulido and Garzon-Ferreira 2002; Umezawa et al. 2002; Leichter et al. 2003; LaPointe et al. 2004; Smith et al. 2004) . Natural sources of nutrients include runoff from rivers and streams (Vitousek et al. 1997), sea-bird guano run-off (Erskine et al. 1998), deep ocean upwelling (Zimmerman and Kremer 1984; Diaz-Pulido and Garzon-Ferreira 2002), pulsed tidal upwelling (Leichter et al. 2003; Smith et al. 2004) and nutrient cycling within the system through nitrogen fixation (Capone et al. 1977; LaPointe et al. 1987; Lobban and Harrison 1997). Anthropogenic sources are derived from run-off of agriculture fertilizers (Beman et al. 2005), animal manure (Carpenter et al. 1998; Howarth et al. 2000), golf courses, and sewage disposal (LaPointe 2004). In addition, the burning of fossil fuels releases large amounts of nitrogen that can be directly deposited on the surface of the ocean or can be added to run-off from land (Vitousek et al. 1997; Carpenter et al. 1998; Howarth et al. 2000).

Methods for examining nutrients limitation and nutrient sources

Nutrients can fluctuate greatly over a short period in the water column, making it difficult to monitor nutrient availability (Wheeler and Bjornsater 1992; Fong et al. 2003). As discussed above, algae uptake nutrients from the water column or sediments and integrate them within cells as stored molecules or as proteins (Lobban and Harrison 1997). Therefore, analyzing algal tissue for nitrogen and phosphorus can indicate the relative amounts of nutrients in the environment over a longer period of time, possibly providing a more accurate indication of nutrient availability and flux than instantaneous water sample determinations (Wheeler and Bjornsater 1992; Costanzo et al. 2000; Fong et al. 2003). Algal tissue analysis has also been used as a biological indicator of heavy metal pollution (Say et al. 1990) and to examine sources of nutrients through stable isotope research (Umezawa et al. 2002).

In order to use algal tissue nutrient content as a proxy for environmental nutrient availability, it has to be assumed that the tissue will reflect ambient available nutrients. This has been shown to be true in many studies (Costanzo et al. 2000; LaPointe et al. 1987; Fong et al. 2003; Smith et al. 2004), although it is necessary to be aware of some variations. Wheeler and Bjornsater (1992) hypothesized that persistent annual species of algae (branched specimen) would have higher storage capacity than opportunistic species, however this was not supported. Instead, they found the highest ratios of N:P in morphologically simple and opportunistic algae and the lowest ratios in persistent branched algae in the temperate Pacific Northwest (Wheeler and Bjornsater 1992). They also found that algal tissue from sheltered and exposed sites had similar N:P ratios despite higher levels of nutrients at the sheltered sites, indicating that environmental

conditions and smaller relative boundary layers may allow for increased nutrient uptake (Wheeler and Bjornsater 1992). However, seasonal changes in tissue N:P ratios did mirror seasonal changes in ambient nutrient levels. Therefore, Wheeler and Bjornsater (1992) concluded that the simultaneous measurement of algal tissue N and P is a useful indicator of nutrient status, however in order to study nutrient limitation, storage capacity and growth rates are also useful.

Ratios of limiting nutrients in algal tissue has been used to study nutrient limitation by examining the ratio of carbon to nitrogen to phosphorus (C:N:P) (Niell 1976; Hanisak 1979; Wheeler and Bjornsater 1992; Larned 1998; Smith et al. 2001; Fong et al. 2003). After extensive analysis of phytoplankton and zooplankton, an average ratio of C:N:P was determined to be 106:16:1 (Redfield et al. 1963), the Redfield ratio. Phytoplankton with a nutrient composition near the Redfield ratio are considered to be growing maximally while those with deviations from this ratio are considered to have nutrient limitation as suggested by the deviation from this ratio (Redfield et al. 1963). Atkinson and Smith (1983) determined that C:N:P for benthic algae was considerably higher (550:30:1) than the Redfield ratio, potentially indicating phosphorus limitation, or conversely nitrogen or carbon storage within the tissues. However, theses values were highly variable, ranging from 143:16:1 to 3,550:58:1, making generalizations in the absence of replication, difficult. Other studies have reported phosphorus values to be higher resulting in lower average C:N:P values but still higher than that of the phytoplankton Redfield ratio (Wheeler and Bjornsater 1992). It is important to realize a ratio compresses multiple values into one value which can be misleading. Therefore, it is

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important to examine individual values such as % N and % P for tissues in addition to the ratio.

Stable isotopes have been used to infer sources of nitrogen and carbon (Peterson and Fry 1987; Griffiths 1991; Smit 2001; Stewart 2001). Natural cellular processes such as photosynthesis can favor the light (C^{12}, N^{14}) or heavy (C^{13}, N^{15}) carbon and nitrogen isotopes, resulting in fractionation (Smit 2001). This ratio of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) is transmitted through the food web and can sometimes be traced to identify sources (Smit 2001; Umezawa et al. 2002; LaPointe et al. 2004). Most ecological studies express this ratio of heavy to light isotopes in terms of δ values: $\delta X = \{(R_{sample}/ R_{standard})- 1\} \times 10^3$ (where $X = {}^{13}C$ or ^{15}N and R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$) (Smit 2001).

Nutrient sources can have known isotopic signals: for example, sewage effluent has a relatively high level of $\delta^{15}N$ (mean = 8.0‰) compared with recycled N from an oligotrophic system (mean = -3.5‰) (Smit 2001). Successful ecological studies using isotopes depend on a high natural isotopic variation between the interrelating components of the ecosystem (Smit 2001). One way which this occurs is through input from animal-derived nitrogen which has enriched levels of $\delta^{15}N$ (i.e. seabirds) relative to depleted ambient conditions (i.e. oceanic systems) (Erskine et al. 1998). Seabird guano has been noted as a significant source of nutrients, allowing for high plant productivity surrounding seabird rookeries (Mazutani et al. 1988; Mazutani et al. 1992; Erskine et al 1998). The elevated $\delta^{15}N$ levels in seabird guano are traceable through the ecosystem (Mazutani et al. 1988; Mazutani et al. 1992; Erskine et al. 1998). Erskine et al. (1998) found that the giant kelp *Durvillaea antarctica* (Chamisso) Hariot on coastlines adjacent

to penguin colonies had significantly greater $\delta^{15}N$ levels (11.9‰) than plants distant from penguin colonies (1.6‰). These findings are similar to other studies and suggest that seabird guano can be a source of nutrients to marine plants (Wada et al. 1981; Mizutani et al. 1988; Mizutani et al. 1992). In addition, seabird guano is rapidly mineralized, releasing ammonia gas (Erskine et al. 1998). This volatilized N has very depleted $\delta^{15}N$ signatures which is reflected in the low δN^{15} (-5.2‰) in upland plants (Erskine et al. 1998).

In coral reefs, $\delta^{15}N$ has been used to determine if nutrients are from natural or anthropogenic sources (Umezawa et al. 2002; LaPointe et al. 2004). Upwelled levels of $\delta^{15}N$ as well as recycled levels of $\delta^{15}N$ are reported to be at/or below zero (Smit 2001; LaPointe et al 2004), therefore levels above this may suggest terrestrially derived nutrients (Umezawa et al. 2002; LaPointe et al. 2004). Umezawa et al. (2002) showed that $\delta^{15}N$ was higher in algae closer to shore as well as in areas with more anthropogenic impact. As seen above, elevated $\delta^{15}N$ levels may also reflect natural nutrient input such as that from seabird guano (Erskine et al. 1998). However, in a study on the Great Barrier reef, $\delta^{15}N$ values did not vary between algae growing adjacent to seabird cays and those at other reefs without seabirds (2.0- 4.5‰) (Stewart 2001). Therefore, the evidence for the nutrient enrichment from seabirds in coral reefs is inconclusive.

While there has been an increase in research on coral reef community regulation, there are very few studies that have applied theories of community regulation to unmanipulated coral reef ecosystems. There is much to be gained from examining these principles in an area removed from human manipulation.

Study area

Pearl and Hermes Atoll is located in the Northwestern Hawai`ian Islands (NWHI). The NWHI are a chain of low lying islands, banks, and reefs that stretch 1200 nautical miles to the North West of the Main Hawai`ian Islands (MHI) (Maragos et al. 2002). This area makes up a large portion of the coral reefs in the United States (Maragos et al. 2002). Because of its remote location, PHA has been largely unimpacted by overfishing and pollution in contrast to many other reefs world wide (Brainard et. al 2002; Sulu et al. 2002). However, it is not immune to the far reaching effects of global climate change as many would have hoped. In 2002, a large scale coral bleaching event (when corals expel their photosynthetic symbionts) was reported after a long period of above average temperatures (Aeby et al. 2003).

At the latitude of 27°N Pearl and Hermes Atoll is one of the most northern atolls in the NWHI (Fig. 1.2). PHA is a large classic atoll with fore reef, back reef, and a large labyrinth of reefs within the lagoon (Maragos et al. 2002) (Fig. 1.3). The south and east side of the atoll has a very defined reef crest that is often emergent. The west side of the atoll has a more open reef crest with a number of large passes into the lagoon.

PHA is home to the endangered Hawai`ian monk seals and supports nesting grounds for the green sea turtle and many seabirds including albatross (Maragos et al. 2002). The reefs are remarkable because of the dominance of apex predators and high abundance of herbivorous fish as well as the occurrence of rare marine plants (Friedlander and DeMartini 2002; Vroom and Abbott 2004 a, b; Vroom 2005). In sum, PHA is an ideal place to try to understand coral reef community regulation in the absence of human manipulation.

Very little is known about the distribution and abundance of algae from PHA. Therefore; one aim of this study is to describe algal distributional patterns and analyze biotic and abiotic factors that might be influencing the distribution. I will assess location, disturbance exposure, herbivory, and nutrient availability as potential regulatory factors in benthic community structure at PHA, and assess potential sources of nutrients using stable isotope analysis of nitrogen from algal tissue.

Project Goals

Description of benthic community structure at PHA along a wave exposure gradient

Due to the shape of Pearl and Hermes Atoll (Fig. 1.3) sites can be divided into 4 exposure categories depending on wave exposure: high, intermediate high, intermediate low, and low. Because each category experiences similar disturbance regimes, it seems logical that biological benthic communities would be similar within a particular each wave exposure category and differ between categories. Additionally, it is thought that sites at the intermediate levels of exposure will have the highest number of species while sites with high exposure and low exposure will have less species richness.

Comparison of PHA to French Frigate Shoals

French Frigate Shoals (FFS) and Pearl and Hermes Atoll (PHA) are approximately 500 miles apart. FFS is closest to the equator of any of the atolls present in the NHWI. Although FFS has less emergent reef and is thus more open than PHA, the shape and size of the two atolls are generally similar. At FFS, Vroom et al. (2005) found

that benthic cover at sites within the lagoon is more heterogeneous than sites in the fore

and back reef. Further, the windward side is more homogenous than the leeward side.

Seven "ecozones" of distinct biological and geomorphic distinction were determined for

FFS. It is hypothesized that there will be some overlap in groups for FFS and PHA (i.e.

some sites from PHA will group more closely to sites in FFS than other sites at PHA).

Also, because of the higher latitude of PHA, it is expected that less coral cover will occur

than in waters of the more southerly islands, resulting in higher algal cover and different

species assemblages.

Factors affecting coral reef benthic community structure at PHA

Much research has been conducted on factors that affect anthropogenically

influenced coral reefs. PHA, however, offers a unique opportunity to look at these

factors in the absence of anthropogenic stressors. I will seek to determine which factors

(herbivorous fish and urchin density, algal tissue nutrient data, or wave exposure) affect

benthic community structure at PHA.
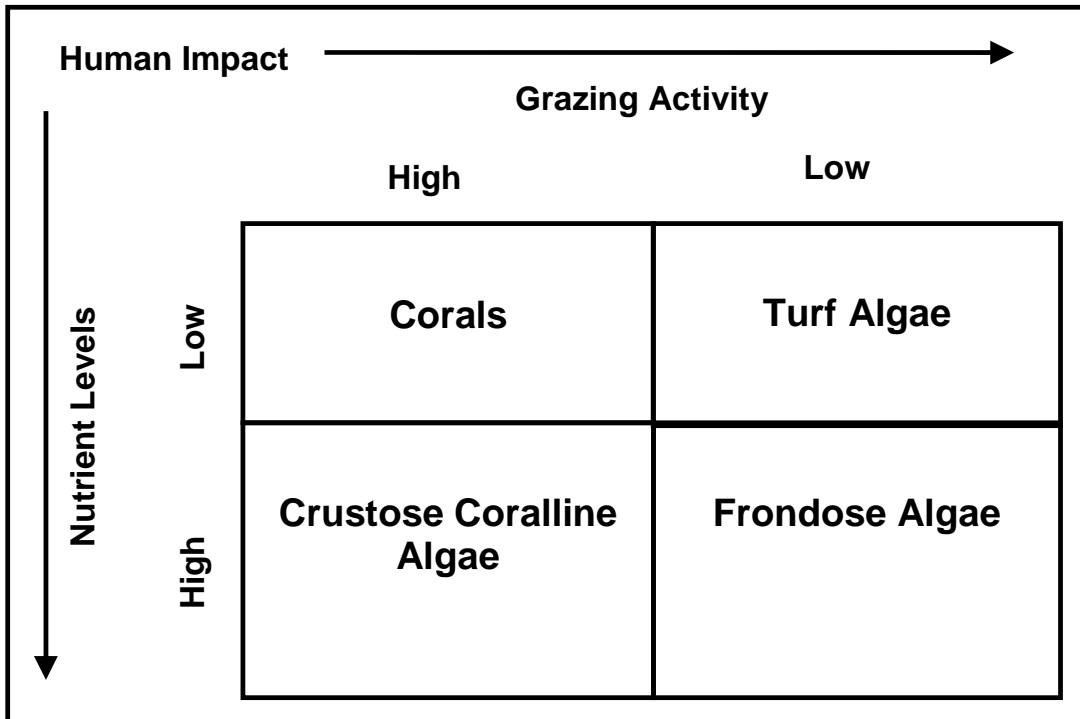
Figure 1.1. This figure is adapted from the Relative Dominance Paradigm (Littler and Littler 1984) and provides testable hypotheses for the interaction among biological causal factors influencing phase shifts. With low nutrient availability and high grazing pressures characteristic of typical of pristine reefs, coral were predicted to dominate. With low nutrient availability and low grazing pressures, turf algae were predicted to dominate. With high nutrient availability and high grazing pressures crustose coralline red algae were predicted to dominate, and finally with high nutrient availability and low grazing pressures typical of anthropogenically impacted reefs, frondose algae were predicted to dominate.
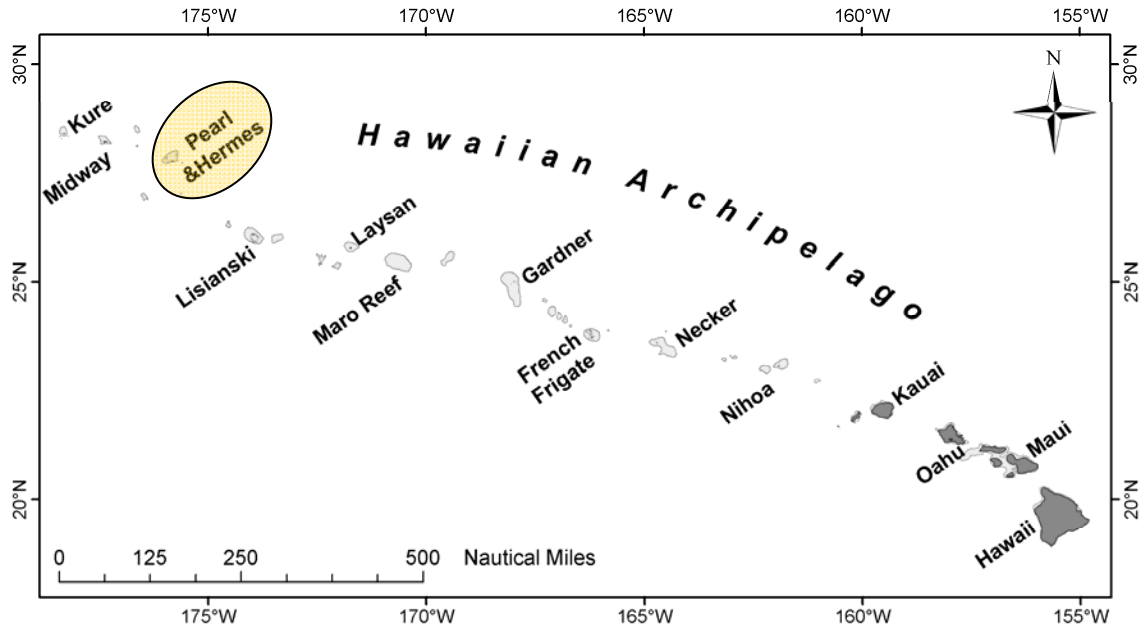
Figure 1.2. Map of the Hawai`ian Island Archipelago including the northwestern

Hawai`ian Islands. Pearl and Hermes Atoll circled in yellow is one of the most northern

in the chain located at 27.8°N and 175.8° W.
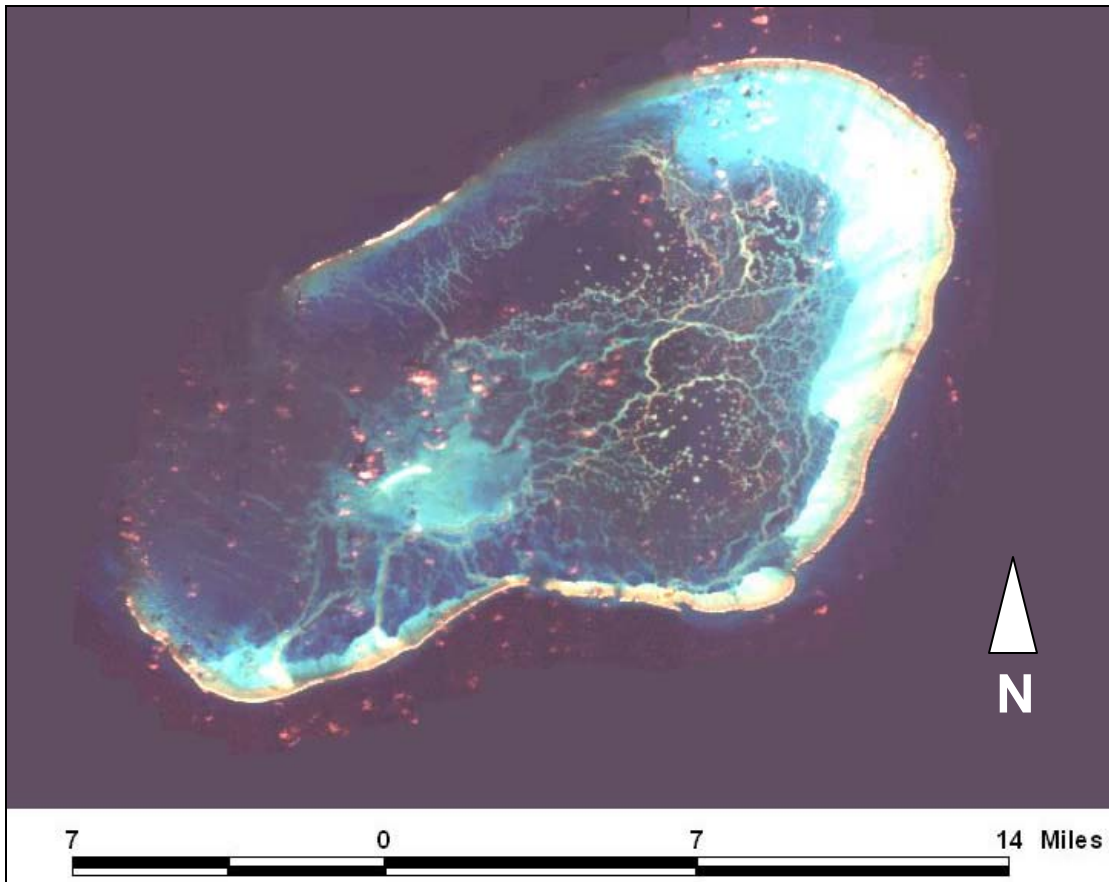
Figure 1.3. This is an Ikonos satellite image of Pearl and Hermes Atoll. While the south and east facing shores have emergent reef, the north and west facing sides have large openings exposing the lagoon to ocean swells. The lagoon is comprised of a labyrinth of patch reefs and numerous small sand islets including 4 vegetated sand islands.

CHAPTER 2

PATTERNS IN BENTHIC COMMUNITIES AT A REMOTE TROPICAL REEF

ALONG A WAVE EXPOSURE GRADIENT

Abstract

Ecologists have long sought to understand mechanisms which determine
distributional patterns of organisms. In this study, we examine wave exposure as a
potential abiotic factor in the determination of benthic community composition at Pearl
and Hermes Atoll, in the Northwestern Hawai`ian Islands that is free from direct
anthropogenic impacts. Benthic community composition was examined along a wave
exposure gradient using multivariate statistical analyses. Our expectation was that sites
with similar levels of wave exposure would exhibit similar benthic community
composition. Additionally, species richness of coral and macroalgae were compared to
predictions from Connell's intermediate disturbance hypothesis with the expectation that
sites with intermediate levels of wave exposure would have the highest coral and
macroalgal species richness. To test each of the above hypotheses, percent cover of
benthic organisms was observed at 34 sites from 4 wave exposure categories: high,
intermediate-high, intermediate-low, and low. Multivariate statistical analyses revealed
that sites from the four wave exposure categories differed significantly, and a non-metric
multi-dimensional scaling ordination (nMDS) and cluster diagram grouped sites from
low, high, and intermediate-high wave disturbance areas into three relatively discrete
clusters. However, sites experiencing intermediate-low wave exposure did not group
together in the nMDS ordination or cluster diagram, suggesting variability in benthic

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compositions among these sites.   SIMPER results identified crustose coralline red algae, the coral *Porites compressa*, and the green alga *Microdictyon setchellianum* as largely responsible for differences among wave exposure groups. In accordance with expectations based on the intermediate disturbance hypothesis, coral and macroalgal species richness was significantly higher at sites with intermediate-high and intermediate-low levels of wave exposure than at sites with low wave exposure, although not significantly higher than sites with high wave exposure.

Introduction

Within any given ecosystem, numerous factors play key roles in influencing patterns of community structure (Hutchinson 1959; Hairston et al. 1960; Connell 1978; Menge and Sutherland 1987; Menge 1992). These include both biotic and abiotic factors such as disturbance, climate, geomorphology, competition, resource limitation, and recruitment (Connell 1978; Menge and Sutherland 1987; Menge 1992; Power 1992). Complex species interactions, temporal variation in physical and biological parameters and anthropogenic manipulation of natural processes often make pinpointing those factors most responsible for determining community structure difficult. Yet with multiple reports of coral reef decline occurring globally (Jackson et al. 2001; Pandolfi et al. 2003; Birkeland 2004), it has become increasingly important for scientist and resource managers to understand the relative roles of various determinants of coral reef community structure and function.

Wave exposure creates a gradient of water motion ranging from low, relatively benign, oscillatory flow to high, potentially destructive flow which is often a source of

disturbance in marine benthic communities (Connell 1978; Huston 1985; Brander et al. 2004; Storlazzi et al. 2005). This disturbance creates flux and maintains a non-equilibrium state within marine ecosystems (Connell 1978; Huston 1985). For many years, it was believed that communities with the highest species diversity functioned at equilibrium and that diversity was attained through niche-partitioning and co-evolution (MacArthur 1960; MacArthur and Levins 1964; Schoener 1974; Diamond 1975; Fox 1981). However, it is now generally held that the most diverse communities are in constant flux due to disturbance and exist in a non-equilibrium state (Connell 1978; Huston 1985). At intermediate levels of disturbance, competitive dominants, climax species in other communities are limited, allowing for a maximum number of species to coexist (Connell 1978). This theory, known as the Intermediate Disturbance Hypothesis, has been widely tested and supported in coral reef communities (Grigg and Maragos 1974; Dollar 1982; Grigg 1983; Kilar and McLachlan 1989; Friedlander et al. 2003). Areas with intermediate levels of wave exposure also have the highest level of species diversity, while areas with extreme levels of wave exposure are often represented by a few species (Grigg and Maragos 1974; Dollar 1982; Grigg 1983; Sousa 1984; Kilar and McLachlan 1989; Friedlander et al. 2003).

Wave exposure is not only important as a mechanism of disturbance on coral reefs but is also a significant contributor to general water motion and circulation across reefs (Atkinson et al. 1981; Brander and et al. 2004; Fulton and Bellwood 2005). Water motion affects numerous biological processes on a coral reef such as larval/ food supply, sedimentation, and diffusion boundary layer thickness of coral and algae and subsequent nutrient availability (Shashar et al. 1996; Larned and Atkinson 1997; Dawes 1998; Hurd

2000). The diffusion boundary layer is a thin layer of water (μm- mm thickness) directly adjacent to the surface of a macrophyte or coral (Shashar et al. 1996; Hurd 2000). This layer of water is more viscous than surrounding water and requires greater force to perturb (Dawes 1998; Hurd 2000). Nutrients and gases diffuse slowly through the boundary layer to the surface of the organism where they are utilized by organisms for cellular processes such as photosynthesis and may become limiting (Shashar et al. 1996; Larned and Atkinson 1997; Hurd 2000). Therefore, disruption of a diffusion limited boundary layer by wave and current induced water movement are likely to be essential for the long term success of sessile coral reef organisms (Larned and Atkinson 1997; Hurd 2000).

Photosynthetic organisms living in an oligotrophic coral reef system (both corals and algae) must achieve a balance that allows for both maximum gas and nutrient exchange and minimum destruction from wave energy (Fig. 2.1). Morphologies with high surface area to volume (SA/V) such as highly branched morphologies allow marine organisms to maximize uptake of nutrients and gases (Hurd 2000; Stewart and Carpenter 2003). This type of morphology is ideal for low wave exposure regimes because boundary layer turnover is slow (Hurd 2000; Stewart and Carpenter 2003). However, a high SA/V ratio morphology increases the vulnerability of an organism to mechanical damage or dislodging in areas with high wave exposure (Ruyter van Stevenick 1988; Stewart and Carpenter 2003). In high wave exposure regimes boundary layer water is replaced rapidly therefore a morphology that is tightly adherent to the substrate such as a prostate encrusting morphology and that is robust to damage from wave exposure is more advantageous. Some organisms, especially species of marine algae, exhibit phenotypic

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plasticity presumably altering their morphology in response to wave exposure (Ruyter van Stevenick 1988; Stewart and Carpenter 2003). For instance, the brown macroalgal species *Lobophora variegata* (Lamouroux) Womersley ex Oliveira exhibits a prostrate encrusting and tightly adherent morphology in high wave exposure conditions and a lobed blade-like morphology with higher SA/V in low wave exposure conditions (Ruyter van Stevenick 1988). However, not all organisms are capable of the phenotypic plasticity seen in *L. variegata*. Therefore a trade off likely exists between a morphology that is robust to wave exposure and one that allows for maximum surface area to volume (Fig. 2.1). This trade-off may result in certain organisms being best suited for specific wave exposure regimes, thus potentially creating distinct communities along a wave exposure gradient.

The geomorphology of a coral reef creates a gradient of wave exposure: ocean facing or fore-reef regions have high to intermediate levels of exposure, back-reefs (lagoon facing reef adjacent to reef crest) have intermediate to low levels of exposure, and inner lagoon reefs have low exposure (Brander et al. 2004; Fulton and Bellwood 2005; Storlazzi et al. 2005). While, complex variations in a suite of physical and biotic factors such as reef crest morphology, temperature, and herbivory may cause differences in benthic community composition among sites within similar wave exposure regimes (Littler and Littler 1984; Huston 1985; Hixon and Brostoff 1996; Connell et al. 1997), we hypothesize that in general, sites with similar wave exposure will have similar benthic communities. We also predict that coral and macroalgal communities will exhibit higher species richness in areas of mid level disturbance than in areas with low or high level disturbance. These predictions were tested by examining benthic biological communities

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along a wave exposure gradient at Pearl and Hermes Atoll (PHA), a large coral reef system located in the Northwestern Hawai`ian Islands (NWHI). To further assess the results at PHA, comparisons with data from French Frigate Shoals (FFS) (Vroom et al. 2005), another Hawai`ian atoll system 926 km southeast of PHA, were analyzed.

Materials and methods

Location and description

PHA, centered at approximately 27° 50' N and 175° 55' W in the NWHI (Fig. 2.2), is the largest atoll in the NWHI, encompassing 1,166 km^2 of reef area and several small sand islands. PHA is semi-elliptical in shape, with its longest axis stretching from the SW to the NE (Fig. 2.3). An exposed reef crest surrounds the majority of the atoll, with the exception of the west facing side, which is largely open to prevailing ocean surface currents. Classic fore-reef and back-reef zones are present along areas with exposed reef crest. The majority of the lagoon area is protected from high energy wave forces and consists of a maze of reticulated and patch reefs with depths ranging from 0 to 26 m.

The remote location and inaccessibility of PHA has limited past research. The earliest known biological assessments of the atoll were conducted by Galtsoff (1933) after significant pearl oyster harvests; however, observations from this expedition were largely subjective in nature (Keenan et al. 2006). Since this early study, most scientific research has been constrained to building species lists or has focused primarily on coral or fish abundances rather than whole ecosystem assessments (Tsuda 1966; Grigg and

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Dollar 1980; Abbott 1989; Friedlander and DeMartini 2002).   Beginning in 2000,

NOAA's Coral Reef Ecosystem Division (National Marine Fisheries' Pacific Islands

Fisheries Science Center) and NWHI Coral Reef Ecosystem Reserve (National Ocean

Service) have led annual, multi-agency expeditions to the NWHI to assess and monitor

coral reef communities. Data presented here represent findings from the 2002 research

expedition.

Data collection

Quantitative data of benthic cover were collected at 34 sites at PHA between 17 to

29 September 2002 using a modified version of the Preskitt method (Preskitt et al. 2004).

Sites were selected to represent a range of habitat types (discussed in Vroom et al. 2005).

At each site, two 25 m transects separated by 10 m were placed along a 10 to 15 m

isobath (shallower at some back-reef and lagoon sites). Using a photoquadrat ($0.18m^2$)

equipped with either a Sony DSC P-9 or an Olympus C-4040 digital still camera and an

Ikelite substrobe DS-50, twelve photos were taken along the two transects: six at

randomly selected points directly adjacent to the transects, and six off the transect, 3-m

from the random points, in the direction of shallow water. In addition, field notes

(including in-depth coral species lists and rankings), and voucher specimens of algae

were collected in order to ensure accurate identification of species in the photos. Samples

of macroalgae were brought aboard the research vessel and frozen in sealable bags. In the

lab, microscope slides and herbarium pressings were prepared from samples for species

identification purposes. Microscopic specimens were examined with a Nikon E400

compound microscope (Nikon, Melville, NY, USA). All microscope slides and

herbarium specimens are currently in the personal herbarium of Peter Vroom (PSV 20017, PSV20097-PSV20122, PSV20124-PSV20190) located in the NOAA Fisheries Coral Reef Ecosystem Division's Phycology lab. Specimens are slated for eventual deposition in the Herbarium at the Bishop Museum, Honolulu, Hawai`i.

406 photoquadrat images were analyzed using PhotoGrid[©] (Bird 2002) to determine percent cover of benthic organisms by placing 100 stratified random points over each image and identifying to highest possible taxonomic level for the organisms under each crosshair. Because of the difficulties in identifying species of turf algae and crustose coralline red algae in the field and in a photo, organisms in these categories were identified to the functional group level only. Highly epiphytized macroalgae or crustose coralline red algae were recorded as both macroalgae and turf, often leading to percent covers exceeding 100%.

Data analysis

Field sites were grouped into *a priori* categories based on wave exposure: high, intermediate-high, intermediate-low, and low (Fig. 2.3) prior to the cruise. Category designations were subjective but based on wave height and period measurements from nearby Kure Atoll (241 km NW of PHA), wave models derived from the US Naval Oceanographic Office, literature on wave exposure in Hawai`i, and on personal observation of these areas. N and NW facing fore-reefs were identified as high wave exposure areas because of large, episodic NW swells (Fig. 2.3, 2.4; Storlazzi et al. 2005). Sites located along the E and S fore-reefs were identified as intermediate-high wave exposure areas. Fore-reef sites along the E side of the atoll experience relatively

consistent moderate to high wave heights because the predominant wind comes from the NE (Fig. 2.3, 2.4; Storlazzi et al. 2005). Similarly, significant swells from the S during summer months expose southern fore-reef sites to episodic long wave periods exceeding 10s and wave heights of greater than 2.5m (Fig. 2.3, 2.4; Storlazzi et al. 2005). All back-reef sites were identified as intermediate-low wave exposure areas, as were exposed patch reefs sites (Fig. 2.3; Brander et al. 2004, Fulton and Bellwood 2005). While sites along these areas can have strong currents, the force of waves is reduced by up to 80% after initial impact on the reef-crest. Patch reef sites located in the interior of the atoll are protected and therefore considered to have low levels of wave exposure (Fig. 2.3; Fulton and Bellwood 2005).

To test for differences among sites and examine patterns of benthic communities, species presence and percent cover data from each photoquadrat were treated as individual replicates within a site (n = 12). A Bray-Curtis similarity matrix of quadrats was created using PRIMER-E® (Clarke and Warwick 2001). A fourth-root transformation was performed on the data to increase the relative weight of rare species (Clarke and Warwick 2001). These data were then rigorously compared using a one-way analysis of similarity (ANOSIM; maximum permutations = 5000). Site comparisons with resulting r- values >0.75 were considered distinct with no to few shared species, while sites with resulting r-values <0.25 were considered to be biologically similar (Clarke and Warwick 2001).

Similarities among benthic communities from *a priori* wave exposure categories were tested using a 2-way nested ANOSIM (maximum permutations = 5000) with sites nested by wave exposure. Non-metric multi-dimensional scaling (nMDS) ordinations

(number of restarts = 30) and cluster diagrams were created from Bray-Curtis similarity matrices of averaged photoquadrat data by site and wave exposure characteristics. A SIMPER analysis was used to determine the level at which each species or functional group contributed to observed differences among sites in different wave exposure categories.

Species richness of coral and macroalgae (the number of species observed at a given site) was compared among wave exposure categories. For each site, macroalgal richness was determined from photoquadrats, and coral richness was determined from combined species lists and photoquadrat data. Because of unequal variances, Welch's one-way ANOVA coupled with Dunnett's T3 pairwise comparisons were used to test for differences in species number among the different exposure categories. A Bonferroni adjustment for multiple comparisons was required ($\alpha = 0.05$, p-value must be < 0.011).

Comparison to FFS

French Frigate Shoals (FFS) is a partially submerged atoll centered at 23°45' N and 166°11' W and approximately 926 km to the SE of PHA (Fig. 2.3; Vroom et al. 2005). While FFS and PHA are similar in size, they exhibit different geomorphologies (Maragos et al. 2002); PHA has a more continuous and defined reef crest surrounding the lagoon (Fig. 2.3), whereas FFS is crescent-shaped with only an E to NE facing emergent reef crest (Vroom et al. 2005). Vroom et al. (2005) conducted a similar study in which percent cover of benthic organisms was determined for FFS in the same manner that it was described for this study of PHA. Percent cover of benthic organisms from FFS and PHA were combined into a single data matrix. The same criteria used to assign wave

exposure categories at PHA were used to assign wave exposure categories at FFS. However, because of the open shape of FFS, no sites were categorized as having low wave exposure. Also, because there are no fore-reef regions facing NW, only 2 outer lagoon sites were categorized as having high wave exposure. nMDS ordinations (number of restarts = 30) and cluster diagrams were created from Bray-Curtis similarity matrixes of photoquadrat data (fourth root transformed) and averaged by site to compare sites from PHA to sites from FFS. Further we sought to determine if results from PHA could be used to explain benthic community patterns observed at FFS.

Results

At Pearl and Hermes Atoll (PHA), benthic cover was determined for 406 photoquadrats from 34 sites representing 4 different wave exposure categories: 6 high, 13 intermediate-high, 12 intermediate-low, and 3 low. Turf algae were the dominant benthic organisms with an average atoll-wide cover of 55.9% (SE = 1.55%) when percent cover data from all sites across the atoll were averaged. Macroalgae, with 36 species recorded (Table 2.1), were the second most abundant functional group with percent cover averaging 15.8% (SE = 1.89%). Of all macroalgal species recorded, 58.3% (21 species) occurred in analyzed photoquadrats; with the remainder being observed along transect lines outside of sampling areas. *Microdictyon setchellianum* Howe was the largest contributor to overall macroalgal cover, and occupied an average of 10.9% (SE = 1.83%) of the substrata when data from all sites were pooled.   Coralline red algae (both encrusting and non-geniculate branching forms) occupied an average of 12.2 % (SE=

1.79%) of the substrata, while scleractinian coral species occupied an average of 8.33% (SE= 1.81%).

One-way ANOSIM

When sites were compared regardless of wave exposure through one-way ANOSIM, differences in percent cover of benthic species occurred among sites at PHA, with 39.1% of the 558 pair-wise comparisons having r-values > 0.75 (global R value = 0.567, number of permutated statistics greater than or equal to Global $R = 0$). Very few site comparisons were statistically similar (6.4% with r- values <0.25). Surprisingly, ANOSIM results did not reveal any apparent pattern among sites, and geographically close locations varied between being highly similar and highly dissimilar. This is exemplified by sites rPHA-43 and rPHA-39 (Fig. 2.3, 2.5 a, b); two geographically close (2.16 km) high wave exposure sites containing similar benthic composition ($r = 0.057$). Yet, other geographically close sites (rPHA-43 and rPHA-44 separated by 3.16 km) were dissimilar in composition and abundance ($r = 0.763$). In contrast, PHA-31 and PHA-26, located on opposite ends of the lagoon (26.4 km apart), were found to have similar benthic community assemblages ($r = 0.252$).

When using the one-way ANOSIM to compare sites from differing wave exposure categories; benthic communities at sites both within and between exposure categories were variable (Table 2.2). 26.7% of 15 pair-wise comparisons among sites assigned to the high wave exposure category were statistically similar. Yet, 66.6% of these comparisons revealed mid-range r-values that indicated neither substantial similarity nor dissimilarity in benthic species composition among sites (Table 2.2). A

similar pattern occurred among sites assigned to the intermediate-high wave category (12.1% of 91 comparisons had r-values <0.250 and 84.7% had r-values ranging between 0.251 and 0.750, Table 2.2). All 3 comparisons among sites assigned to low levels of wave exposure were similar, while comparisons among sites assigned to the intermediate-low category of wave exposure had the lowest occurrence of similarity (only 7.2% of comparisons had r-values <0.250). Additionally, the highest number of comparisons indicating dissimilarity occurred among sites experiencing intermediate-low levels of wave disturbance (29.1%, Table 2.2).

When comparing benthic composition among wave exposure categories, all comparisons indicated moderate to high dissimilarity with 66.9 to 100.0% having r-values greater than 0.5 (Table 2.2). No comparisons of benthic community composition (0.0%) indicated similarity between low wave exposure sites and sites with high, intermediate-high, or intermediate-low wave exposure. The highest number of comparisons indicating similarity occurred between sites with intermediate-high and intermediate-low levels of wave exposure with 33.1% of comparisons having r-values < 0.5 (Table 2.2).

Two-way nested ANOSIM

When sites within and between *a priori* wave exposure categories were compared using a two-way nested ANOSIM (sites nested within wave exposure categories), strong differences were observed between sites from the intermediate-high and low wave exposure categories ($r = 0.897$) and between sites from high and low wave exposure categories ($r = 0.556$, global r-value $= 0.199$, p$= 0.1\%$). Sites assigned to intermediate-

high and high wave exposure categories exhibited a moderate degree of similarity ($r = 0.354$), although comparisons between sites from intermediate-low and high levels of wave exposure and sites from intermediate-high and intermediate-low levels of wave exposure were found to be statistically similar ($r = 0.192, 0.124$, respectively). A higher degree of variation existed among sites within intermediate-low and low wave exposure categories than between the wave exposure categories themselves (r-value $= -0.386$).

Non-metric multi-dimensional scaling (nMDS) ordination and cluster diagram

The nMDS ordination and cluster diagram (Fig. 2.5 a, b) showed that sites experiencing high wave exposure (N facing fore-reef) were highly similar in terms of benthic species (composition and percent cover), as were sites among the low wave exposure category (lagoonal reefs). Similarly, sites assigned to intermediate-high exposure grouped together. The back-reef sites rPHA-32 and rPHA-34 also clustered with the intermediate-high wave exposure sites, indicating that benthic community composition, at these sites was more closely aligned to intermediate-high wave exposure sites than other intermediate-low wave exposure sites. Sites characterized by intermediate-low wave exposure were the most variable in terms of benthic species (composition and percent cover), and subsequently exhibited the greatest separation in the nMDS ordination and cluster analysis dendrogram (Fig. 2.5 a, b). In the nMDS ordination and the cluster diagram, the NW patch reef sites PHA-23 and PHA-24, which were characterized by high macroalgal cover (25.67% and 28.75% respectively), were distinct from other sites.

SIMPER analysis

Sites within each of the wave exposure categories exhibited highly similar benthic communities with the highest similarity occurring among sites assigned to the category of low wave exposure (77.09% similarity among sites) and the lowest similarity occurring among sites assigned to the intermediate-low category of exposure (58.99% similarity among sites).

The high wave exposure category located on the NW fore-reef had an average dissimilarity of 44.78% when compared to other wave exposure categories. This area was characterized by the highest abundance of crustose coralline red algae (36.53% cover) which contributed to 5.54% of the dissimilarity (Table 2.3). The rarity of *Microdictyon setchellianum* (Table 2.3) also contributed significantly to the dissimilarity between high wave exposure areas to other wave exposure categories (11.26 %). Additionally, the highest percent cover of the calcified green algal genus, *Halimeda,* and the encrusting morphology of the brown alga, *Lobophora variegata*, were found at sites with high wave exposure and were responsible for 5.49% and 6.46% of the dissimilarity, respectively (Table 2.3). Many sites categorized as high wave exposure located along the northwest fore-reef were also characterized by high relief with pinnacles of crustose coralline red algae. These sites also exhibited the highest density of *Porites lobata* Dana (6.49% cover)*,* a massive reef building species known to withstand high wave energy (responsible for 6.53% of the dissimilarity). Cover by turf algae and sand were relatively low at these sites (Table 2.3).

Areas with intermediate-high wave exposure were located along E and S facing fore-reefs and had an average dissimilarity of 41.88% when compared with other wave

exposure categories. These areas ranged in morphology from classic spur and groove formations to flat pavements, and were typically characterized by a diversity of benthic species. The largest abundance of *Microdicyton setchellianum* coupled with a relatively high occurrence of sand were found at these sites (Table 2.3) and were responsible for 9.32% and 4.12% of dissimilarity, respectively, when compared to other wave exposure categories. Species of coral, *Pocillopora,* were also most abundant at sites with intermediate-high levels of exposure (1.92% cover) with *P. meandrina* contributing 5.06% to the dissimilarity (Table 2.3).

Areas with intermediate-low wave exposure were located in both back-reef and lagoonal regions and had an average dissimilarity of 44.45% when compared to sites from other wave exposure categories. Sites within this category were variable in terms of their benthic community assemblages, and were the only locations containing the coral *Montipora capitata* Dana and *M. turgescens* Bernard (contributing 3.47% and 1.96% to the dissimilarity, respectively). These sites had the highest abundances of turf and macroalgae (Table 2.3; *Padina* sp., *Codium edule* Silva, *C. arabicum* Kützing, *Laurencia galtsoffii* Howe, *Liagora pinnatum* Harvey, *Dictyota* sp., and *Dictyosphaeria verslyusii* Weber-van Bosse). Additionally, relatively high percent cover of species of *Halimeda* was responsible for 9.47% of the dissimilarity observed, and low levels of crustose coralline red algae were responsible for 4.90% of the dissimilarity.

Areas of low wave exposure were located within the central part of the lagoon and surrounded by a network of reticulated reefs and had an average dissimilarity of 54.08% when compared to sites from other wave exposure categories. These sites were dominated by the finger coral *Porites compressa* Dana (37.77% cover), with very few

other coral species present. *P. compressa* contributed 15.10% to the dissimilarity between low wave exposure areas and other wave exposure categories. The absence of *M. setchellianum* was responsible for 10.72% of the dissimilarity of these sites. Turf algae were relatively low in abundance, although crustose coralline red algae commonly overgrew older portions of branched coral skeletons.

Species richness

Species richness of macroalgae and coral was found to be significantly higher at sites with both intermediate-low and intermediate-high levels of wave exposure than at sites with low wave exposure ($p = 0.0013$, $p = 0.0011$; Fig. 2.6 a, b, c). Sites with low wave exposure had relatively few species, with *Porites compressa, Cyphastrea ocellina* Dana, *Pocillopora damicornis* Linnaeus, and *Montipora capitata* being the only coral, and *Halimeda opuntia* (Linnaeus) Lamouroux and *Laurencia nidifica* J. Agardh being the only macroalga recorded. Sites with high wave exposure had moderate numbers of coral species, but were found to have significantly lower macroalgal species richness than sites with intermediate-high levels of wave exposure ($p = 0.0013$; Fig. 2.6 a, b). Results of ANOVAs using combined coral and macroalgal species richness suggest that sites with intermediate-high and intermediate-low levels of wave exposure contained significantly higher numbers of species than sites experiencing low levels of exposure while sites with high exposure had moderate numbers of species and were not significantly lower than sites with intermediate levels of wave exposure ($p = 0.0001$; Fig. 2.6 c).

Comparison to FFS

The 3-dimensional nMDS ordination grouped sites along the E and NE facing fore-reef at FFS together with intermediate-high wave exposure sites at PHA sites (Fig. 2.7 a). The cluster analysis reflects a similar pattern as seen at PHA (Fig. 2.7 b). As seen at PHA with sites rPHA-32 and rPHA-34 (Fig. 2.5 a, b) back reefs near the reef crest at FFS group with sites experiencing intermediate-high wave exposure (Fig. 2.7 b). Lagoonal sites at FFS exhibited a similar pattern to sites at PHA that had intermediate-low wave exposure. These sites exhibited relatively high spatial heterogeneity, similar to the highly variable intermediate-low wave exposure sites at PHA. Sites categorized as having high wave exposure at FFS did not form a distinct group as did high wave exposure sites at PHA (Fig. 2.7 a, b).

Discussion

Patterns of benthic communities

At Pearl and Hermes Atoll (PHA), sites assigned to high, low and intermediate-high wave exposure categories had similar benthic composition and abundance within each category and formed three distinct communities (Table 2.2; Fig. 2.5 a, b). Relative abundance of specific organisms was largely responsible for trends observed (Table 2.3). However, sites grouped within the intermediate-low wave exposure category were variable in benthic community composition (Table 2.2; Fig. 2.5 a, b). Therefore, our hypothesis that sites experiencing similar levels of wave exposure exhibit similar benthic community composition was partially supported.

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Low wave exposure sites had the highest degree of similarity among sites (Table 2.2; Fig. 2.5 a, b). With limited wave exposure in the inner lagoon, the scleractinian coral *Porites compressa* was the dominant species, forming nearly monospecific stands. Similar patterns have been reported to occur throughout Hawai`i, and show that protected areas such as embayments, lagoons, and deeper fore reef areas commonly contain monospecific stands of *Porites compressa* (Grigg and Maragos 1974; Dollar 1982; Grigg 1983; Storlazzi et al. 2005). While several researchers have noted the competitive dominance of this species, there have been very few studies that examine the mechanisms that give *P. compressa* a competitive edge over other corals in Hawai`i.

Most corals have reduced photosynthetic and calcification rates with reduced water motion (Dennison and Barnes 1988; Lesser et al. 1994). This leads us to question how *P. compressa* is able succeed in low water motion conditions. One possible explanation for the success of *P. compressa* in low wave exposure conditions is that its finger-like morphology and subsequent high surface area to volume ratio (SA/V) increase gas and nutrient exchange as well as increasing its ability to capture prey (Sebens and Johnson 1991; Lesser et al. 1994; Shashar et al. 1996). *P. compressa* has also been shown to have thinner diffusion boundary layers than other corals (possibly due to its high SA/V), and the length of some of the "fingers" may enable *P. compressa* to stimulate turbulent mixing at least in small scales (Shashar et al. 1996). Therefore, the same morphology that renders *P. compressa* vulnerable in high wave conditions potentially enables *P. compressa* to have better gas and nutrient exchange than other organisms in low wave exposure conditions, with the benefit of increased photosynthesis and calcification rates. This mechanism may allow *P. compressa* to out-compete other

organisms in the absence of wave exposure, thus creating a highly homogeneous benthic community dominated by *P. compressa*.

Sites characterized with high wave exposure exhibited greater variability than the reciprocal situation, however they still formed a rather distinct group largely characterized by the abundance of crustose coralline red algae (Table 2.2, Fig. 2.5 a, b). The dominance of crustose coralline red algae as a functional group at high wave exposure sites is likely an example of disturbance-mediated competition (36.53% cover; Table 2.3) but this concept awaits rigorous testing. Because of the encrusting nature of crustose coralline red algal species, these organisms are often highly resistant to extreme wave energy (MacCaughey 1918; Adey and Vassar 1975). High wave energy decreases the effectiveness of grazers and increases nutrient availability by constantly perturbing the diffusion boundary layer (Steneck 1986; Hurd 2000). This combination makes areas with high wave energy a productive refuge for crustose coralline red algae (Adey and Vassar 1975). Because other organisms especially non-encrusting organisms are more susceptible to damage at high wave exposure (Storlazzi et al. 2005), crustose coralline red algae can competitively dominate these high energy areas.

Sites categorized as having intermediate-high wave exposure were fore-reef sites along the east and south sides of Pearl and Hermes Atoll. These sites exhibited a relatively high degree of similarity in benthic community composition (Fig. 2.5 a, b). Although not as frequent or intense as sites with high wave exposure, episodic high wave heights and periods occur at sites with intermediate-high wave exposure, (Fig. 2.4) resulting in periodic disturbance conditions for many organisms. This disturbance may explain the relative high abundance of the colonizing coral species *Pocillopora*

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meandrina and the robust coral species *Porites lobata* (Grigg and Maragos 1974;

Storlazzi et al. 2005). *Pocillopora meandrina* is commonly referred to as the

"cauliflower" coral due to its compact branching morphology. Not only is this species

one of the first species to colonize disturbed habitats (Grigg and Maragos 1974), but its

thick branches are capable of withstanding relatively high wave energy (Storlazzi et al.

2005).

The intermediate level of water motion may also provide an ideal midpoint

between nutrient delivery and disturbance for *Microdictyon setchellianum*. Although the

"net" like morphology of *M. setchellianum* would seem to be favored in low wave energy

sites, its distribution is limited to sites with intermediate levels of wave exposure (Table

2.3). One explanation for this discrepancy is the high occurrence of epiphytes on tissue

of *M. setchellianum*. Epiphytes have been observed to completely cover *M.

setchellianum* at PHA making the alga nearly undetectable to divers in the field. While in

some cases epiphytes have been shown to benefit the host alga by increasing surface area,

epiphytes can also increase the thickness of the diffusion boundary layer making gas and

nutrient exchange more difficult (Hurd 2000). This, in addition to other potential limiting

factors such as high herbivory, may limit *M. setchellianum* in low wave exposure areas.

In high wave exposed areas, the morphology of *M. setchellianum* is likely not sufficiently

robust to remain attached to the substrate thus limiting its distribution to sites with

intermediate levels of wave exposure.

Benthic composition at sites with intermediate-low wave exposure was highly

variable among sites and did not support our hypothesis that sites experiencing similar

wave exposure regimes would have similar benthic composition. However, the

intermediate-low wave exposure category is comprised of both patch reefs and back reefs that are located at varying distances from the reef crest (Fig. 2.3). Variations in the morphology of the reef crest likely effects intensity of wave exposure at sites within the lagoon (Fulton and Bellwood 2005). Those sites near emergent reef crests are likely more protected from wave exposure than those near a submerged reef crest (Fulton and Bellwood 2005). For instance sites rPHA-32 and rPHA-34, located just 10 meters from a partially submerged reef crest have benthic compositions more similar to sites with intermediate-high wave exposure than that of the intermediate-low wave exposure category (Fig. 2.3).

Seasonal differences in the wave exposure may also play a role in the variability of benthic composition observed at sites with intermediate-low wave exposure (Storlazzi et al. 2005). The NW side of the lagoon likely experiences higher wave energy and subsequent water motion in the winter whereas the southern side of the lagoon likely experiences higher wave energy and water motion in the summer. This variation in wave exposure on a temporal scale, may influence spatial differences of benthic community structure within the lagoon. Since this study was conducted in the summer, it is likely that fewer disturbances from wave exposure were occurring at NW reefs in the lagoon than at Southern reefs in the lagoon. If sampling were possible during winter months when wave exposure was higher at NW lagoonal reefs, we would expect to see less abundance of macroalgal species that are susceptible to being damaged from waves than were present in the summer months. Lagoonal sites that make up the intermediate-low wave exposure category likely experience more variable wave intensity and frequency than sites within the other wave exposure categories. Long term, fine scale measurements of wave energy

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and water motion within the lagoon at PHA would provide essential quantification of this relationship between wave exposure and benthic community structure.

While *a-priori* wave exposure categories were supported by our results, some comparisons among sites within wave exposure categories were found to be statistically dissimilar (Table 2.2). Such dissimilarities occurred in three of four wave exposure categories with low wave exposure sites being the outlier (Table 2.2). Additionally, the 2-way nested ANOSIM results showed that some groups were not statistically distinct. This may be due to the large variation in benthic community composition at sites with intermediate-low wave exposure which allowed for some sites within the intermediate-low wave exposure group to be more similar to sites in other groups than sites within the intermediate-low wave exposure group. However, it is likely that there are many structuring forces other than wave exposure at play at PHA. Differences in resource availability, herbivory, competition, etc. within each wave exposure category may cause within category variation in benthic communities (Hutchinson 1959; Menge and Sutherland 1987; Menge 1992; Power 1992). Therefore, while wave exposure appears to be a dominant determinant in benthic community structure at PHA, additional factors such as herbivory may play a significant role.

Coral and macroalgal species richness

In accordance with the intermediate disturbance hypothesis (IDH), species richness of coral and macroalgal communities was higher at sites with intermediate wave exposure (both intermediate-high and intermediate-low) than in areas of low wave exposure (Fig. 2.6 a, b, c). Within and among site heterogeneity, observed at

intermediate-high and intermediate-low wave exposure sites respectively, are explanations for higher numbers of species in these areas (Table 2.2; Fig. 2.5 a, b). Seasonal storms and variation in the vulnerability of sites to disturbance creates temporal and spatial heterogeneous habitats or patches within ecosystems (Levin and Paine 1974; Connell 1978; Wooten 1998). These patches allow for organisms at different successional stages (primary to climax) to coexist and create areas with maximum species coexistence (Grigg and Maragos 1974; Connell 1978). Therefore, the co-occurrence of species representative of multiple stages of succession (seasonal macroalgae, late succession coral species: *Montipora capitata,* and early succession coral species: *Pocillopora meandrina*) at sites with both intermediate-high and intermediate-low levels of wave exposure at PHA supports predictions from the IDH (Table 2.3; Grigg and Maragos 1974; Grigg 1983).

It is tempting to speculate that highest species richness at sites with intermediate levels of wave exposure is associated with extreme high and low wave exposure that limit the distributional range of some organisms. Some organisms at PHA have large distributional ranges occurring in each wave exposure regime such as species of the green alga *Halimeda* while other organisms have a more limited distribution such as the green alga *Microdictyon setchellianum* and species of the scleractinian coral *Montipora* (Table 2.3). Sites with intermediate wave exposure are less extreme in terms of both damage from waves and boundary layer thickness, less specialization and/ or adaptation is likely required to be successful in these areas. Therefore, limitation of distribution at the extremes by a number of potential mechanisms (i.e. physiological limitation, disturbance,

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competition) may cause there to be greater overlap in the distribution of organisms at a mid level, thus explaining highest species richness at intermediate levels.

Turf and crustose coralline red algae were abundant at many sites. Increasing our taxonomic resolution of these fundamental groups would impact the results of this study by either (1) altering the patterns observed, or by (2) reinforcing our observed trends. For example, turf algae accounted for 53% of algal diversity observed at French Frigate Shoals (Vroom et al. 2006). Crustose coralline red algae were also abundant, and in a similar study, Kilar and McLachlan (1989) found 17 species of crustose coralline red algae in high wave exposure areas in Panama. At PHA, field observations characterize sites with high wave exposure as having large expanses of what appears to be a few dominant species of crustose coralline red algae. This leads us to believe that crustose coralline red algal diversity would follow a similar pattern to that observed in coral and macroalgal communities in these areas (Fig. 2.4), although this awaits testing.

Comparison to FFS

Patterns of benthic community structure observed at PHA were compared with those observed at French Frigate Shoals (FFS) by combining data sets from this study with a similar analysis recently completed at FFS (Vroom et al. 2005). Vroom et al. (2005) examined differences in benthic communities among geomorphic zones: fore-reef, back-reef and lagoon reefs, and found most fore- and back-reef sites to be biologically similar along the E and NE emergent reef. Sites within the lagoon were highly variable (Vroom et al. 2005). Based on this comparative approach, it is likely that wave exposure may also influence benthic community structure at FFS but geomorphology of FFS also

plays an important role. Multivariate analyses yielded some similar results at both FFS and PHA (Fig. 2.7 a, b). Sites along the east and NE emergent reef crest sites at FFS formed a relatively distinct group in the 3-dimensional nMDS ordination and the cluster diagram (Fig. 2.7 a, b). Some back and patch reefs near the reef crest grouped more closely with intermediate-high wave exposure sites at FFS than intermediate-low, similar to the back reef sites rPHA-32 and rPHA-34 at PHA (Fig. 2.5 a, b; 2.7 a, b). Additionally, variability of benthic composition within the lagoon at FFS was similar to that seen in comparable areas at PHA and may indicate that FFS experiences variable levels of water motion similar to that expected at intermediate-low wave exposure sites at PHA. Interestingly, sites identified as high wave exposure areas at FFS were distinct from one another and were not similar to high wave exposure sites at PHA. Since an emergent reef crest facing NW was absent at FFS, sites characterized as have high wave exposure were patch reefs rather than fore-reefs as seen at PHA. One of these two sites was La Perouse pinnacle, a basaltic pinnacle surrounded by a coral shoal which makes it unique from most areas in the Northwestern Hawai`ian Islands. While the two high wave exposure sites at FFS may experience similar wave conditions as PHA, the morphology of the reef likely influence the level of force experienced (Fulton and Bellwood 2005).

Results of one-way ANOSIM at FFS showed fewer differences among overall site comparisons with only 7.67% having r-values greater than 0.75 (Vroom et al. 2005) as compared to 39.1% at PHA. In addition, site comparisons were more frequently similar at FFS with 21.69% having r-values < 0.25 compared to only 6.42% at PHA. One possible explanation for the higher variability at PHA is the existence of a defined reef crest along all sides of the atoll with the exception of the SW side. The role of

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geomorphology as an factor impacting long term fine scale hydrodynamic features of NWHI awaits future examination.

Conclusion

This study used multivariate statistics to test predictions regarding the influence of wave exposure on the structure of benthic communities at PHA. Results indicate that sites experiencing high, intermediate-high and low wave exposure had similar benthic community composition as hypothesized, while sites with intermediate-low levels of wave exposure had variable benthic community composition. In addition, sites experiencing intermediate-low and intermediate-high wave exposure had the highest coral and macroalgal species richness supporting expectations based on Connell's Intermediate Disturbance Hypothesis. The ability of specific organisms (i.e. *Porites compressa* or crustose coralline red algae) to cope with destructive wave energy at high levels of wave exposure and/or reduced gas exchange and nutrient availability at low levels of wave exposure likely contributes to the patterns observed in benthic community composition. Increased knowledge on the taxonomy, ecology, and physiology of significant organisms such as crustose coralline red algae, turf algae, *Porites compressa*, and *Microdictyon setchellianum*, continued long-term and seasonal monitoring, and additional fine-scale long-term estimate of the hydrodynamic regime (wave energy and water movement) across atolls, will further enable scientists to examine and understand the role of the physical environment as a structuring force for the benthic community. Experimental studies on coral reefs controlling for variables of wave exposure, herbivory, and nutrient availability in areas removed from human impact would additionally

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enhance our understanding of factors that influence these communities. While it is likely

that multiple factors are important in structuring coral reef communities, results from the

current study suggest that wave exposure has a notable influence on benthic community

assemblages at PHA.

Table 2.1. Macroalgal Species list from Pearl and Hermes Atoll, Northwestern Hawai`ian Islands.  Validity of species and authors ascertained through AlgaeBase (Guiry et al. 2006). * = new record for Pearl and Hermes Atoll;† = new record for the Northwestern Hawai`ian Islands.

RHODOPHYTA
  Ceramiales
   Ceramiaceae
    Haloplegma duperreyi Montagne
   Dasyaceae
    Dasya iridescens* (Schlech) Millar & Abbott
   Rhodomelaceae
    Amansia fimbrifolia Norris
    Chondrophycus parvipapillatus* (Tseng) Garbary & Harper
    Laurencia crustiformans* † McDermid
    L. decumbens* Kützing
    L. galtsoffii Howe
    L. mariannensis* Yamada
    L. nidifica* Agardh
  Corallinales
   Corallinaceae
    Jania adhaerens Lamouroux
  Gigartinales
   Peyssonneliaceae
    Peyssonnelia sp. Decaisne
  Nemaliales
   Liagoraceae
    Liagora pinnata* Harvey
  Rhodymeniales
   Faucheaceae
    Halichrysis coalescens* (Farlow) Norris & Millar
   Rhodymeniaceae
    Chrysymenia okamurae* Yamada & Segawa
CHLOROPHYTA
  Bryopsidales
   Caulerpaceae
    Caulerpa serrulata (Forsskål) Agardh
    C. webbiana Montagne

   Codiaceae
    Codium arabicum Kützing
    C. hawaiiense* Silva & Chacana
    C. subtubulosum* Okamura
   Halimedaceae
    Halimeda discoidea Decaisne
    H. distorta* (Yamada) Hillis-Colinvaux
    H. opuntia (Linnaeus) Lamouroux
    H. velasquezii Taylor
  Cladophorales
   Anadyomenaceae
    Microdictyon setchellianum Howe
   Siphonocladaceae
    Boodlea composita* (Harvey) Brand
    Dictyosphaeria cavernosa* (Forsskål) Børgesen
    D. versluysii* Weber-van Bosse
  Chlorococcales
    Palmophyllum crassum (Naccari) Rabenhorst
  Dasycladales
   Dasycladaceae
    Neomeris van-bosseae* Howe
PHAEOPHYTA
  Dictyotales
   Dictyotaceae
    Dictyota sp. Lamouroux
    Lobophora variegata* (Lamouroux) Womersley ex Oliveira
    Padina boryana* Thivy
    Stypopodium flabelliforme Weber-van Bosse
  Fucales
   Sargassaceae
    Turbinaria ornata (Turner) J. Agardh

Table 2.2. Comparison of pairwise *r*-statistics from one-way ANOSIM of sites at PHA. Sites from within and among exposure categories were compared and the number of comparisons that fell within each *r*-statistic range are presented as percentages. *N* = number of pairwise comparisons in each group.

Sites compared	*r*-values			
	Statistically similar			Statistically dissimilar
	0.000-0.250	0.251- 0.500	0.501-0.750	0.751-1.000
High (*n*= 15)	26.7%	53.3%	13.3%	6.7%
Intermediate high (*n*= 91)	12.1%	40.7%	44%	3.3%
Intermediate low (*n*= 55)	7.2%	36.4%	27.3%	29.1%
Low (*n*= 3)	100.0%	0%	0%	0%
High to intermediate high (*n*= 84)	1.2%	10.7%	46.4%	41.7%
High to intermediate low (*n*= 69)	2.9%	4.3%	24.6%	68.1%
High to low (*n*= 18)	0%	0%	33.3%	66.7%
Intermediate high to intermediate low (*n*= 154)	7.8%	25.3%	36.4%	30.5%
Intermediate high to low (*n*= 42)	0%	0%	21.4%	78.6%
Intermediate low to low (*n*= 33)	0%	3%	24.2%	72.7%

Table 2.3. Average percent cover of organisms within wave exposure categories. Percent cover (standard deviation) of major space occupying organisms within the four wave exposure categories. Bold numbers indicate the wave exposure category with the highest average percent cover of a particular organism.

	High	Intermediate high	Intermediate low	Low
Algae				
Turf	57.32 (6.23)	73.95 (9.63)	**75.11** **(9.77)**	52.66 (7.33)
Coralline	**36.65** **(10.49)**	13.76 (9.28)	6.47 (5.64)	16.82 (8.28)
Halimeda spp.	**5.50** **(0.93)**	2.70 (2.59)	5.42 (12.27)	0.18 (0.26)
Microdictyon setchellianum	0.06 (0.14)	**23.10** **(14.14)**	18.33 (16.30)	0.00 (0.00)
Other Macroalgae	3.47 (4.22)	1.05 (0.79)	**3.94** **(4.12)**	0.00 (0.00)
Coral				
Montipora spp.	0.00 (0.00)	0.00 (0.00)	**5.14** **(9.73)**	0.00 (0.00)
Pocillopora spp.	1.71 (2.58)	**1.92** **(2.67)**	1.08 (1.42)	0.00 (0.00)
Porites compressa	0.31 (0.46)	0.12 (0.24)	0.19 (0.62)	**37.77** **(11.21)**
Porites lobata	**6.49** **(7.14)**	2.36 (3.52)	0.71 (2.02)	0.00 (0.00)
Other Coral	**1.47** **(2.84)**	0.76 (0.81)	0.03 (0.08)	0.03 (0.04)
Other				
Cyanobacteria	0.00 (0.00))	0.13 (0.46)	0.45 (1.41)	**0.56** **(0.79)**
Sand	3.60 (3.36)	6.31 (5.71)	**7.65** **(4.69)**	3.76 (5.00)
Other	**4.46** **(2.83)**	2.90 (1.07)	1.15 (0.95)	3.98 (2.02)
# of Scleractinian Coral Species	6.50 (4.55)	7.31 (2.84)	6.75 (2.60)	4.00 (0.00)
# of Macroalgal Species	2.83 (1.33)	5.39 (1.19)	4.75 (2.18)	0.67 (1.16)
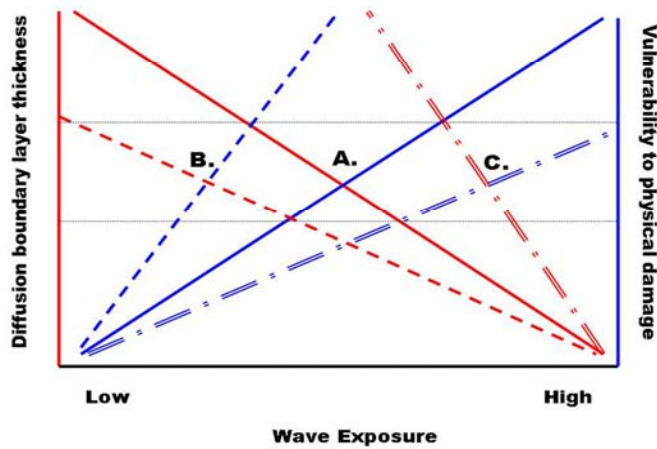
Figure 2.1. Morphological trade-offs of photosynthetic marine organisms along a wave exposure gradient. Diffusion boundary layer (DBL) thickness (left vertical axis) decreases with increasing wave exposure (red lines). Vulnerability of organisms to physical damage (right vertical axis) increases with increasing wave exposure (blue lines). In this model, particular morphological strategies are represented by the intersections of red and blue lines. The intersection space is bounded at the top of the graph by the Maximum Survival Threshold (MST, upper grey line), which represents both maximum DBL thickness and maximum vulnerability, and at the bottom of the graph by the morphological trade-off limitation (lower grey line). Morphological strategies (intersections) in this model are limited to the intersection space bounded by these two lines. The solid line intersection (a) represents a morphological strategy suited to intermediate levels of wave exposure. The dashed line intersection (b) represents a morphological strategy suited to low wave exposure. This strategy requires an organism to decrease its DBL thickness (slope of red dashed line) to remain below the maximum threshold. However, to remain above the morphological tradeoff limitation requires a concomitant increase in vulnerability to physical damage (slope of blue dashed line). The dot-dash line intersection (c) represents a morphological strategy suited to high wave exposure. This strategy requires an organism to decrease its vulnerability to physical damage (slope of blue dot-dash line) with a concomitant increase in DBL thickness (slope of red dot-dash line).

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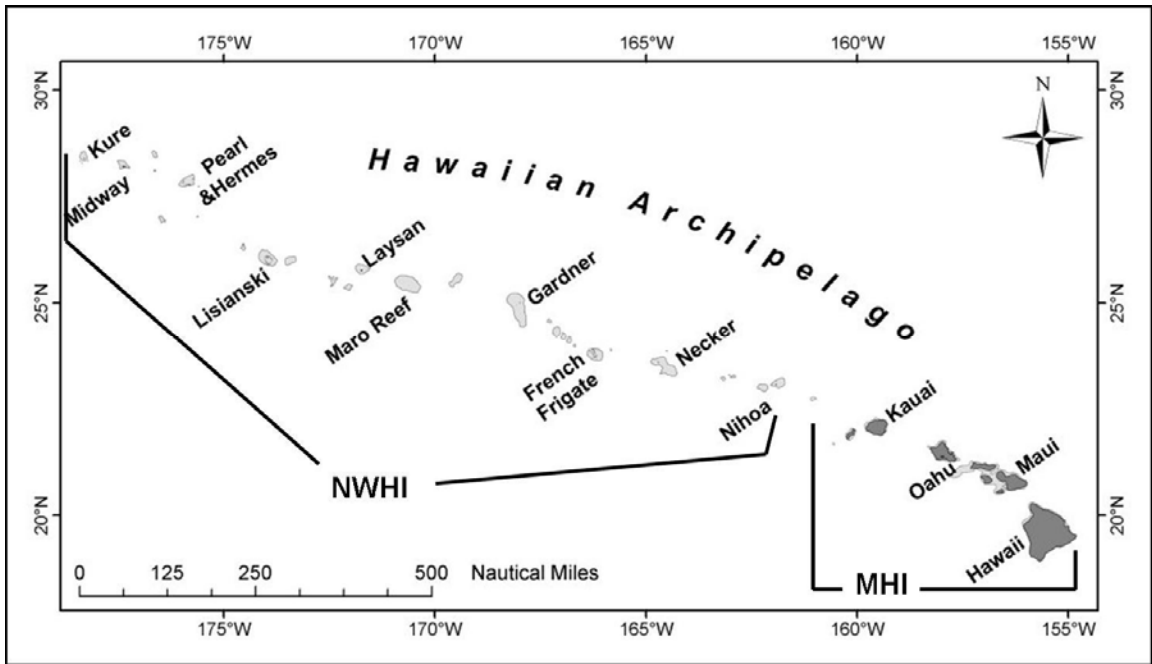
Figure 2.2. Map of the Hawai`ian Archipelago depicting the location of Pearl and

Hermes Atoll in the Northwestern Hawai`ian Islands (NWHI). The NWHI are a chain of

low lying islands, banks and atolls that are federally protected and located to the NW of

the Main Hawai`ian Islands (MHI).
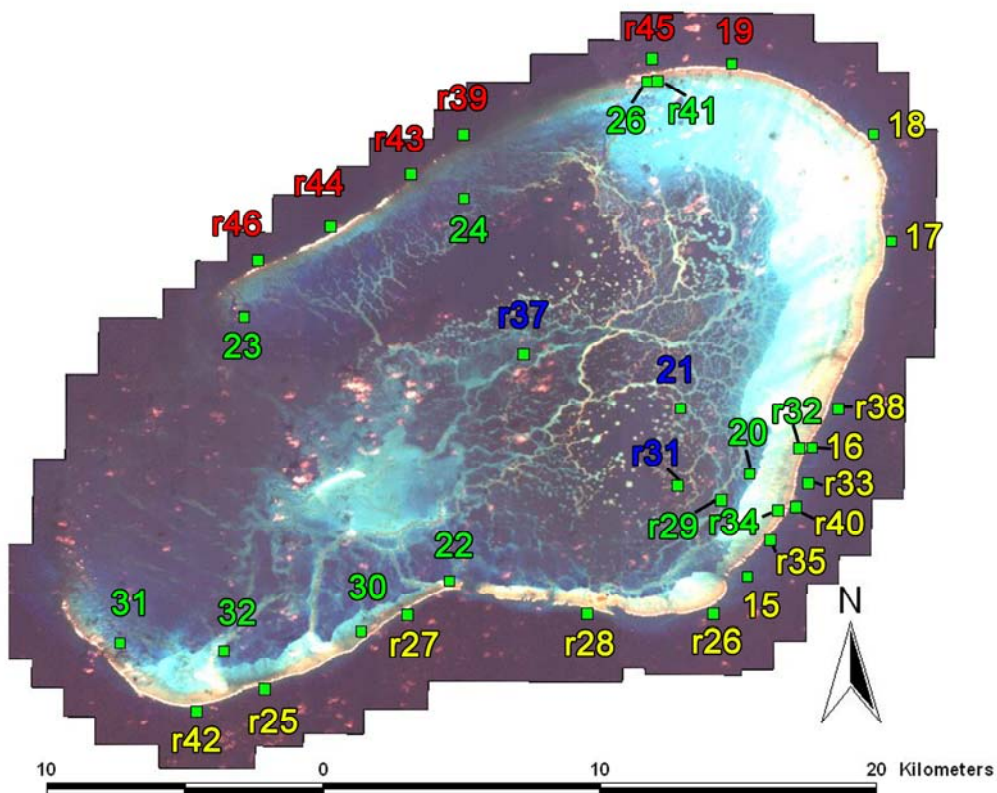
Figure 2.3. Ikonos satellite image of Pearl and Hermes Atoll. Numbers represent study sites. Colors of each number represent wave exposure categories: red = high, yellow = intermediate- high, green = intermediate-low, blue = low.

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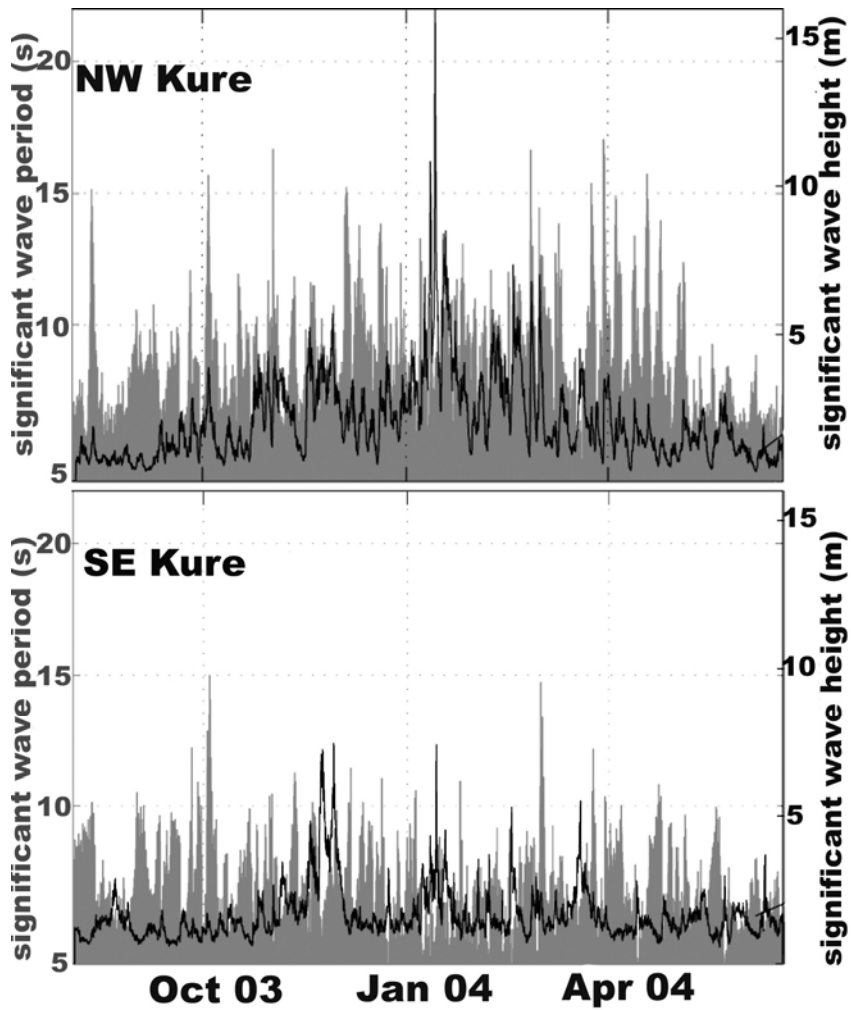
Figure 2.4. Significant wave height (m) and wave period (s) for two sites, one on the NW facing fore-reef and one on the SE facing fore-reef, at Kure Atoll in the NWHI. Wave height was measured from August 2003- June 2004 using Seabird Electronics SBE, in-situ wave gauges moored at each of the locations.
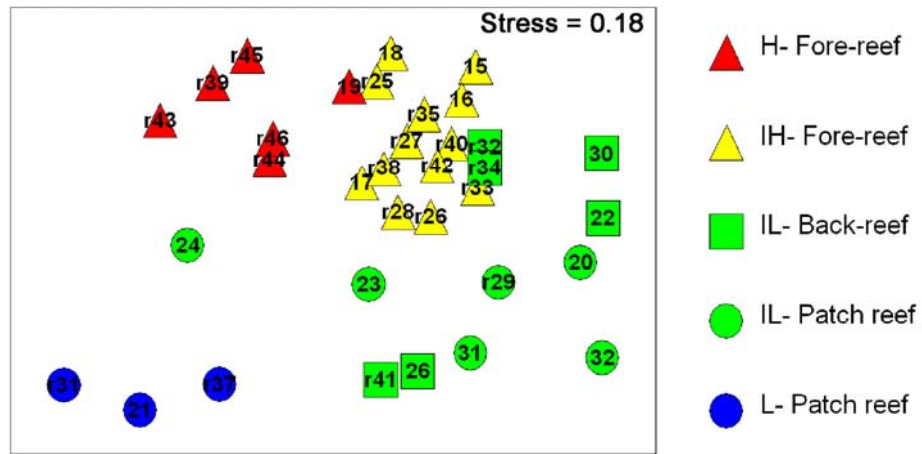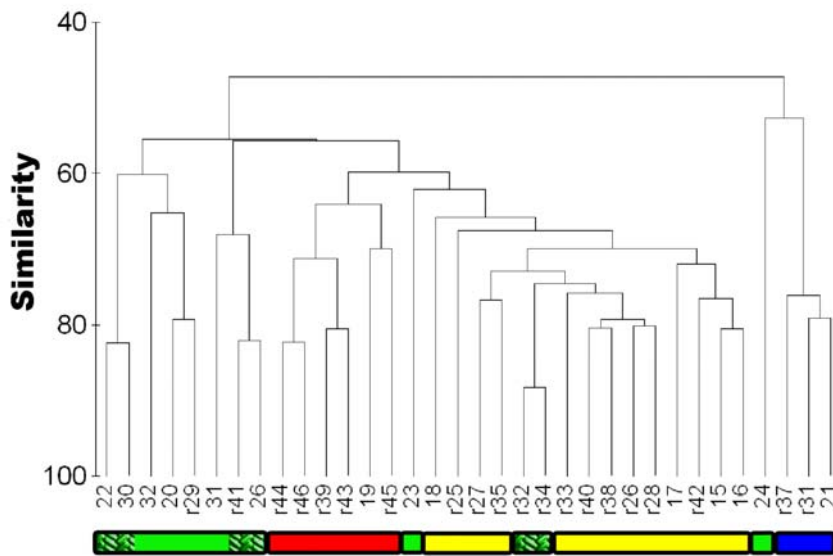
Figure 2.5. (a) Non-metric multi-dimentional scaling (nMDS) plot and (b) cluster diagram showing relationships of sites to one another. For both A and B, colors represent wave exposure categories: red= high, yellow = intermediate-high, green = intermediate-low, blue = low. In A, shapes represent geomorphology zones (fore-reef, back-reef, and patch reef). In B, cross hatching represents back-reef sites.

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a. macroalgae species richness

F = 13.819
p = 0.0013

b. coral species richness

F = 9.855
p = 0.0011

c: macroalge and coral species richness

F = 19.581
p = 0.0001
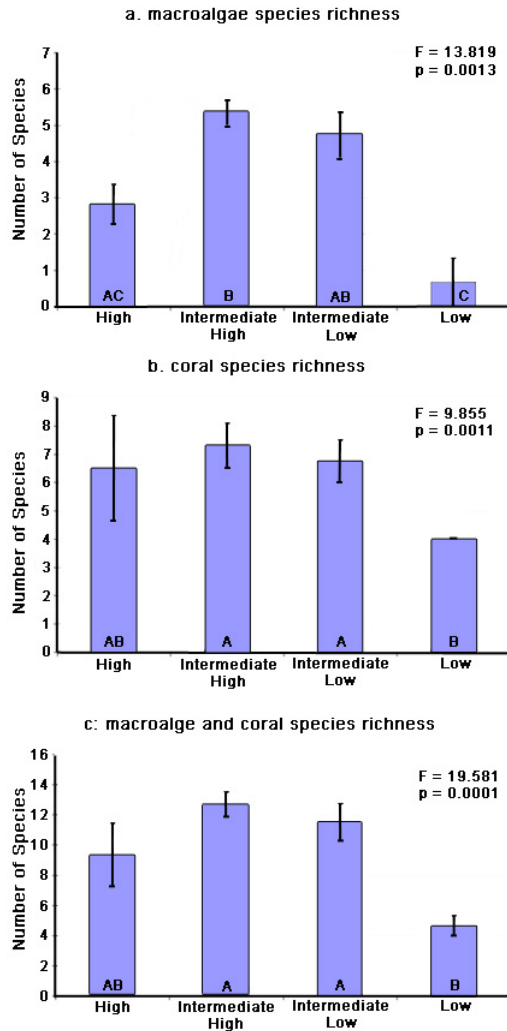
Figure 2.6. Comparison of species richness among wave exposure categories for (a) macroalgae, (b) coral, and (c) combined macroalgae and coral. Values for macroalgae were based on photoquadrat percent cover data and values for coral were based on *in situ* species lists combine with percent cover photoquadrat data. Error bars represent one standard error of the mean. Statistical results of Welch's one-way ANOVA are shown, differences were significant after Bonferroni adjustment for multiple comparison (α = 0.05). Exposure groups with different letters are significantly different (Dunnett's T3 pair-wise comparisons).

Figure 2.7. (a) 3-dimensional Non-metric multi-dimentional scaling (nMDS) plot and (b) cluster diagram showing relationships of sites to one another and comparing PHA to FFS. Colors represent wave exposure categories: red= high, yellow = intermediate-high, green = intermediate-low, blue = low. For a, filled in shapes represent PHA and open shapes represent FFS. For b, the letter F stands for FFS and the letter P represents PHA.

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CHAPTER 3

FACTORS INFLUENCING BENTHIC COMMUNITY STRUCTURE ON A NEAR-PRISTINE CORAL REEF

Abstract

Biotic and abiotic factors structure coral reef communities in tropical regions worldwide. The dominant factors are likely determined, in part, by the level of anthropogenic impact present at any particular location. Variations in anthropogenic impact as well as natural variations in biotic and abiotic factors have limited the ability of scientists to make global comparisons among benthic coral reef communities. Rather than one single factor being most influential in structuring coral reef benthic communities, reefs likely exist along a gradient of health and the factors that determine benthic community structure likely vary along this gradient. Here we examine potential determinants of coral reef community structure in a near-pristine system, Pearl and Hermes Atoll (PHA) of the Northwestern Hawai`ian Islands. We measured percent cover of benthic organisms along with herbivorous fish density and biomass, urchin density, nutrient availability, and wave exposure. Multi-linear regressions revealed that for each of the benthic functional groups examined (coral, frondose macroalgae, crustose coralline red algae, and turf algae) herbivorous fish density was a significant explanatory factor. Herbivorous fish biomass, urchin density and wave exposure were additionally significant in models explaining benthic community composition. When all benthic functional groups were combined in a multivariate analysis, herbivorous fish density combined with wave exposure was identified as having the highest significant correlation

with benthic community composition at PHA. Nutrient availability, based on algal tissue nutrient content, did not correlate with percent cover of benthic organisms. Our results suggest for this site which represents one end of a global continuum ranging from near-pristin to highly degraded, top-down mechanisms have primacy over bottom-up mechanisms in an ecosystem free from direct anthropogenic impacts, including fishing. Additionally, the role of wave exposure is emphasized along with the potential of direct competition between coral and frondose algae.

Introduction

As natural ecosystems become increasingly encroached upon by human activity (Vitousek et al. 1997), many are being altered to a less functional and less desirable state, a phenomenon known as a phase shift (Hughes 1994; Folke et al. 2004). In tropical reef ecosystems, these phase shifts specifically refer to once coral dominated reefs changing to algal dominated reefs (Pastorok and Bilyard 1985; Hughes 1994; Hunter and Evans 1995). Past research has suggested that the two main factors linked to reef phase shifts are over-fishing and increased nutrient loads, theories commonly known as "top-down" and "bottom-up" mechanisms, respectively (Hughes 1994; Stimson et al. 1996; 2001; Hughes et al. 1999; LaPointe 1997; 1999; Aronson and Precht 2000). In addition to anthropogenic influence on coral reefs, natural processes and physical parameters such as wave exposure and depth affect community structure on coral reefs (Connell 1978; Littler and Littler 1984; Huston 1985; Kilar and McLachlan 1989; Connell et al. 1997). The goal of this study was to quantify the extents to which each of these well-studied factors (i.e. herbivory, nutrient availability or wave exposure) influence community structure in a

near-pristine tropical reef system. Because of the increased stressors to many reef ecosystems and the desire to protect the remaining coral reefs on a global scale, understanding the extents to which factors influence coral reef communities in near pristine environments is of great importance.

Complex interactions along with spatial and temporal variability among both biotic and abiotic factors make pinpointing a single dominant factor responsible for regulating community structure an extremely difficult and often confounded task (Connell 1978; Menge and Sutherland 1987; Hunter and Price 1992; Menge 1992; Power 1992). Despite such complexities, researchers often argue in favor of one particular factor (e.g. disturbance or trophic interactions) as being more important than others (Hairston et al. 1960; Connell 1978; Hughes 1994). One of the most debated factors held to determine community structure is interactions among trophic levels (Hairston et al. 1960; Ehrlich and Birch 1967; Power 1992; Menge 1992; Hughes 1994; LaPointe 1997). Ecologists are largely separated into two camps, those that support top-down determination of community structure, and those that support bottom-up determination of community structure. The "world is green" hypothesis (Hairston et al. 1960), one of the first arguments that favored top-down control, states that the plants dominate because predators (including parasites) control herbivore populations. Although subsequent investigations provided further evidence that favor top-down mechanisms (Paine 1966; Menge et al. 1986; Hughes 1994), substantial evidence also exist for bottom-up control especially in resource limited ecosystems (Pastorak and Bilyard 1985; Hunter and Evans 1995; Smith et al. 2001). The importance of primary producers was simply stated by Hunter and Price (1992) who wrote, "removal of higher trophic levels leaves lower levels

present (if perhaps greatly modified), whereas the removal of primary producers leaves no system at all."

Coral reef ecology has been a more recent focus of the debate over top-down (herbivory) vs. bottom-up (nutrient availability) structuring of communities. Whether the phase shift from a coral to algal dominated reef at Discovery Bay in Jamaica was due to release from urchin grazing (top-down) or nutrient pollution (bottom-up) has been hotly debated for many years (Hughes 1994; LaPointe 1997; 1999; Hughes 1999; Aronson and Precht 2000; NOAA's Coral Health and Monitoring Program (CHAMP) list-serve for coral reef information and news 2006). Both herbivory and nutrient availability have been shown to effect coral reef communities. For instance, high levels of herbivory have been shown to increase algal diversity, and herbivore (fish and urchins) exclusion has been shown to increase algal abundance and/ or biomass (Hatcher and Larkum 1983; Lewis 1985; 1986; Carpenter 1986; Hixon and Brostoff 1996; Hay 1997; Miller et al. 1999; Smith et al. 2001; Thatcher et al. 2001). Additionally, increases in nutrient availability to tropical algae have been shown to increase algal growth rates (LaPointe et al. 1987; Larned 1998; Smith et al. 2001; Stimson et al. 2001; Fong et al. 2003; and LaPointe et al. 2004). Therefore, both herbivory and nutrient availability appear to influence benthic community structure.

Recognizing that both herbivory and nutrient availability likely explain algal and coral distributional patterns on tropical reefs, Littler and Littler (1984) published the Relative Dominance Paradigm (RDP). According to the RDP, reefs exhibiting low nutrients and high grazing pressures (hypothetically characteristic of pristine reefs with low human impact) were hypothesized to be dominated by scleractinian coral species

while those with high nutrients and low grazing (hypothetically characteristic of areas

with high human impact) were hypothesized to be dominated by frondose algae (Fig.

1.1). The RDP was experimentally tested and supported in coral reef ecosystems by

Smith et al. (2001). The additive effect of herbivore removal and high nutrient

availability allowed experimental tiles to have the greatest biomass of algae, supporting

the theory that both top-down and bottom-up trophic level interactions are important in

shaping tropical reef communities. However, in other experiments examining these two

factors only herbivory showed significant changes in benthic communities (Miller et al.

1999; Thacker et al. 2001). Hatcher and Larkum (1983) found that removing herbivores

consistently impacted community structure while nutrient addition had lesser and more

variable results. The consistency of experimental results using herbivore exclusion in

contrast to the inconsistency of experiments exploring the addition of nutrients,

stimulates a continued debate over which factor, herbivory or nutrient availability, has

primacy in structuring benthic coral reef communities and therefore which factor has

highest priority for management (NOAA's CHAMP list-serve for coral reef information

and news 2006).

In addition to herbivory and nutrient availability, there are many other factors that

potentially influence coral reef structure. For instance, wave exposure has been shown to

effect coral reef community assemblages with areas experiencing intermediate levels of

disturbance from waves containing the highest diversity of coral reef organisms (Grigg

and Maragos 1974; Dollar 1982; Grigg 1983; Kilar and McLachlan 1989; and

Freidlander et al. 2003). Areas with low levels of wave exposure often exhibited less

diverse yet highly abundant coral communities (Grigg and Maragos 1974; Dollar 1982;

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Grigg 1983; Chapter 2). Other factors such as depth, temperature, inter- and intra-specific competition are also known to affect coral reef community structure (McCook et al. 2001).

Coral reefs are complex systems that have been shown to have less similarity and more variability within and among locations than predicted from neutral models as well as observed in other systems (Dornelas et al. 2006). Variation in reefs is likely due to differences in both natural processes (environmental stochasticity) and degrees of anthropogenic impact (Pandolfi et al. 2003; Dornelas et al. 2006). One way in which reefs world-wide have been compared is by placing them along a continuum from near-pristine to highly degraded (Pandolfi et al. 2003). Rather than one single factor being the most influential in determining benthic community structure in coral reefs world-wide, it is likely that reefs exist along a gradient and factors most responsible for determining benthic community structure vary along this gradient. For the purpose of this study we will examine factors that influence coral reef community structure in a near-pristine reef one end of this continuum.

In this study, observational data herbivorous fish density and biomass, urchin density, wave exposure, and depth were collected in concert with benthic percent cover data in a near-pristine reef, Pearl and Hermes Atoll located in the Northwestern Hawai`ian Islands. Nutrient availability was indirectly estimated. It is our goal to 1) determine which factors best explain benthic community composition in a natural reef system that is free from direct human impacts, and 2) provide a baseline of a natural functioning tropical reef system in which reefs world-wide may be compared. Finally,

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values of tissue nutrients were compared to others collected in the Main Hawai`ian Islands to further assess the status of nutrient availability at PHA.

Materials and Methods

Location and description

Centered at approximately 27° 50' N and 175° 55' W (Fig. 3.1), Pearl and Hermes Atoll (PHA) is the largest atoll in the Northwestern Hawai`ian Islands (NWHI). It contains several small sand islands (total land area= 0.36 km^2) and encompasses 1,166 km^2 of reef area. A more complete description of Pearl and Hermes Atoll can be found in Chapter 2.

The remote location and inaccessibility of PHA has limited past research. Beginning in 2000, NOAA's Coral Reef Ecosystem Division (National Marine Fisheries' Pacific Islands Fisheries Science Center) and NWHI Coral Reef Ecosystem Reserve (National Ocean Service) have led annual, multi-agency expeditions to the NWHI to assess and monitor coral reef communities. Data presented here represent findings from the 2002 and 2004 research expedition.

Field Data collection

Quantitative data of benthic cover and herbivorous fish abundances were collected at 34 and 32 sites at PHA, respectively, between 17-29 September 2002. Sites were selected as discussed in Vroom et al. (2005) and represent a range habitat types. Quantitative benthic cover was collected using a modified version of the Preskitt method

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as described below (Preskitt et al. 2004). At each site, two 25-m transects separated by 10 meters were placed along a 10-15 m isobath (shallower at some back-reef and lagoon sites). Using a photoquadrat ($0.18 \ m^2$) equipped with either a Sony DSC P-9 or an Olympus C-4040 digital still camera and an Ikelite substrobe DS-50, 12 photos were taken along the two transects: six at randomly selected points directly adjacent to the transects, and six off the transect, three-m perpendicular to the random points, in the direction of shallow water. In addition, field notes (including in-depth coral species lists and ranking), and voucher specimens of algae were collected in order to ensure correct identification of species in the photos. Herbivorous fish densities were collected by *in situ* diver surveys along the same two- 25 m transects surveyed for benthic cover plus an additional third 25 m transect following Brock (1954, 1982). Standard underwater visual belt transect methods were used to enumerate fish encountered to the lowest possible taxon (Brock 1954; 1982). Total lengths (TL) of the fish were estimated to the nearest centimeter by reference to size standards (Friedlander and DeMartini 2002). Quantitative counts for urchin abundance were also conducted along the same two 25 m transects at 20 of the 32 sites surveyed. At each site surveyed, a Global Positioning System (GPS) point was created, habitat was described, and maximum depth was recorded.

Algal tissue nutrient content has been shown to be useful *in situ* measurement of nutrient availability (Wheeler and Bjornsater 1992). To test relative nutrient availability at PHA, algal samples at PHA were haphazardly collected at all sites encountered between 26-30 September 2004. Due to their ubiquitous distribution, two species of the calcified chlorophyte genus *Halimeda* were collected from 12 sites (*H. discoidea* Decaisne and *H. velasquezii* Taylor), 10 of which correspond to sites sampled in 2002 for

quantitative benthic cover and herbivorous fish abundance. Epiphytes were removed

from algal samples on board the NOAA R.V. *Hi`ialakai*. Samples were rinsed in DI

water, patted dry, wrapped in aluminum foil, and placed directly in a 60°C drying oven

until constant weight was achieved following Wheeler and Bjornsater (1992).

Data and sample processing

Each of 406 photoquadrat images were analyzed using PhotoGrid$^©$ ver 1.0 beta

(Bird 2002) where percent cover of algae and invertebrates was determined at the species

level (when possible) by placing 100 stratified random points over each image. This

number of points assured identification of rarer organisms. Because of the difficulties in

identifying species of turf algae and crustose coralline red algae, organisms in these

categories were identified to the functional group level only. Highly epiphytized

macroalgae or crustose coralline red algae were recorded as both macroalgae and turf,

leading to percent covers often exceeding 100%.

Urchin counts were converted to urchin density by calculating the average

number of urchins per unit area.

 Mean numerical densities of fish were determined by pooling individuals of all

body lengths in a 10 m^2 area. Biomass of herbivorous fish was determined by converting

lengths to weight using the allometric length-weight conversion: W= aSL^b, where

parameters a and b are species specific constants, SL is standard length in mm, and W is

the weight in grams. Total length (TL) estimated in the field was converted to SL by

using published and web-based conversion factors (Froese and Pauly 2006). Length-

weight constants were available for 150 species commonly seen on transects (Hawai`i

Cooperative Fishery Research Unit unpubl. data) with supplements from other published and web-based sources (Froese and Pauly 2006). Mean biomass was then calculated in grams per 10 m^2 of the transect area.

For nutrient analysis, algal tissues were brought into the lab where portions of tissue were ground to a fine powder using a mortar and pestle. Algal tissue carbon (C) and nitrogen (N) were obtained at the University of Hawai`i Isotope Biogeochemistry Laboratory using a Carlo Erba NC 2500 Elemental Analyzer coupled with a Thermo Finnigan Delta S Mass Spectrometer (Fry et al. 1992). To obtain organic carbon percentages, *Halimeda* species were first fumed with hydrochloric acid to remove calcium carbonate from samples according to methods described in Yamamuro and Kayanne (1995). These de-calcified portions were then analyzed in triplicate to obtain percentages of organic carbon (Fry et al. 1992). To obtain percent nitrogen, triplicates of calcified portions of tissue were analyzed. Phosphorous amounts were analyzed at the University of Hawai`i's Agriculture Diagnostics Service Center where algal tissue were ashed in a furnace at 550°C, dissolved in Hydrochloric acid (5N), and run through an Inductively Coupled Plasma Spectrophotometer following Isaac and Johnson (1985).

C:N, N:P and C:N:P ratios were calculated by averaging the triplicates samples run each species at each site. Rather than using the typical format for C:N:P which portrays both C:P value and the N:P value (i.e., 106:16:1), this number was modified by dividing the C:N ratio by the value for P. This transformation enabled greater freedom in statistical analyses. In order to assess nutrient limitation at PHA, tissue nutrient concentrations from *Halimeda discoidea* collected at PHA were compared to two sets of samples collected on the Main Hawai`ian Island of O`ahu. These samples were collected

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by the author in an earlier experiment using the same methods described above. Tissue nutrient values were also compared to published values (Atkinson and Smith 1983).

Sites surveyed were grouped into *a priori* categories based on wave exposure and given numerical ranking: high (4), intermediate-high (3), intermediate-low (2), and low (1) as described in chapter 2 (Fig. 3.1).

Statistical analysis

In order to look for relationships between benthic cover and herbivorous fish, urchin density, tissue nutrient content, depth, and wave exposure, Pearson's correlation analysis was run on all corresponding data (n= 9 sites). Algal tissue nutrient samples were the limiting factor allowing for only nine sites to be analyzed (Appendix 1). Extremely high abundance and biomass of herbivorous fish at site PHA 22, warranted the removal of this data outlier and Pearson correlation analyses were repeated (n= 8 sites). To further investigate relationships with herbivorous fish density and biomass (n= 32 sites), as well as urchin density (n=20 sites), additional Pearson's correlations were run with the additional corresponding data for these variables (Appendix 1).

To detect differences in tissue nutrients of *Halimeda discoidea* between PHA and samples collected on O`ahu, the non-parametric mood's median analysis was employed.

Multiple-linear regressions were run to further test the relationship between benthic cover and herbivorous fish data, urchin data, wave exposure, and depth (benthic cover was the response variable). Regression were run including algal tissue nutrient data; however are not reported because of (1) a lack of correlation present and (2) the few sample sites constrained the number of sites that could be included in broader analyses.

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Best subsets regressions were used to help determine which model best explained each of the benthic parameters (coral, frondose macroalgae, turf algae, and crustose coralline red algae). Models with the highest adjusted r^2, lowest Mallow's C-p, and the lowest square root of the mean square error (MSE) are presented.

To further analyze relationships of benthic cover to herbivorous fish density and biomass, urchin density, wave exposure and depth, the multivariate BIO-ENV test was employed using PRIMER-E[®] (Clarke and Warwick 2001). The BIO-ENV procedure uses a Spearman coefficient to compare the Bray-Curtis similarity matrix of fourth-root transformed benthic percent cover data at sites to a normalized Euclidean distance similarity matrix of herbivorous fish abundance, herbivorous fish biomass, depth, urchin abundance, and wave exposure. The resulting sample statistic, rho (ρ), lies in the range (-1, 1), with $\rho = -1$ indicating that data matrices are in complete opposition and with $\rho = +1$ indicating that data are in complete agreement. BIO-ENV procedure was run on Bray-Curtis similarity matrices of: (1) benthic cover functional group percent cover data (scleractinian coral, frondose macroalgae, crustose coralline red algae, turf algae, and other (i.e. sand, other invertebrates)), (2) macroalgal species level percent cover data, (3) coral species level percent cover data, and (4) a combination of coral species, macroalgal species, crustose coralline red algal, and turf algal percent cover data. In each test benthic data were transformed using the fourth root function and a global BEST permutation test (999 permutations) was run to determine the significance level of the sample statistic (significant when p<1%).

Results

Descriptive statistics

Descriptive statistics of benthic percent cover data are presented in Chapter 2. At the 32 sites where herbivorous fish data were collected, the mean density of herbivorous fish was 6.33 fish/ 10 m^2 (SE= 1.01) and the mean biomass of herbivorous fish was 388 g/10 m^2 (SE= 56.3). At the 20 sites where urchin data were collected, the mean urchin density was 0.09 urchins/ m^2 (SE= 0.0310).

Tissue of *Halimeda discoidea* had a mean percent nitrogen (N) concentration of 1.96% (SE = 0.139%), a mean percent organic carbon (OC) of 17.27% (SE= 1.42 %), a mean percent phosphorous (P) of 0.061% (SE = 0.003%), and a mean C:N:P ratio of 147.79 (SE= 8.74). *H. velasquezii* was found to have a mean tissue nutrient content of: N = 0.653 % (SE= 0.032%), OC= 4.853% (SE= 0.238%), and P= 0.022% (SE= 0.0017%) with an average C:N:P ratio of 360.3 (SE= 31.3).

When comparing tissue nutrient values of *H. discoidea* from PHA with those found O`ahu, the June 2004 samples from O`ahu had significantly higher %N and %P (3.753% N, 0.140% P) and significantly lower OC than those recorded at PHA (Chi-square= 6.97, p= 0.031; Chi-square= 4.55, p= 0.033; Chi-square= 7.57, p= 0.023; Table 3.1). However, the *H. discoidea* tissue samples collected from O`ahu in May 2005 had very similar nitrogen and organic carbon concentrations to those recorded from PHA (Table 3.1). *H. discoidea* at PHA had the lowest C:N ratio and was significantly different from both O`ahu samples (Chi-square= 13.39, p= 0.001; Table 3.1). While no significant differences were detected between C:N:P ratios of *H. discoidea* between the different

locations, the C:N:P at PHA was nearly double that of the samples collected from O`ahu in June 2004 (Table 3.2).

Correlations

Benthic function group: benthic functional group

Correlative analyses found percent cover of both frondose and turf algae exhibited a significant negative correlation with percent cover of corals and coralline red algae (Table 3.2). However the most distinct relationship occurred between frondose algal cover and coral cover, with a quadratic function best fitting this relationship (Table 3.2; Fig. 3.2).

Benthic functional group: herbivorous fish

After removal of the outlier (site PHA-22), due to a skewed value of herbivorous fish density and biomass, herbivorous fish density (number/ 10 m^2) had a significant positive correlation with coral cover ($r = 0.605$, $p < 0.001$) and a significant negative correlation with frondose algal cover ($r = -0.542$, $p = 0.001$) (Table 3.2, Fig. 3.3 a, d). Unlike herbivorous fish density, biomass of herbivorous fish was not significantly correlated with coral cover but was however negatively correlated with frondose algal cover as well as the "other" category (percent cover of sand was determined to drive this correlation). Herbivorous fish biomass was also positively correlated with coralline red algal cover (Table 3.2).

Three lagoonal and one back-reef site largely contributed to the correlations between benthic percent cover and herbivorous fish density (Fig. 3.3 a, d). At the lagoonal sites (rPHA-31, rPHA-37 and PHA-21) the scarid *Chlorurus sordidus* was more

than 90% of herbivorous fish encountered and *Porites compressa* was the dominant coral. The back-reef site (rPHA-41) contained a diverse coral and fish community with three species of scarids, one Pomacentrid (*Stegastes fasciolatus*), and four species of Acanthurids, making up 54.6, 23.5, 19.4 percent of herbivorous fish recorded respectively. Two species of *Montipora* were the dominant coral cover.

Benthic functional group: urchin density

Urchin density was not significantly correlated with coral, frondose algae, or coralline red algae, but was significantly and positively correlated with cover if turf algae ($r = 0.451$, $p = 0.046$; Table 3.2).

Benthic functional group: tissue nutrient content

Concentrations of tissue nutrients for *Halimeda discoidea* and *H. velasquezii* did not significantly correlate with any of the benthic functional groups.

Benthic functional group: physical parameters

The four assigned wave exposure regimes (high, intermediate-high, intermediate-low, and low) were significantly and negatively correlated with coral cover, and significantly and positively correlated with cover of coralline red algae cover (Table 3.2). No correlation however existed between wave exposure and percent cover of frondose or turf algae (Table 3.2). Additionally, depth was significantly and negatively correlated with turf algae but was significantly and positively correlated with coralline algae (Table 3.2).

Benthic species level correlations

When individual benthic species were considered instead of functional groups, the scleractinian coral, *Porites compressa*, was significantly correlated with herbivorous fish

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density (r = 0.651, p <0.001). No other dominant coral species exhibited significant correlations with herbivorous fish density. The most dominant frondose algae, *Microdictyon setchellianum,* was significantly and negatively correlated with both herbivorous fish density (r = -0.523, p <0.002) and biomass (r= -0.552, p = 0.001). Other common frondose algae i.e. *Halimeda* spp. had no significant correlation to herbivorous fish parameters.

Multiple-linear Regression

Results of the multiple-linear regression for the different functional groups are summarized in Table 3.3. Coral cover was best explained by wave exposure, herbivorous fish density, and depth in the multi-linear regression (r^2 = 52.8%, r^2 (adj.) = 47.7%, p <0.001, Table 3.3, Fig. 3.3a). The same model chosen to explain combined species of coral cover also explained a greater amount of the variability in the finger coral *Porites compressa* when analyzed as a single species (r^2 = 71.8%, r^2 (adj.) = 68.7%, p <0.001). The best model explaining frondose algal cover included wave exposure, herbivorous fish density, and urchin density, such that as any one of these variables increased, frondose algal cover decreased (r^2 = 49.0%, r^2 (adj.) = 38.1%, p = 0.021, Table 3.3, Fig. 3.3). For the dominant green frondose algae, *Microdictyon setchellianum*, incorporating depth created the best fit regression (r^2 = 52.9%, r^2 (adj.) = 38.4%, p = 0.033). Cover by turf algae was best explained by urchin density, herbivorous fish density, herbivorous fish biomass, and depth (r^2= 61.7%, r^2 (adj.) = 50.0%, p = 0.010, Table 3.3, Fig. 3.3). Urchin density was the largest contributor to this model, such that as urchin density increased turf algal cover increased. Coralline algal cover was best explained by just two variables -

wave exposure and herbivorous fish density ($r^2 = 67.1\%$, r^2 (adj.) = 64.8%, p>0.001, Table 3.3, Fig. 3.3, 3.4).

BIO-ENV

For each of the four BIO-ENV analyses run, percent cover of benthic organisms correlated greatest with wave exposure and herbivorous fish density. Percent cover of benthic organisms at the functional group level was highly correlated with both herbivorous fish density ($\rho = 0.530$) and wave exposure ($\rho = 0.436$) (Fig. 3.5) with a combination of these two variables having the highest significant correlation ($\rho = 0.553$, p = 0.1%). Frondose macroalgal species abundances were most highly correlated to wave exposure ($\rho = 0.583$) followed by herbivorous fish density ($\rho = 0.515$). The BIO-ENV results for coral species level data exhibited little correlation to any of the variables tested (p = 8.4%; wave exposure $\rho = 0.196$; herbivorous fish density $\rho = 0.123$). However, the BIO-ENV results of the combination of data for frondose algae and coral species with functional group percent cover data, wave exposure alone was the highest significant correlation ($\rho = 0.574$, p = 0.1%), with the correlation to herbivorous fish density closely following ($\rho = 0.516$).

Discussion

Our data identified herbivorous fish density/ biomass, wave exposure, and urchin density as factors explaining benthic coral reef community structure in this near-pristine ecosystem (Table 3.3; Fig. 3.3, 3.4, 3.5). Wave exposure and herbivorous fish density were the most consistent predictors of benthic functional groups (Fig. 3.4, 3.5; Page et al.

in prep). This is especially apparent for coralline algae where 67.1 % of the variation in cover of coralline algae was explained by herbivorous fish density along with wave exposure (Fig. 3.4). While strong correlations of benthic functional groups occurred between herbivore and wave exposure measurements, none were found to occur between nutrient availability and benthic functional groups (Table 3.2). This suggests that herbivory may be more influential than nutrient availability in this near-pristine coral reef.

Top-down: herbivory

Our results clearly identify herbivorous fish as well as urchins as significant explanatory variables for cover of benthic functional groups suggesting that top-down factors are important in structuring benthic communities at PHA (Table 3.3; Fig. 3.3 a, d; Fig. 3.5b). Specifically, as herbivorous fish density increased, coral cover increased and frondose algal cover decreased (Table 3.3, Fig. 3.3 a, d). Numerous studies have shown that exclusion of herbivores results in increased growth of frondose algae which can alter coral reef community structure (Hatcher and Larkum 1983; Carpenter 1986; Lewis 1986; Miller et al. 1999; Smith et al. 2001; Thatcher et al. 2001). Lewis (1986) found that after 10 weeks of herbivore exclusion on a Caribbean reef, macroalgal abundance increased significantly compared to control sites, and some species of macroalgae directly overgrew coral colonies. Although, experimental manipulation was not feasible at PHA, our correlative results taken into consideration with the overwhelming amount of experimental evidence in the literature (Hatcher and Larkum 1983; Lewis 1985; Hay 1985; Carpenter 1986; Lewis 1986; Hixon and Brostoff 1996; Hay 1997; Miller et al.

1999; Smith et al. 2001; Thatcher et al. 2001) indicates that grazing of herbivorous fish at PHA is likely a dominant factor regulating the structure of benthic communities in this near-pristine atoll.

Our findings of a positive relationship of coral cover and negative relationship of frondose algal cover with herbivore abundance were similar to predictions based on the RDP (Fig. 1.1; Fig. 3.4 a, d). However, because there is minimal human impact on herbivorous fish populations at PHA (i.e., no fishing), the RDP would predict that all sites should have high abundance of herbivores and corals. These patterns were not found consistently at PHA; some sites had high cover of frondose algae (low cover of coral) and low numbers of herbivores. Because PHA has higher biomass of apex-predators than any other Hawai`ian island or atoll (Friedlander and DeMartini 2002), we speculate that habitat structure formed by benthic organisms e.g., the coral *Porites compressa*, regulates herbivorous fish communities by providing refuge from predation.

Increasing habitat complexity or rugosity has been shown to provide shelter or refuge from predation to smaller fish with numbers of fish increasing with increasing shelter (Hixon and Beets 1993, Friedlander and Parrish 1998, Friedlander et al. 2003). At PHA, the highest numbers of herbivorous fish were located within lagoonal patch reefs and back reefs (Fig. 3.1, 3.3). Monospecific stands of the finger coral *Porites compressa* characterized patch reef sites. The morphology of this coral makes it an ideal shelter for small fish (Atkins 1981). Conversely, areas with the highest abundance of frondose algae (*Microdictyon setchellianum*) are generally less topographically complex and thus offer less shelter to small herbivorous fish from predation. In addition, areas dominated by *M. setchellianum* (south fore-reefs) are characterized by high abundances of large predatory

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fish (Friedlander and DeMartini 2002). Therefore, one reason that our results from PHA vary from the expectation that coral dominate pristine reefs (based on the RDP), is that the abundance of predators indirectly affects algal abundance by directly effecting herbivorous fish communities. This possibility is similar to early top-down hypotheses (Hairston et al. 1960). Predation pressure along with lack of shelter may limit herbivorous fish abundance, thus allowing for abundances of frondose algae. In order to verify this hypothesis, questions such as the palatability of the *M. setchellianum* should be examined as well as whether increasing shelter of herbivorous fish from top predators would have a cascading affect on frondose algal abundance. These questions await further testing.

Within the *Porites compressa* dominated lagoon, the parrotfish *Chlorurus sordidus* was the dominant herbivore and largely drove the correlations observed between herbivorous fish density and coral percent cover (Fig. 3.1, 3.3). *C. sordidus* is omnivorous until it reaches 15mm TL at which time it has been shown to feed on turf algal patches or epilithic algal communities as well as detritus (Chen 2002; Wilson et al. 2003). In addition to *C. sordidus*, there are large schools of herbivorous Acanthurids that frequent these areas but were not recorded in these censuses (Page pers. obs.). Exclusion of similar herbivorous fish in the Caribbean resulted in significant increases in macroalgal biomass (Carpenter 1986). While shelter may play a role in the abundance of herbivores within the lagoon, we feel confident that lagoonal sites were intensively grazed and that this grazing likely contributed to maintaining high coral cover. Rather than one structuring the other (i.e., herbivores structuring benthic communities); it is likely that there is a mutually beneficial relationship between herbivorous fish and coral.

Coral provide shelter for the small herbivorous fish (Atkins 1981) and the herbivorous fish remove macroalgae that compete with coral (Carpenter 1986; McCook et al. 2001).

At PHA, urchin density was partially responsible for explaining both turf and frondose algal percent cover (Table 3.2, 3.3). As urchin density increased, frondose algal percent cover decreased and turf algal percent cover increased (Table 3.2, 3.3). Through urchin removal experiments as well as the mass mortality of herbivorous urchins in the Caribbean, the role of urchins in grazing macroalgae has been firmly established (Carpenter 1986; Morrison 1988; Hughes 1994; Aronson and Precht 2001). Therefore the negative relationship between frondose algae and urchin density may be explained by grazing pressure of herbivorous urchins. The positive relationship between urchin density and turf algal biomass that occurred at PHA has also been observed experimentally (Williams and Carpenter 1990; McClanahan 1997). Urchin grazing can increase the productivity of turf algae by two to 10 times the productivity of non-grazed communities (Williams and Carpenter 1990). The relationship of urchin density with both turf algae and frondose algae percent cover further suggests that top-down forces are influential in structuring benthic communities in this near-pristine atoll.

Extremely high herbivorous biomass (3021.0 g 10m^{-2}) recorded at the back reef site PHA-22 (Fig. 3.1) warranted the removal of this site from analysis (Appendix 1). This value was over double the second highest biomass recorded from site rPHA-39 (1,123.9 g 10m^{-2}). PHA-22 was unique in that it was very close to a large channel in the reef which acted as a corridor between the outside of the atoll and the lagoon. Strong currents and large schools of fish characterized this site. Despite the high biomass of herbivorous fish (primarily species of *Kyphosus*), PHA-22 was dominated by the

epiphytized macroalgae *M. setchellianum* as well as turf algae. The concurrence of high

herbivorous fish biomass and frondose algae is opposite of the general trend observed at

PHA. This intriguing occurrence may indicate that reef channels are unique habitats and

justifies further research on the dynamics of trophic interactions at this site and other

similar sites.

Bottom-up: Nutrient Availability

Although herbivory showed correlation with features of the benthic community,

there was no correlation for nutrient availability (%N, %P, C:N:P of algal tissue) with

coral, frondose algae, crustose coralline red algae or turf algae cover or with any of the

physical parameters (Table 3.2). Nutrients are generally regarded as limiting on coral

reefs (Hatcher 1990; Fong et al. 2003). Nutrient limitation is a form of bottom-up control

in tropical algae (LaPointe et al. 1987; Hatcher and Larkum 1983; Hatcher 1990; Larned

1998; Smith et al. 2001; Stimson et al. 2001; Fong et al. 2003; and LaPointe et al. 2004).

However, there is some debate over whether or not nutrients are limiting on coral reefs

(Fong et al. 2003; Koope et al. 2001), certain functional groups of algae, primarily the

turf algae, also referred to as the epilithic algal community, have been shown to be highly

productive in low nutrient environments (Odum and Odum 1955, Russ 2003, Hatcher and

Larkum 1983). Since PHA has no human induced nutrient pollution, it seems likely that

nutrients are limiting. However, some sites at PHA had very high frondose algal cover

such as site rPHA-33 that exhibited 46.33% cover of *M. setchellianum*, suggesting that

nutrients are not limiting. Nutrient limitation at PHA was further assessed by comparing

tissue nutrient values of *Halimeda discoidea* from PHA to samples collected on the island

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of O`ahu (Table 3.1, Atkinson and Smith 1983). PHA has significantly lower concentrations of %N, %P, and %C than some of the samples collected from O`ahu (Table 3.1). Generally, higher C:N:P value indicates greater nutrient limitation. While the C:N:P at PHA was found to be less than the published value (Atkinson and Smith 1983), it was nearly double that of one sample collected from O`ahu (Table 3.2). Therefore, *H. discoidea* can have higher concentrations of carbon and related compounds stored within its tissues than what was recorded at PHA. The relatively low values of tissue %C, %N, and %P and the high values of C:N:P may indicate that *H. discoidea* at PHA are nutrient deplete or limited during the season of sampling, however further *in situ* experimentation is needed.

Even if nutrients are limiting, there is still a question of whether or not nutrient pollution alone can alter a coral reef ecosystem (Miller et al. 1999). One study showed that herbivorous fish preferred frondose algae that had higher tissue nutrient content (Boyer et al. 2004). If herbivorous fish can respond by preferentially choosing algae with higher tissue nutrients, than the presence of herbivores may ultimately control benthic communities. While our results do not indicate that nutrient availability plays a decisive role in benthic community assemblages at PHA, nutrient limitation thus bottom up control can not be ruled out. Intensive water and algal tissue sampling throughout the year as well as manipulative experiments would be necessary to firmly understand the role of nutrient availability at PHA.

Coral/ macroalgal competition

Competition between coral and macroalgae is also thought to play a significant role in community structure on coral reefs (McCook et al. 2001, Jompa and McCook 2002). Coral and algae both require light for photosynthesis as well as space for settlement and growth. Under reduced grazing pressure macroalgae have been shown to outcompete coral (Hughes 1994, McCook et al. 2001, Jompa and McCook 2002). Recent evidence also shows that dissolved organic carbon (DOC) released from algae act to increase microbial activity on corals resulting in coral mortality (Smith et al. 2006). A significant inverse relationship of coral percent cover to frondose algal percent cover at PHA, is consistent with intense competition at least for space on a reef (Fig. 3.2). While this relationship is simply correlative and could be the result of external factors such as herbivory and/ or wave exposure as discussed above, it is also likely that coral and frondose algae compete directly at PHA. Two species primarily drive the trends observed at PHA, the scleractinian coral *Porites compressa* and the green alga *Microdictyon setchellianum*. Focused attention on interaction between these species as well as on the physiology of these species would greatly increase our knowledge of competition between coral and macroalgae at PHA.

Wave Exposure

Wave exposure was significant in explaining both coral and coralline algae in the multiple-linear regression analyses (Table 3.3) and was additionally significant in explaining benthic communities including the frondose algal species level data in the multivariate Bio-Env procedure (Fig. 3.5a). Wave exposure can be both a destructive

force to certain coral reef organisms in areas with high wave exposure (Storlazzi et al. 2005) and a necessary force that perturbs boundary layers allowing organisms to receive required nutrients (Hurd 2000). From our results it appears that coral (primarily *Porites compressa*) have a greater affinity for areas with low wave exposure and crustose coralline algae have an affinity for areas with high wave exposure (Table 3.3, Fig. 3.4). The affinity of both coral and crustose coralline algae to opposite wave exposure regimes is tightly coupled with an affinity of both organisms for areas with high abundances of herbivores as mentioned above (Table 3.3, Fig. 3.4). While it is apparent that biotic interactions, especially herbivory, play a role in benthic community structure, physical parameters, such as wave exposure, can not be overlooked.

Conclusion

The results of this study give us a glimpse into the functioning of a near-pristine coral reef- an increasingly rare field site. Wave exposure, herbivorous fish density, and urchin density are factors that influence cover of benthic organisms in this near-pristine coral reef. The tight correlation of benthic functional groups with herbivore abundance, and the lack of correlation with nutrient availability suggest that top-down factors (herbivory) play a strong role in regulating benthic community structure at PHA and that bottom-up factors may be more uniform or possibly strongly seasonal.

This study provides insight into one-end of the continuum of coral reef health. We encourage other coral reef biologist to establish where their study systems lie within this continuum, and determine whether the factors that influence benthic communities in coral reefs change along this continuum of human impact. With continued research on

factors that influence benthic communities, it is hoped that we can reach a point in which

scientists and managers are able to predict how changes in one of these factors (i.e., loss

of particular herbivores) would alter benthic communities in coral reefs.

Table 3.1. Mean values of algal tissue nutrients in *Halimeda discoidea* from PHA, O`ahu, and Hawai`i. Italicized values are the standard error of the mean.

Sample ID	%C	%N	%P	C:P	N:P	C:N	C:N:P
PHA August 2004 (n= 10)	17.27 *1.42*	1.96 *0.14*	0.061 *0.003*	283.3 *17.70*	32.31 *1.52*	8.76 *0.29*	147.79 *8.74*
O`ahu June 2004 (n=3)	41.50 *0.84*	3.75 *0.10*	0.140 *0.01*	297.70 *16.02*	26.94 *1.68*	11.06 *0.10*	79.22 *2.56*
O`ahu May 2005 (n=4)	22.43 *0.06*	1.51 *0.01*	NA	NA	NA	14.85 *0.06*	NA
Hawai`i, Atkinson and Smith 1983 (n=1)	33.00	3.10	0.066	499.0	47.0	10.64	161.19

Table 3.2. Replace with additional print out.

Table 3.3. Multi-linear best subsets regression models for each of the benthic functional groups. (+) indicates a positive relationship between the response variable and the explanatory variable within each model, while (–) indicates a negative relationship. (o) indicates an explanatory variable that was used in creating the best model but had no significant relationship with the response variable. These models represent those with the highest adjusted r^2, lowest Mallow's C-p, and the lowest square root of the mean square error (MSE).

Response variables	Explanatory variables					
	Herbivorous fish density	Herbivorous fish biomass	Urchin density	Wave exposure	Depth	Adjusted r^2, p-value
Coral	+			-	+	47.7% $p < 0.001$
Frondose algae	-		-	o		38.1% $p = 0.021$
Turf algae	o	+	+		-	50.0% $p = 0.010$
Crustose coralline algae	+			+		64.8% $p < 0.001$
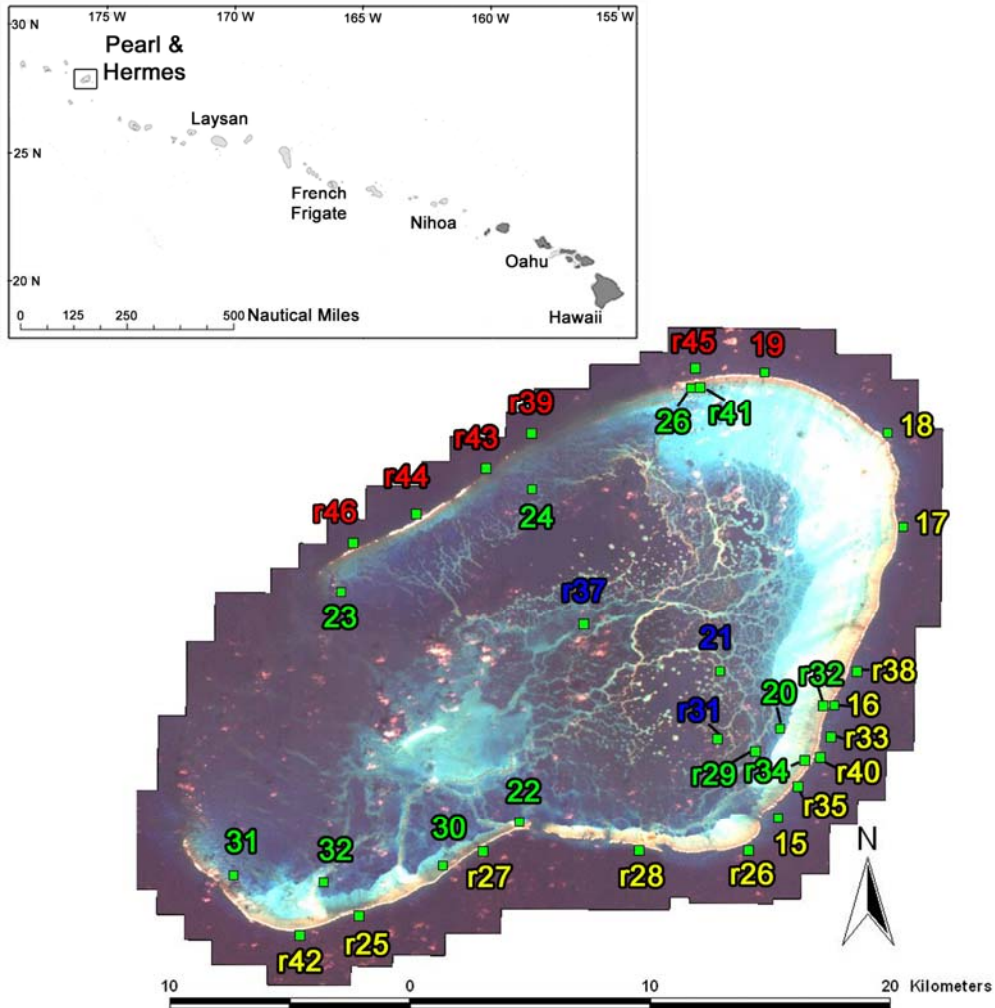
Figure 3.1. Top left corner, map of the complete Hawai`ian island archipelago including the Northwestern Hawai`ian Islands (NWHI) with the position of the study atoll Pearl and Hermes indicated. Bottom right corner, Ikonos image of Pearl and Hermes Atoll indicating sites sampled. Different colors represent the 4 wave exposure regimes, NW fore-reef sites had high wave exposure (red), E and S fore-reef sites have intermediate-high wave exposure (yellow), the lagoonal patch reef sites had low wave exposure (blue), and the other sites within the lagoon (remaining patch and back reef sites) had intermediate-low wave exposure (green).
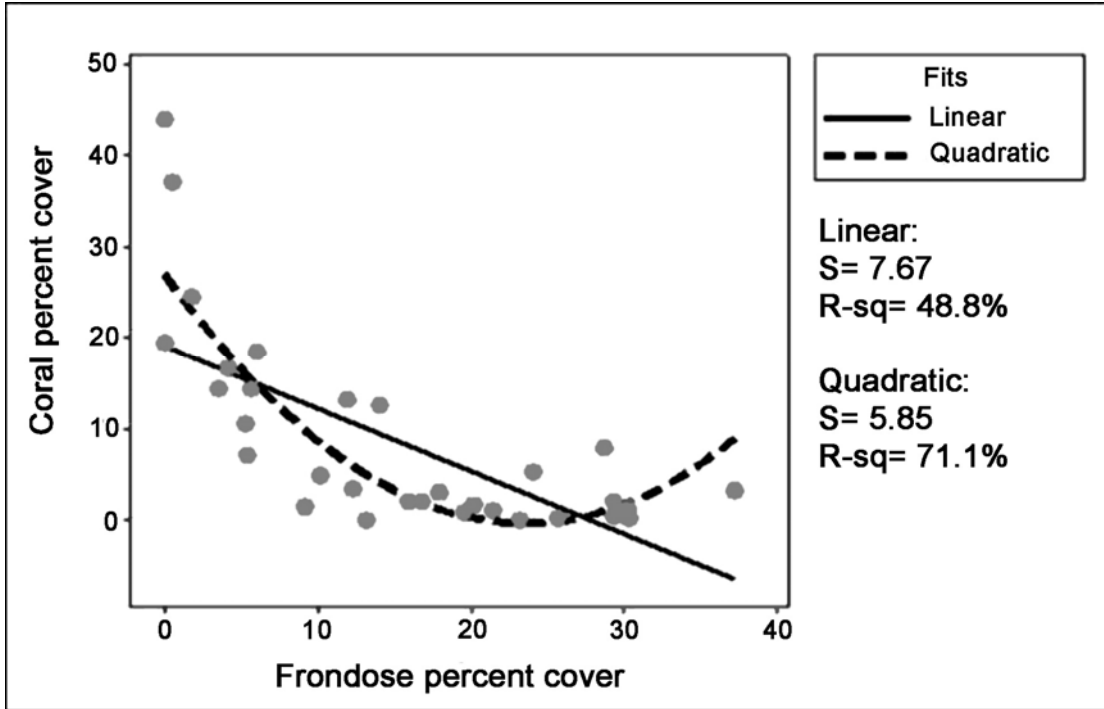
Figure 3.2. Scatter plot of coral vs. frondose algae percent cover with both a linear and quadratic regression fit.
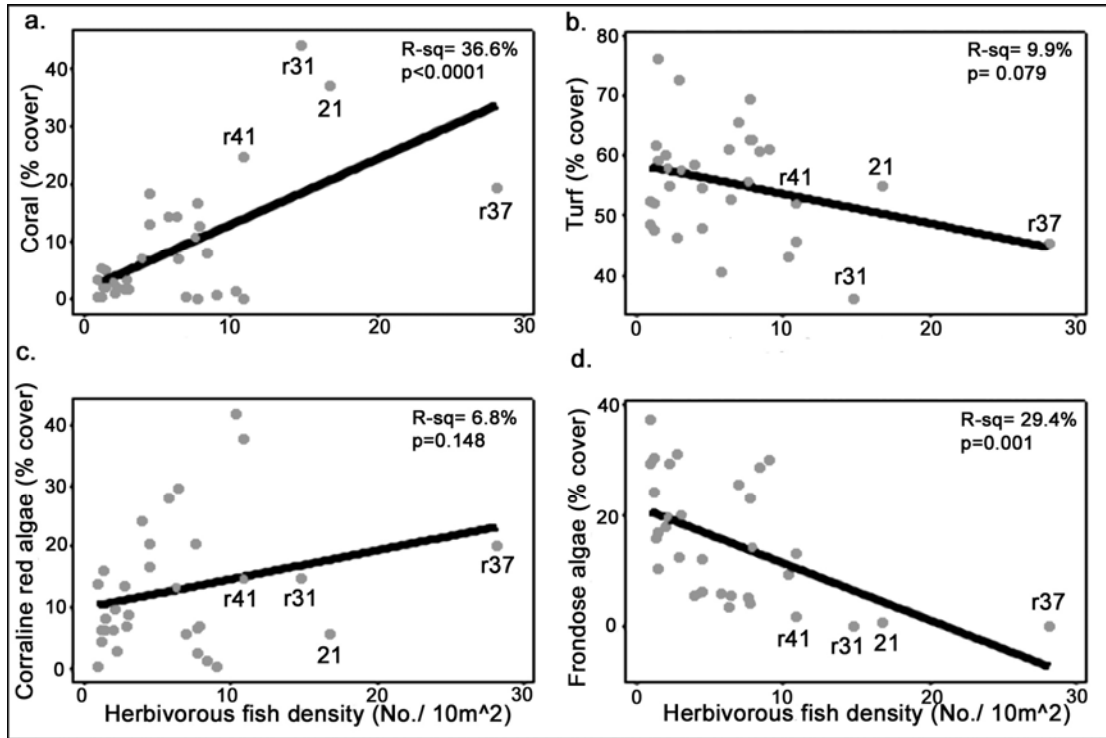
Figure 3.3. Regression fit of benthic functional group cover (a. coral, b. turf algae, c. coralline red algae, and d. frondose algae) to herbivorous fish density. a, c: Coral and coralline red algae percent cover are positively correlated with herbivorous fish density with coral having a significant correlation. b, d: Turf algae and frondose algae percent cover are negatively correlated with herbivorous fish density with frondose algae having a significant correlation.
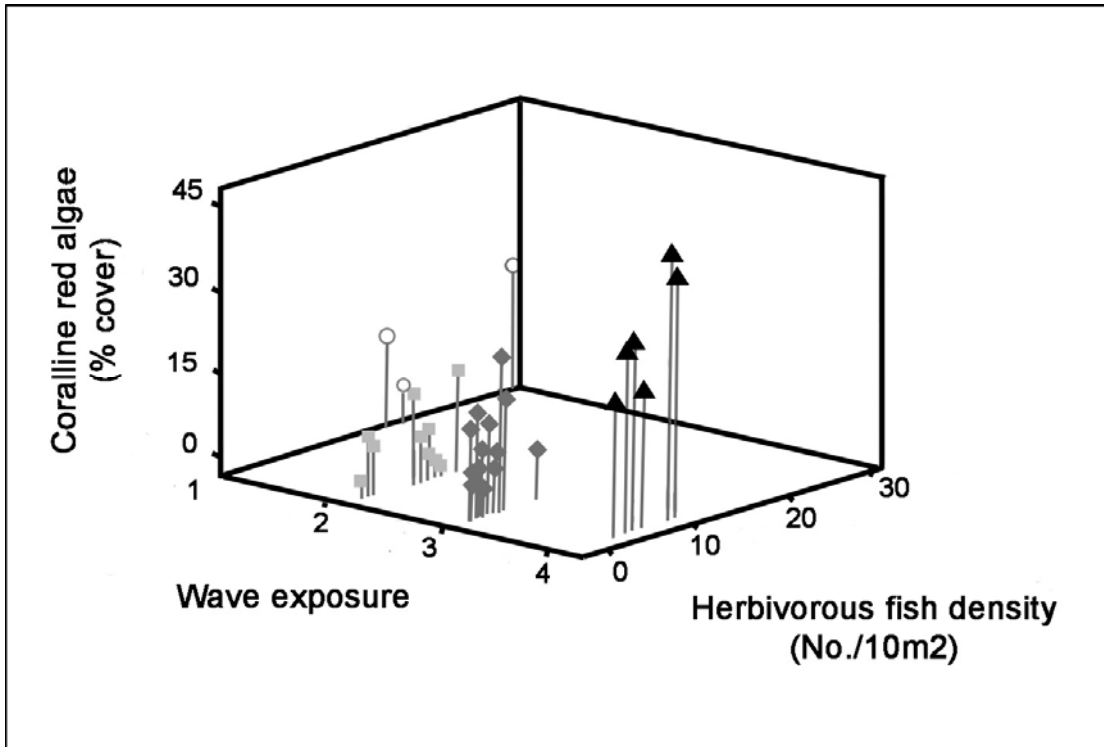
Figure 3.4. 3-dimensional scatter plot of coralline red algae verses herbivorous fish density and wave exposure. Combined herbivorous fish density and wave exposure explain 67.1% of the variability in the coralline red algae percent cover data.

Figure 3.5. Multi-dimensional scaling ordinations of fourth root transformed functional group percent cover data. a: Bubble sizes indicate wave exposure levels, 1 is low wave exposure and 4 is high wave exposure. b: Bubble sizes indicate the number of herbivorous fish/ 10 m^2 area.

APPENDIX

Appendix 1: Data Table

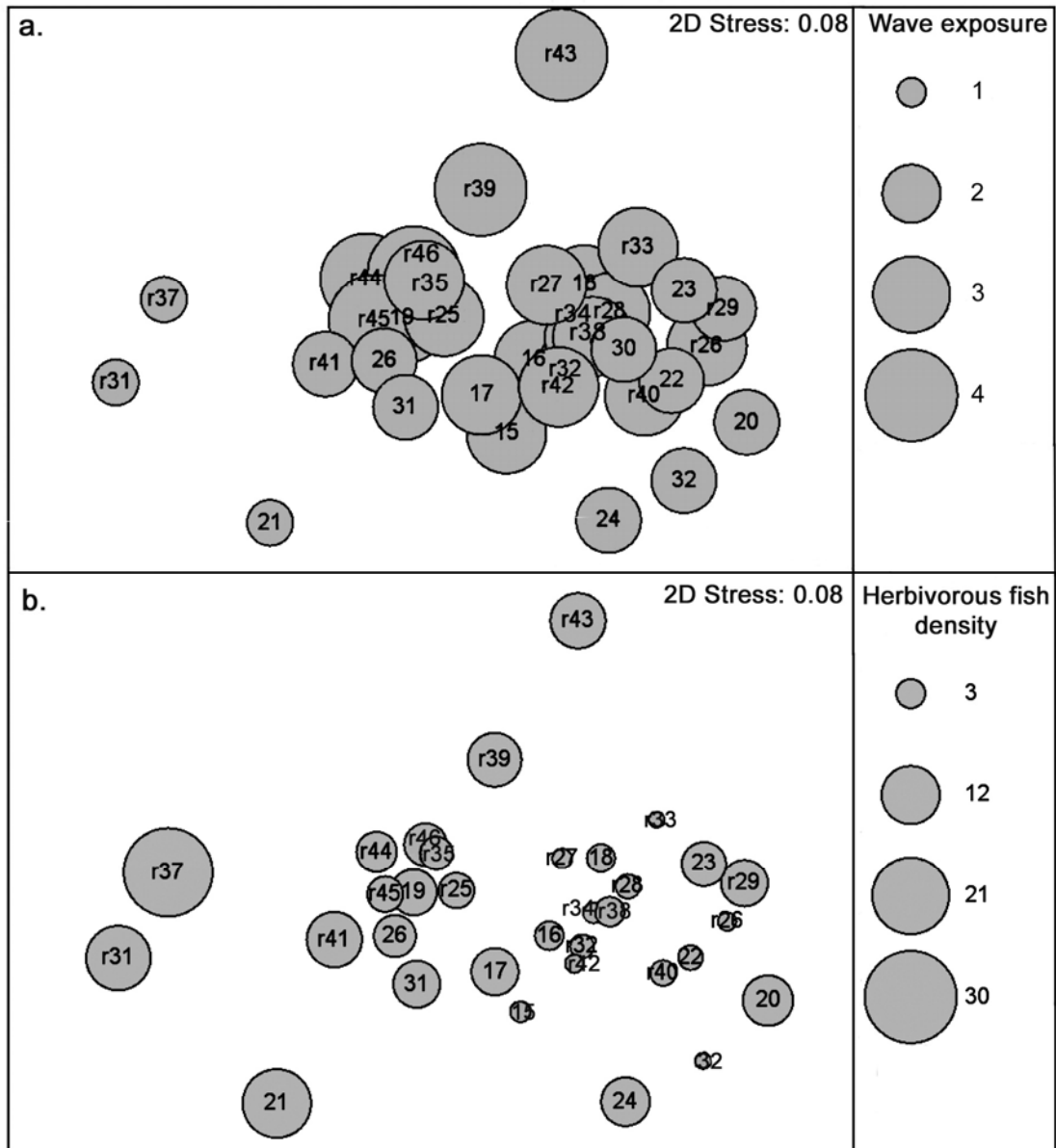| Site	Coral	Frondose	Corallines	Other	Turf	Wave exposure	Depth	Average No. urchins/ m2	No. of Herbivorous fish (n/10m2)
PHA-15	4.92	10.17	6.23	2.33	76.35	Intermediate High	30.25	0.486	1.50
PHA-16	3.39	12.34	6.83	4.63	72.82	Intermediate High	32.17	0.157	2.90
PHA-17	12.63	14.07	6.78	3.71	62.80	Intermediate High	38.00	0.065	7.90
PHA-18	1.68	31.34	13.37	7.33	46.28	Intermediate High	37.42	0.082	2.80
PHA-19	10.61	5.22	20.20	8.20	55.76	High	35.75	0.018	7.60
PHA-20	0.60	29.96	0.21	8.24	60.99	Intermediate Low	9.58	0.032	9.00
PHA-21	37.02	0.47	5.49	1.93	55.08	Low	29.00	0.000	16.70
PHA-22*	1.23	30.20	2.04	8.22	58.31	Intermediate Low	4.67	0.104	23.50
PHA-23	0.25	25.67	5.45	2.98	65.64	Intermediate Low	22.75	0.011	7.00
PHA-24	7.94	28.75	1.02	1.38	60.91	Intermediate Low	13.75	0.018	8.40
PHA-26	14.41	3.49	12.97	7.97	61.16	Intermediate Low	5.08	0.015	6.30
PHA-30	1.00	21.42	4.39	7.64	65.55	Intermediate Low	7.33	0.250	
PHA-31	16.59	4.13	6.40	10.30	62.57	Intermediate Low	20.25	0.035	7.80
PHA-32	3.28	37.28	0.25	10.80	48.39	Intermediate Low	22.83	0.024	0.90
rPHA-25	13.13	11.91	16.60	3.66	54.70	Intermediate High	60.00		4.50
rPHA-26	0.22	30.34	4.25	17.62	47.57	Intermediate High	50.00	0.000	1.20
rPHA-27	2.05	15.90	15.95	4.41	61.69	Intermediate High	45.00		1.40
rPHA-28	0.87	19.55	9.53	12.06	57.98	Intermediate High	40.00		2.10
rPHA-29	0.11	23.25	2.40	4.91	69.34	Intermediate Low	15.00		7.80
rPHA-31	44.00	0.00	14.65	5.60	35.75	Low	35.00	0.000	14.80
rPHA-32	3.11	17.96	6.31	12.55	60.06	Intermediate Low	5.00	0.085	2.00
rPHA-33	0.35	29.37	13.69	4.10	52.48	Intermediate High	50.00		0.90
rPHA-34	2.05	16.80	8.03	13.81	59.31	Intermediate Low	15.00		1.50
rPHA-35	7.12	5.35	24.27	4.59	58.67	Intermediate High	30.00		3.90
rPHA-37	19.39	0.00	20.01	15.25	45.35	Low	15.00		28.10

rPHA-38	1.73	20.15	8.61	12.01	57.50	Intermediate High	50.00		3.10
rPHA-39	1.51	9.21	41.75	4.52	43.01	High	41.00	0.002	10.30
rPHA-40	2.16	29.29	2.71	10.99	54.85	Intermediate High	37.00		2.30
rPHA-41	24.61	1.82	14.62	6.76	52.18	Intermediate Low	10.00		10.90
rPHA-42	5.29	24.10	6.06	12.42	52.14	Intermediate High	46.00	0.419	1.20
rPHA-43	0.00	13.15	37.79	3.50	45.57	High	28.00		10.90
rPHA-44	14.44	5.68	28.00	11.31	40.57	High	47.00	0.023	5.80
rPHA-45	18.42	6.02	20.36	7.45	47.75	High	67.00		4.50
rPHA-46	7.11	5.40	29.31	5.37	52.80	High	41.00		6.50

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