

Patterns in benthic coral reef communities at Pearl and Hermes Atoll along a wave exposure gradient

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Abstract

This study compares percent cover of benthic organisms at the species level at Pearl and Hermes Atoll (PHA), the largest atoll in the Northwestern Hawaiian Islands, in order to determine 1) the degree of difference among sites, 2) whether wave exposure zones explain observed patterns in benthic community structure, and 3) whether species richness differs among wave exposure zones. Thirty-four sites representing four categorical wave exposure regimes were surveyed: high, intermediate-high, intermediate-low, and low. A two-way nested ANOSIM found there to be significant differences among sites and found that wave exposure explained some, but not all of this variation. High and low wave exposure zones were found to differ significantly from other zones. Low wave exposure sites exhibited the highest similarity to each other, and were dominated by the finger coral, *Porites compressa* (38% cover). High wave exposure sites were also similar to each other, and were dominated by crustose coralline red algae (37% cover). Sites within the intermediate-high zone exhibited substantial variability; however, the presence of the green alga *Microdictyon setchellianum* was a unifying characteristic among many sites in this zone. Finally, intermediate-low wave exposure sites exhibited the greatest degree of variability among sites, and also exhibited the greatest level of benthic species diversity including the presence of rarer species. Wave exposure proved a useful tool in describing the diverse assemblages of benthic communities at PHA, especially for sites experiencing extreme high and low wave exposure.

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Introduction

Pearl and Hermes Atoll (PHA) is located in the Northwestern Hawaiian Islands and is part of the Papahānaumokuākea Marine National Monument (PMNM). This region was protected for centuries from most direct human impacts due to its remote location, and is now considered to be one of the least impacted coral reef wildernesses left on the planet (Friedlander et al. 2008). These reefs have a high abundance of apex predators such as the Galapagos reef shark (*Carcharhinus galapagensis*) and Giant Trevally (*Caranx ignobilis*) and are the home to many rare and endangered species such as the Hawaiian monk seal (*Monachus schauinslandi*) (Maragos et al. 2002, Sulu et al. 2002). Nevertheless, the reefs of PHA have endured some direct and indirect human impacts. For example, populations of black lipped pearl oyster (*Pinctada margaritifera*) have never recovered from heavy harvesting that occurred from 1928–1930 (Keenan et al. 2006). Additionally, two large scale coral bleaching events in 2002 and 2004 have affected many reefs (Kenyon and Brainard 2006). PHA remains highly vulnerable to indirect human impacts of global warming specifically coral bleaching and marine debris such as derelict fishing gear (Dameron et al. 2006, Kenyon et al. 2007).

As part of an initiative to explore vast areas of uncharacterized reef habitat in the PMNM, a large-scale, multi-agency, interdisciplinary effort began in 2000 to assess and monitor biological communities and oceanographic parameters at the islands, atolls, and banks situated inside the Monument. This effort continues today on an annual basis. As part of this work, Kenyon et al. (2007) documented coral abundance at PHA, and found that three genera (*Porites*, *Montipora*, and *Pocillopora*) make up 97% of all coral cover. While other manuscripts have documented relative abundance of benthic species at PHA, and made broad scale comparisons of benthic communities at PHA to other island groups (e.g. Vroom and Page 2006, Vroom and Braun 2010, and Vroom 2011) the current study represents the most comprehensive synthesis of

benthic data (both corals and algae) to date for PHA, and will serve as a baseline for future management and monitoring efforts.

Establishing patterns of similarity within ecosystems facilitates the description of overall heterogeneity and is a valuable tool for understanding trophic functions and interactions. Numerous factors can influence patterns of community structure including both biotic and abiotic factors such as physical 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 it difficult to pinpoint those factors most responsible for determining community structure. However, abiotic factors that can be determined categorically based on climate and geomorphology offer a good starting point for formulating hypotheses that lead to better understanding of patterns within communities.

Wave exposure is known to be a prominent factor contributing to benthic community composition on coral reefs (Dollar 1982, Storlazzi et al. 2005, Jokiel 2006). Wave exposure creates a gradient of water motion ranging from low, relatively benign flow to high, potentially destructive, oscillatory flow and associated bed shear stresses (Connell 1978, Dollar 1982, Huston 1985, Brander et al. 2004, Storlazzi et al. 2005). Such shear stresses are often a source of disturbance in marine benthic communities (Connell 1978, Dollar 1982, Huston 1985, Brander et al. 2004, Storlazzi et al. 2005). This disturbance creates flux and maintains a nonequilibrium state within marine ecosystems (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 (IDH), 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 have been shown to contain the highest level of species diversity, while areas with extreme levels of wave exposure are often represented by few species (Grigg and Maragos 1974, Dollar 1982, Grigg, 1983, Sousa, 1984, Kilar and McLachlan 1989, Friedlander et al. 2003).

Wave-induced oscillatory flow and associated bed shear stresses are not only important as a mechanism of disturbance on coral reefs, but they are also a significant contributor to general (residual) water motion and circulation across reefs (Atkinson et al. 1981, Brander et al. 2004, Fulton and Bellwood 2005). Water motion affects numerous processes on a coral reef such as larval/food supply, sedimentation, and diffusion boundary layer thickness for coral and algae and subsequent nutrient availability (Shashar et al. 1996, Larned and Atkinson 1997, Dawes 1998, Hurd 2000, Falter et al. 2006). 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 water layer 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, are removed 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 is likely to be essential for the long-term success of sessile coral reef organisms (Larned and Atkinson 1997, Hurd 2000).

In order to describe and explain patterns of benthic community structure at PHA, we addressed three hypotheses: (1) multivariate statistical approaches will reveal differences in benthic community structure among sites (2) general qualitative wave exposure categories will explain observed differences, and (3) species richness will vary based on wave exposure zone.

The results of this work will prove valuable as a tool to make predictions of community assemblages in the NWHI based on basic wave exposure knowledge.

Methods and Materials

Location

PHA, centered at approximately latitude 27° 50' N and longitude 175° 55' W (Figure 1), is the largest atoll in the NWHI, encompassing 1166 km² of reef area to 100 m depth and several small sand islands (Maragos et al. 2002). PHA is semi-elliptical in shape, with its longest axis stretching 34 km from the southwest (SW) to the northeast (NE) (Figure 1). 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 currents and waves. Classic forereef and backreef 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.

Wave climate and category descriptions

The wave climate of PHA is dominated by trade wind conditions that are characterized by locally generated 1-3 m wave heights from an easterly direction (Figure 2, Moberly and Chamberlain 1964, Rooney et al. 2008, Hoeke et al. 2011). Between the months of October and May, however, episodes of much higher swell from the northwest (NW) occur, generated from more distant temperate storms; swell heights during the more energetic episodes may be up to 11.6 m (Figure 2, Moberly and Chamberlain 1964, Rooney et al. 2008, Hoeke et al. 2011). As waves impinge the forereefs of PHA, they break and dissipate their energy, applying force to the seabed. NW forereef areas are oriented towards the highest episodic wave heights and can be assumed to experience the highest levels of exposure on the atoll. Other forereef areas along the east (E) and south (S) of PHA typically experience lower, yet relatively high levels of exposure.

Breaking and frictional processes generally reduce wave heights to less than 1 m at the reef crests and reduce orbital wave velocities up to 90%. Thus, backreefs (lagoon facing reefs adjacent to the reef crest) receive intermediate-to-low levels of exposure. Inner lagoon reefs are generally completely sheltered from breaking waves, and subsequently have low exposure to wave forcing (Brander et al. 2004, Fulton and Bellwood 2005, Lowe et al. 2005, Storlazzi et al. 2005).

Field sites at PHA were grouped into four zones based on the generated wave climate for PHA (Figure 2) and generally accepted knowledge of the interaction between local wave conditions and reef geomorphology: high, intermediate-high, intermediate-low, and low wave exposure (Figure 1). North (N) and NW facing fore-reefs were identified as high wave exposure zones. Sites located along the E and S forereef were identified as intermediate-high wave exposure zones (Figure 1). All backreef sites were identified as intermediate-low wave exposure areas, as were patch reefs sites near the reef crest (Figure 1). Sites within the inner lagoon were categorized as low wave exposure (Figure 1).

Quantitative wave exposure estimates

Quantitative estimates of both maximum and modal significant wave height (H_s) and bed shear stress (τ) for the four wave exposure categories were determined by using a one-dimensional Simulating Waves Nearshore (1-D SWAN) model (Table 1, Supplementary methods, Booij et al. 1999 and Ris et al. 1999). Input parameters for the model were PHA wave climate data (Figure 2, Supplementary Table 1) and 12 bathymetric transects at PHA (Supplementary Figure 1). Results from the 1-D SWAN model support our categorical designation of wave exposure zones (Table 1). However, for lagoon reefs, the model resulted in an unrealistically high decadal max for both H_s and τ (Table 1). Due to wave reflection and refraction, it is highly unlikely that waves with a height of 2.9 m would ever propagate into the

inner lagoon. Despite the simplicity of our categorical designations of wave exposure, they are supported by the model-derived quantitative estimates and are additionally robust to the potential inadequacies of the 1-D SWAN model which does not account for multi-dimensional processes such as reflection and refraction.

Benthic data collection

Quantitative data of benthic cover were collected at 34 sites at PHA from September 17 to September 29, 2002 on a research cruise of the NOAA Ship *Townsend Cromwell* (TC-02-07) and M/V *Rapture* 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, Figure 1). At each site, two 25-m transects separated by 10 m were placed along a 10 to 20 m isobath on fore reef sites and at shallower depths for backreef and lagoon sites (Appendix 1). Using a photoquadrat (0.18 m²) 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 2 transects: 6 at randomly selected points directly adjacent to the transects and 6 off the transect, 3 m from the random points, in the direction of shallow water. In addition, field notes (including relative abundance estimates of algal and coral species) and voucher specimens of algae were collected to ensure accurate identification of species in the photos. All microscope slides and herbarium specimens of algal samples are currently in the Coral Reef Ecosystem Division (CRED) herbarium (PSV20017, PSV20097–PSV20122, PSV20124–PSV20190). Specimens are slated for eventual deposition in the *Herbarium Pacificum* at the Bishop Museum, Honolulu, Hawai`i.

A total of 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 the highest possible taxonomic level 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%.

Benthic data analysis

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[®], version 5 (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). Similarities among benthic communities from *a priori* wave exposure zones were tested using a two-way nested ANOSIM (maximum permutations = 5000) with sites nested by wave exposure. Nonmetric multidimensional 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 within different wave exposure zones.

Species richness of coral and macroalgae was compared among wave exposure zones. For each site, macroalgal richness was determined from photoquadrats, and coral richness was determined from combined species lists assembled in the field and photoquadrat data. 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 zones. A Bonferroni adjustment for multiple comparisons was required ($\alpha = 0.05$, p value must be < 0.011).

Results

At Pearl and Hermes Atoll (PHA), benthic cover was determined for 406 photoquadrats from 34 sites representing four different wave exposure zones: 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%). Macroalgae, with 36 species recorded (Table 2), were the second most abundant functional group with atoll-wide percent cover averaging 15.8% (SE = 1.89%). Of the 36 species found, thirteen were new records for PHA (see Abbott 1989, Vroom and Braun 2010) and one (*Laurencia crustiformans* McDermid) was a new record for the Northwestern Hawaiian Islands (Table 2). *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%).

Multivariate analysis

Significant differences were found when all sites at PHA were compared regardless of wave exposure through a two-way nested ANOSIM (Global R = 0.447, p-value < 0.001). The Bray-Curtis similarity matrix revealed that 39.1% of the 558 pair-wise comparisons were different (r-values >0.75) while very few site comparisons were similar (6.4% with r-values < 0.25). Surprisingly, geographically close locations varied between being highly similar and highly dissimilar suggesting high variability on both small and large spatial scales. This is exemplified by sites rPHA-43 and rPHA-39 (Figures 1, 2); 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 ($r = 0.763$).

The two-way nested ANOSIM (sites nested within wave exposure) did not find global significant differences among benthic communities based on wave exposure zones (Global $R = 0.199$, p -value = 10.0), but did indicate differences between a subset of wave exposure categories. For instance, pair-wise comparisons among the four wave exposure zones revealed significant differences in benthic communities between high/low ($r = 0.556$, p -value = 0.024), intermediate-high/low ($r = 0.897$, p -value = 0.002), and high/intermediate-high ($r = 0.354$, p -value = 0.004) wave regimes. Benthic communities were statistically similar between intermediate-low/high levels of wave exposure and between intermediate-low/intermediate-high levels of wave exposure ($r = 0.192$, p -value = 0.059; $r = 0.124$, p -value = 0.008, respectively). A higher degree of variation existed among sites within the intermediate-low and low wave exposure zones than between the wave exposure zones themselves (r -value = - 0.386).

Nonmetric multidimensional scaling (nMDS) ordination and cluster diagram

An nMDS ordination and cluster diagram (Figure 3) show that sites experiencing high wave exposure (N/NW-facing forereefs) were highly similar to each other in terms of benthic species composition and percent cover, as were sites experiencing low wave exposure (lagoonal reefs). Although greater variability was present, sites assigned to intermediate-high exposure also grouped together. The backreef sites rPHA-32 and rPHA-34 were found to cluster with intermediate-high wave exposure sites, indicating that benthic community assemblages in these areas were more closely similar to benthic communities from 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 (Figure 3).

SIMPER analysis and description of zones

Photoquadrats from sites within each of the wave exposure zones exhibited similar benthic assemblages, with the highest similarity of benthic cover occurring among low wave exposure sites (77.1% similarity, n = 36 photoquadrats) and the lowest similarity occurring among intermediate-low wave exposure sites (59.0% similarity, n = 144 photoquadrats).

Photoquadrats from high and high-intermediate wave exposure zones exhibited 68.7% (n = 72 photoquadrats) and 71.1% (n = 156 photoquadrats), respectively.

High wave exposure zones located on the NW forereef were characterized by the highest percent covers of encrusting crustose coralline red algae (36.5%) and the mound forming coral *Porites lobata* Dana (6.5%) and a scarcity of the fleshy green macroalga *M. setchellianum* (Table 3). Geomorphologically, high wave exposure sites often consisted of highly rugose spur and groove environments containing pinnacles of crustose coralline red algae. Cover by turf algae and sand were relatively low (Table 3).

Areas with intermediate-high wave exposure were located along E and S facing forereefs. The geomorphology of these sites ranged from classic spur-and-groove formations to flat pavements and benthic assemblages were typically characterized by a diversity of species. These sites were unified by the large abundance of *M. setchellianum* coupled with a relatively high occurrence of sand (Table 3) when compared to other wave exposure zones. Species of the coral genus, *Pocillopora*, were also most abundant at sites with intermediate-high levels of exposure (1.9%, Table 3).

Areas with intermediate-low wave exposure were located in both backreef and lagoonal regions. Sites within this zone were variable in terms of their benthic community assemblages and were the only locations containing the coral *Montipora capitata* Dana and *M. turgescens* Bernard. These sites had the highest abundances of turf and macroalgae (Table 3). Additionally,

relatively high percent cover of species of *Halimeda* and low levels of crustose coralline red algae were observed.

Areas of low wave exposure located within the central part of the lagoon were dominated by the finger coral *Porites compressa* Dana (37.8%) with very few other coral species present (Table 3). A complete absence of *M. setchellianum* also separated these sites from other wave exposure zones.

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 ($F=13.819, p=0.0013$; $F=9.855, p=0.0011$; Figure 4). Sites with low wave exposure had relatively few species, with *P. compressa*, *Cyphastrea ocellina* Dana, *Pocillopora damicornis* Linnaeus, and *M. capitata* as the only corals, and *Halimeda opuntia* (Linnaeus) Lamouroux and *Laurencia nidifica* J. Agardh as the only macroalgae recorded. Sites with high wave exposure had moderate numbers of coral species, but were found to have significantly fewer macroalgal species than sites with intermediate-high levels of wave exposure (Figure 4a). Results of ANOVA 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 ($F=19.581, p=0.0001$).

Discussion

Pearl and Hermes Atoll contains a rich diversity of coral reef communities with high variability among sites on both large and small scales. Patterns among benthic community assemblages based on wave exposure were also apparent. Sites occurring in high and low wave

exposure zones each supported similar types of benthic organisms in similar abundances, and formed two distinct groups (Table 3, Figure 3). Intermediate wave exposure zones were more variable in benthic community composition and formed less distinct groups (Figure 3).

Therefore, our hypothesis exploring whether sites experiencing similar levels of wave exposure would support similar types of benthic community assemblages was only partially supported.

Regardless, key differences supported by ANOSIM among wave exposure zones at PHA provide a useful measure for categorizing the broad community patterns observed.

Patterns of benthic communities

Inter-site similarity was highest among sites within low wave exposure zones (Figures 2, 3), which also exhibited the lowest diversity of benthic organisms. Low wave exposure favored the growth of the scleractinian coral *P. compressa* that formed nearly monospecific stands in these areas. A link between low wave energy and high *P. compressa* growth has been reported to occur throughout Hawai`i, and demonstrates that protected areas such as embayments, lagoons, and deeper forereefs foster the competitive dominance of *P. compressa* (Grigg and Maragos 1974, Dollar 1982, Grigg 1983, Storlazzi et al. 2005). The occurrence of a competitive dominant species as well as low species diversity with little disturbance supports the concepts proposed by the Intermediate Disturbance Hypothesis (IDH, Connell 1978).

While several researchers have noted the competitive dominance of *P. compressa*, very few studies have examined the mechanisms that give it 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); however, *P. compressa* seems to thrive in calm conditions. One possible explanation for the success of *P. compressa* in low wave exposure conditions is that its fingerlike morphology and subsequent high surface area/volume ratio (SA/V) increase gas and nutrient exchange resulting in increased photosynthetic and

calcification rates (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 small spatial scales (Shashar et al. 1996). Therefore, the same morphology that renders *P. compressa* vulnerable in high wave conditions potentially enables *P. compressa* to out compete other organisms in low wave exposure conditions.

Sites from high wave exposure zones formed a distinct group and were characterized by a high abundance of crustose coralline red algae and occurrence of the robust mound forming coral *P. lobata* (Table 3, Figure 3). Because of the encrusting nature of many coralline red algal species, these organisms are highly resistant to extreme wave energy (MacCaughey 1918, Adey and Vassar 1975). High wave energy decreases the effectiveness of grazers, increases nutrient availability by constantly perturbing the diffusion boundary layer, and damages branching organisms (Steneck 1986, Storlazzi et al. 2005 and Hurd 2000). This combination makes areas with high wave energy a productive refuge in which crustose coralline red algae can become the competitive dominant (Adey and Vassar 1975).

Forereef sites in the intermediate-high wave exposure zone along the E and S sides of Pearl and Hermes Atoll supported greater benthic community variability than either the high or low wave exposure zones, but still exhibited a relatively high degree of similarity in benthic community composition (Figure 3). Although not as high as those for sites in the high wave exposure zone, 1-D SWAN wave forces estimates for the intermediate-high wave exposure zone were considerable (Table 2) and likely result in periodic disturbance conditions for many organisms (Storlazzi et al. 2005). Disturbance may explain the relatively high abundance of the colonizing coral species *P. meandrina* and the robust coral species *P. lobata* (Table 3, Grigg and Maragos 1974, Storlazzi et al. 2005). *P. meandrina* is commonly referred to as the “cauliflower”

coral based on 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).

Benthic composition within the intermediate-low wave exposure zone was highly variable among sites and appears to not support the hypothesis that sites experiencing similar wave exposure regimes would support similar benthic assemblages. However, the intermediate-low wave exposure zone at PHA is a large area composed of both patch reefs and backreefs adjacent to NW, W, S, and E facing forereefs (Figure 3). The high residual flows and bed shear stress (Table 2) in backreef areas during large wave events may differ substantially depending on the wave height and period impacting adjacent forereefs and depending on to the geomorphology of the adjacent reef crest (Rooney et al. 2008). For instance, those sites near emergent reef crests are likely more protected from wave exposure than those near a submerged reef crest (Fulton and Bellwood 2005). While wave exposure is likely one mechanism involved in structuring benthic communities at PHA, it is not surprising that high variability occurred within the intermediate-low wave exposure zone. In the absence of a strong disturbance regime as well as strong competitive interactions common in low disturbance conditions, a suite of other abiotic and biotic factors (such as temperature, nutrients, herbivory, etc.) may influence the variability of communities within these reefs (Connell 1978, Menge and Sutherland 1987, Menge 1992, Power 1992).

Intermediate low and high wave exposure zones were also characterized by the abundance of the green alga *Microdictyon setchellianum*. The level of water motion experienced at these sites may provide an ideal balance between nutrient delivery and disturbance for *M. setchellianum*. Thick boundary layers and high epiphyte cover may limit growth of *M. setchellianum* in low wave regimes; while the delicate morphology of *M. setchellianum* may

prevent it from remaining attached to the substrate in high wave regimes. Thus, *M. setchellianum* might be limited in its distribution to sites with intermediate levels of wave exposure.

Species Richness

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 (Figure 4). 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: *M. capitata*, and early succession coral species: *P. meandrina*) at sites with both intermediate-high and intermediate-low levels of wave exposure at PHA supports predictions from the IDH (Table 3, Grigg and Maragos 1974, Grigg 1983).

Morphological Patterns

Our results highlight the importance of organismal morphology in different wave exposure regimes (Table 3). It is likely that a morphological tradeoff exists between species that are robust to high wave exposure (e.g. crustose coralline algae) and species that allow for maximum surface area to volume (SA/V, e.g. *Porites compressa*). 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 (Figure 5). Morphologies with high SA/V, such as the highly branched *Porites compressa* (the dominant species in our low wave exposure zone), allow for maximum uptake of nutrients and gases (Hurd 2000; Stewart and Carpenter 2003). While this type of morphology is ideal for

low wave exposure regimes because boundary layer turnover is slow (Hurd 2000, Stewart and Carpenter 2003), the high SA/V ratio morphology increases the vulnerability 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 the prostrate encrusting morphology of crustose coralline red algae (the dominant group in our high wave exposure category) , and that is robust to damage from wave exposure is more advantageous. Some organisms, especially species of marine algae, exhibit phenotypic 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). This species was found at nearly all sites at PHA regardless of wave exposure. However, not all organisms are capable of the phenotypic plasticity seen in *L. variegata*. Therefore, a tradeoff likely exists between a morphology that is robust to wave exposure and one that allows for maximum SA/V (Figure 5). This tradeoff may result in certain organisms being best suited for specific wave exposure regimes, and is likely partially responsible for creating distinct communities observed in the low and high wave exposure zones at PHA.

Conclusion

While it is apparent that wave exposure is a determinant in coral reef community structure, analyses only partially supported our hypothesized wave exposure zones. Two-way nested ANOSIM results showed that some zones were not statistically distinct. More precise measurements of wave force and current velocity may reveal a more robust relationship between

benthic communities and wave energy and possibly form more informative zones. However, wave exposure alone will never be sufficient in explaining all variation within coral reef community structure. Other structuring forces, such as resource availability, herbivory and competition, are also responsible for variation in benthic communities within and among wave exposure regimes (Menge and Sutherland 1987, Menge 1992, Power 1992). Regardless, we found wave exposure provided a useful measure for categorizing the broad community patterns observed in benthic assemblages at PHA.

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Table 1: Calculated estimates of wave height (H_s) and bed shear stress (τ) for both 10-year extreme events and modal conditions for the four wave exposure categories using results from the 1-D SWAN model.

Wave Exposure Zones	Site ID	10-year max H_s (m)	Modal mean (SE) H_s (m)	10-year max τ (N/m²)	Modal mean (SE) τ (N/m²)
High: NW facing fore-reefs	R46, r44, r43, r39, r45, 19	12.379	3.337 (0.005)	131.074	27.405 (0.225)
Intermediate High: E and S facing fore-reef	r42, r25, r27, r28, r26, 15, r35, r40, r33, 16, r38, 17, 18	6.638	NA*	76.401	NA*
Intermediate Low: Back and patch reefs near reef crest	31, 32, 30, 22, r29, r34, 20, r32, 23, 24, 26, r41	4.044	0.576 (0.085)	64.8	7.344 (1.021)
Low: Lagoon	r37, 21, r31	2.904	0.444 (0.061)	34.197	2.519 (0.661)

* Modal conditions from the S sector were not considered because waves so infrequently originate from this direction. Therefore, not enough information was available to summarize modal conditions for the intermediate-high wave exposure category.

Table 2: Macroalgal species list from Pearl and Hermes Atoll, Northwestern Hawaiian 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 Hawaiian Islands.

RHODOPHYTA	Codiaceae
Ceramiales	<i>Codium arabicum</i> Kützing
Ceramiaceae	<i>C. hawaiiense</i> * Silva and Chacana
<i>Haloplegma duperreyi</i> Montagne	<i>C. subtubulosum</i> * Okamura
Dasyaceae	Halimedaceae
<i>Dasya iridescens</i> (Schlech) Millar and Abbott	<i>Halimeda discoidea</i> Decaisne
Rhodomelaceae	<i>H. distorta</i> (Yamada) Hillis-Colinvaux
<i>Amansia fimbriifolia</i> Norris	<i>H. opuntia</i> (Linnaeus) Lamouroux
<i>Chondrophycus parvipapillatus</i> * (Tseng) Garbary and Harper	<i>H. velasquezii</i> Taylor
<i>Laurencia crustiformans</i> * † McDermid	Cladophorales
<i>L. decumbens</i> * Kützing	Anadyomenaceae
<i>L. galtsoffii</i> Howe	<i>Microdictyon setchellianum</i> Howe
<i>L. mariannensis</i> * Yamada	Siphonocladaceae
<i>L. nidifica</i> * Agardh	<i>Boodlea composita</i> * (Harvey) Brand
Corallinales	<i>Dictyosphaeria cavernosa</i> (Forsskål) Børgesen
Corallinaceae	<i>D. versluisii</i> Weber-van Bosse
<i>Jania adhaerens</i> Lamouroux	Chlorococcales
Gigartinales	<i>Palmophyllum crassum</i> (Naccari) Rabenhorst
Peyssonneliaceae	Dasycladales
<i>Peyssonnelia sp.</i> Decaisne	Dasycladaceae
Nemaliales	<i>Neomeris van-bosseae</i> * Howe
Liagoraceae	PHAEOPHYTA
<i>Ganonema pinnatum</i> * (Harvey) Huisman	Dictyotales
Rhodymeniales	Dictyotaceae
Faucheaceae	<i>Dictyota sp.</i> Lamouroux
<i>Halichrysis coalescens</i> * (Farlow) Norris and Millar	<i>Lobophora variegata</i> (Lamouroux) Womersley ex Oliveira
Rhodymeniaceae	<i>Padina boryana</i> * Thivy
<i>Chrysomenia okamurae</i> * Yamada and Segawa	<i>Styopodium flabelliforme</i> Weber-van Bosse
CHLOROPHYTA	Fucales
Bryopsidales	Sargassaceae
Caulerpanceae	<i>Turbinaria ornata</i> (Turner) J. Agardh
<i>Caulerpa serrulata</i> (Forsskål) Agardh	
<i>C. webbiana</i> Montagne	

Table 3: Average percent cover of organisms within wave exposure zones. Percent cover (standard deviation) of major space occupying organisms within the four wave exposure zones. Bold numbers indicate the wave exposure zone with the highest average percent cover of a particular organism. CCA = crustose coralline red algae.

	Morphology	High	Intermediate high	Intermediate low	Low
Algae					
Turf	flexible	57.32	73.95	75.11	52.66
	filamentous	(6.23)	(9.63)	(9.77)	(7.33)
CCA	inflexible	36.65	13.76	6.47	16.82
	encrusting	(10.49)	(9.28)	(5.64)	(8.28)
<i>Halimeda</i> spp.	flexible	5.50	2.70	5.42	0.18
	branching	(0.93)	(2.59)	(12.27)	(0.26)
<i>Microdictyon setchellianum</i>	flexible	0.06	23.10	18.33	0.00
	blades	(0.14)	(14.14)	(16.30)	(0.00)
Other		3.47	1.05	3.94	0.00
Macroalgae		(4.22)	(0.79)	(4.12)	(0.00)
Coral					
<i>Montipora</i> spp.	inflexible	0.00	0.00	5.14	0.00
	encrusting	(0.00)	(0.00)	(9.73)	(0.00)
<i>Pocillopora</i> spp.	inflexible	1.71	1.92	1.08	0.00
	branching: compact	(2.58)	(2.67)	(1.42)	(0.00)
<i>Porites compressa</i>	inflexible	0.31	0.12	0.19	37.77
	branching: fingerlike	(0.46)	(0.24)	(0.62)	(11.21)
<i>Porites lobata</i>	inflexible	6.49	2.36	0.71	0.00
	mound forming	(7.14)	(3.52)	(2.02)	(0.00)
Other Coral		1.47	0.76	0.03	0.03
		(2.84)	(0.81)	(0.08)	(0.04)
Other					
Cyanobacteria	flexible	0.00	0.13	0.45	0.56
	filamentous	(0.00)	(0.46)	(1.41)	(0.79)
Sand		3.60	6.31	7.65	3.76
		(3.36)	(5.71)	(4.69)	(5.00)
Other		4.46	2.90	1.15	3.98
		(2.83)	(1.07)	(0.95)	(2.02)
# of Scleractinian Coral Species		6.50	7.31	6.75	4.00
		(4.55)	(2.84)	(2.60)	(0.00)
# of Macroalgal Species		2.83	5.39	4.75	0.67
		(1.33)	(1.19)	(2.18)	(1.16)

Figure 1: (a) Ikonos satellite image of Pearl and Hermes Atoll. Numbers represent study sites. Colors of each number represent wave exposure zones: red = high, yellow = intermediate- high, green = intermediate-low, blue = low; (b) Map of the Hawaiian Archipelago depicting the location of Pearl and Hermes Atoll in the Northwestern Hawaiian 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 Hawaiian Islands (MHI).

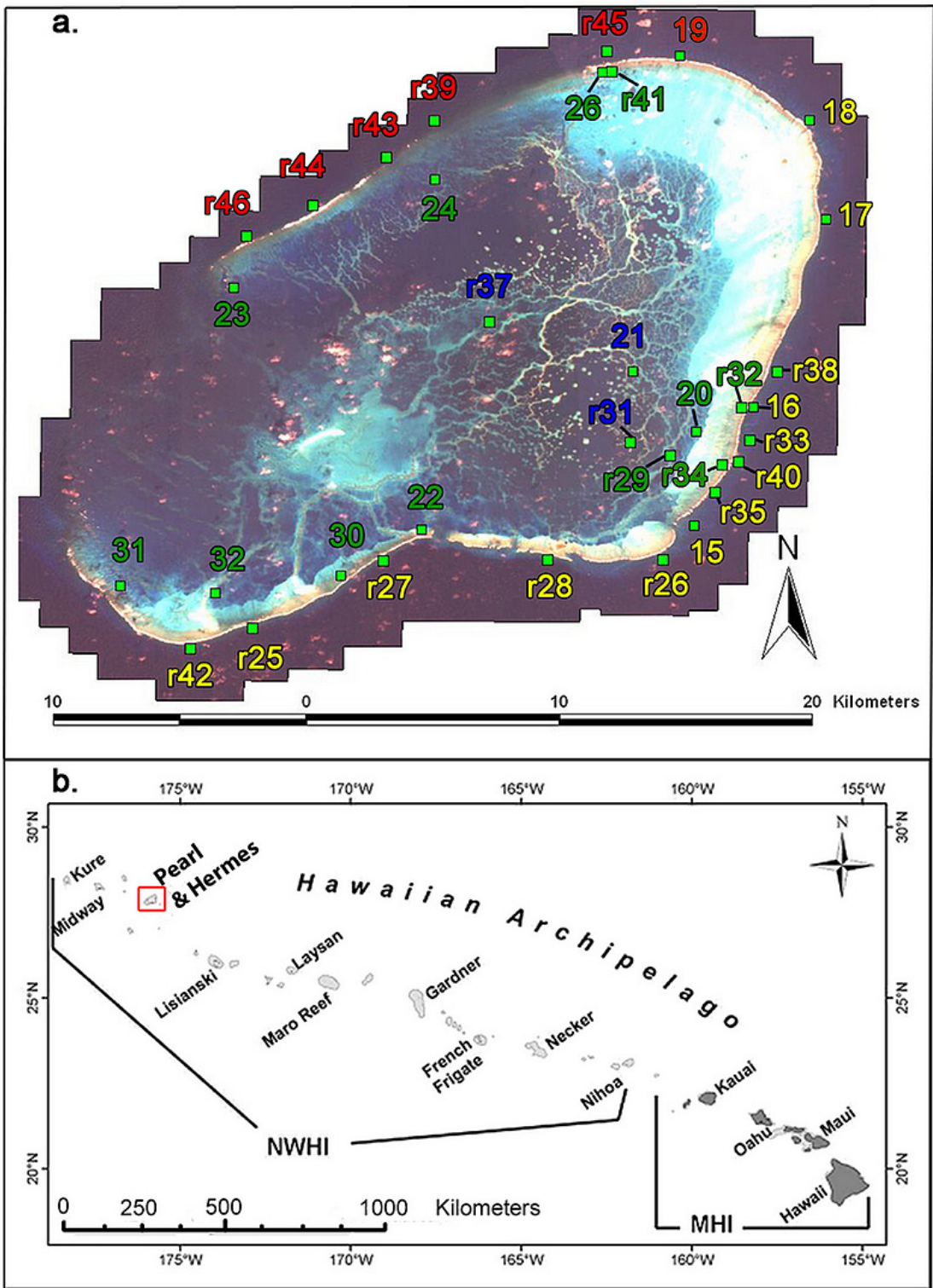


Figure 2: (a) Monthly mean, standard deviation, mean monthly min/max and total observed min/max significant wave height (H_s) at Pearl and Hermes Atoll from NOAA/NCEP Wave Watch III (WW3) global model (Tolman 2002, <http://polar.ncep.noaa.gov/waves>). (b) Frequency of occurrence of peak wave direction (θ_p , 5° bins) and peak wave period (T_p , 2 s bins) from WW3 hindcast data for the months of November through March 1997-2010. (c) Same as (b), but for the months of May through September. Events occurring during the transition months of April and October are omitted from (b) and (c) for clarity.

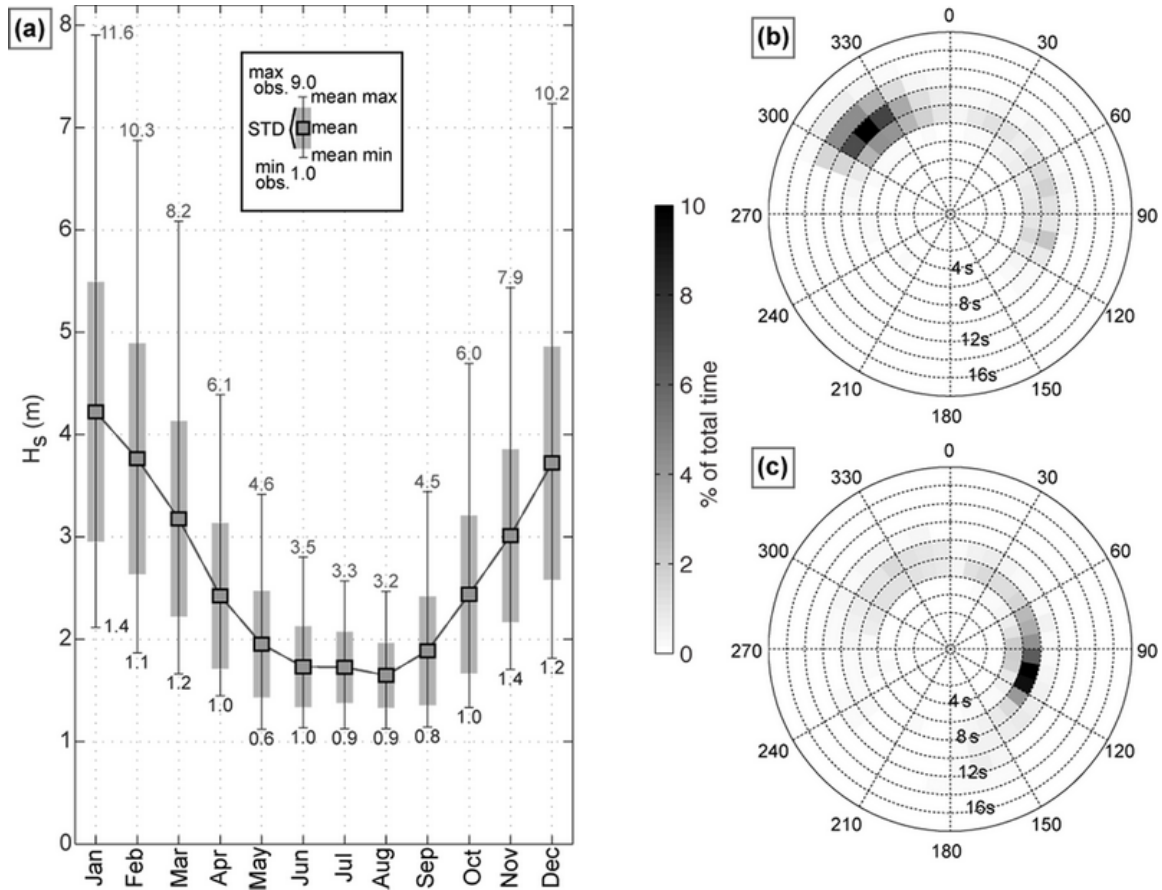
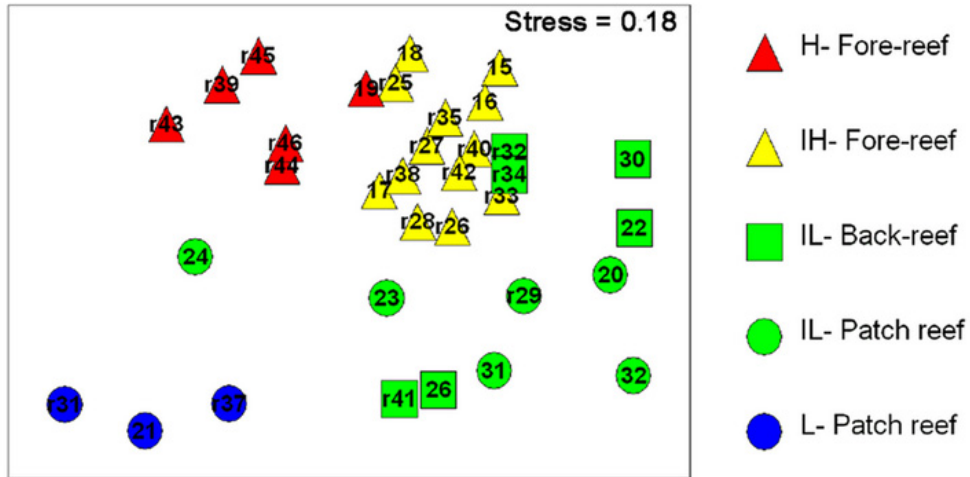


Figure 3: (a) Nonmetric multidimensional scaling (nMDS) plot and (b) cluster diagram showing relationships of sites to one another. For both A and B, colors represent wave exposure zones: red= high, yellow = intermediate-high, green = intermediate-low, blue = low. In A, shapes represent geomorphology zones (forereef, backreef, and patch reef). In B, cross hatching represents backreef sites.

a.



b.

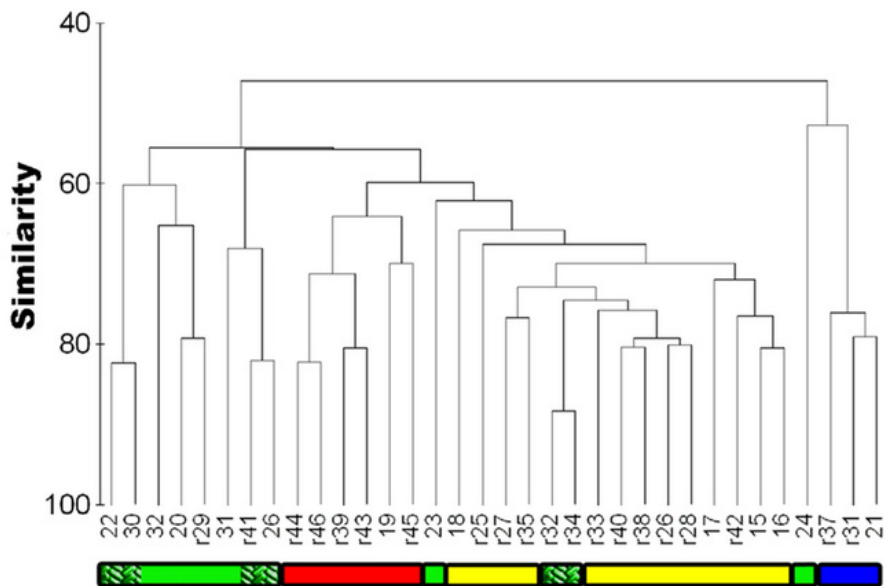


Figure 4: Comparison of species richness among wave exposure zones for (a) macroalgae and (b) coral. Values for macroalgae were based on photoquadrat percent cover data and values for coral were based on *in situ* species lists combined with percent cover photoquadrat data. Error bars represent one standard error of the mean. Statistical results of Welch's one-way ANOVA are shown, differences were significant after Bonferroni adjustment for multiple comparison ($\alpha = 0.05$). Exposure groups with different letters are significantly different (Dunnett's T3 pair-wise comparisons).

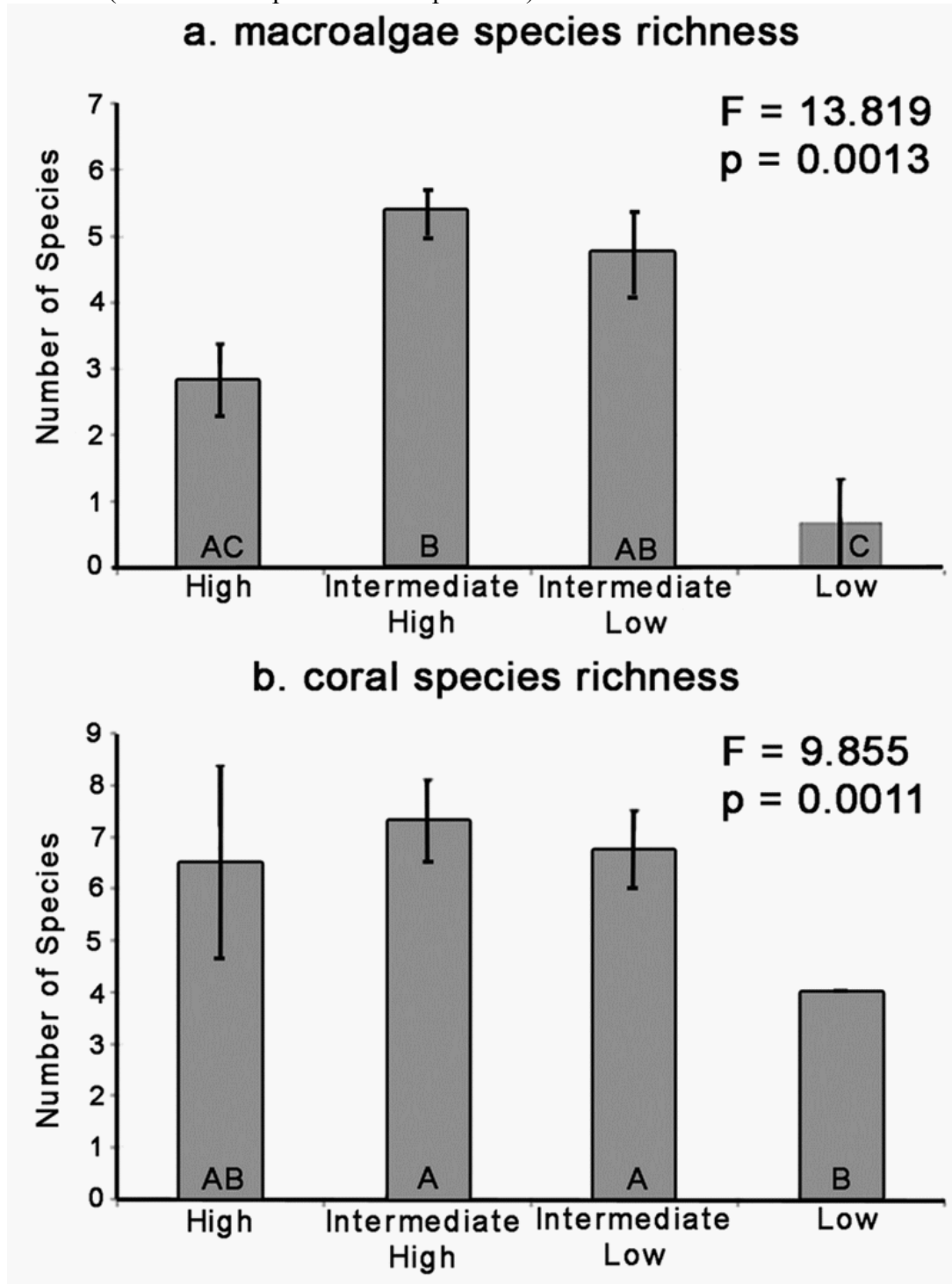
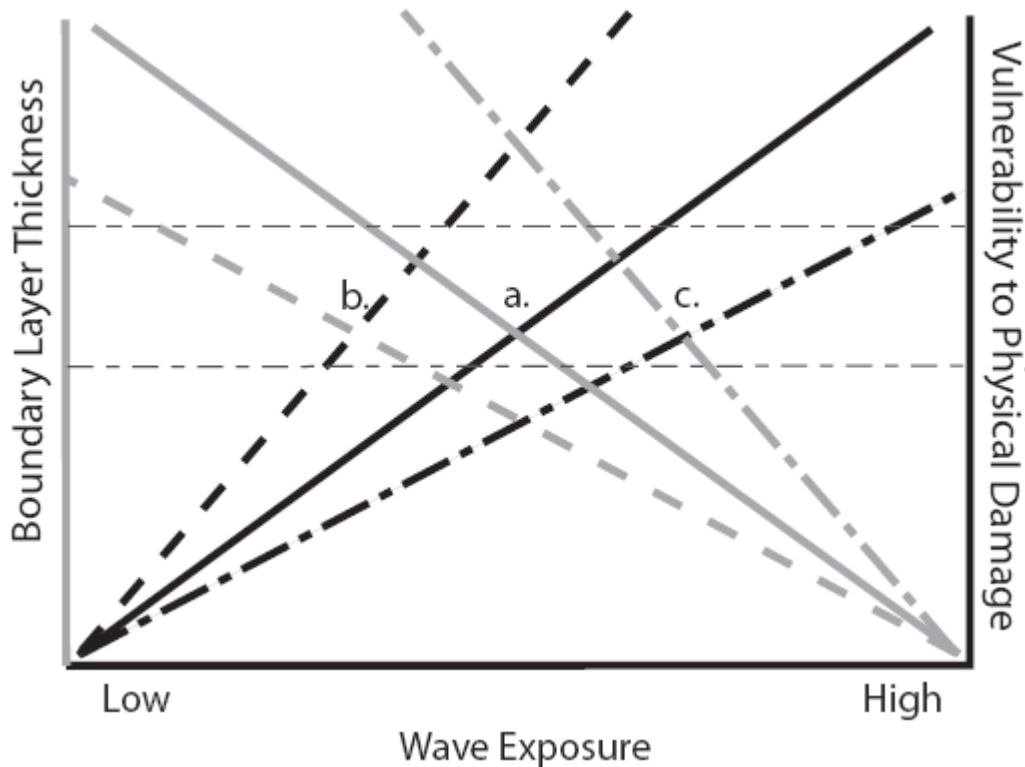


Figure 5: Morphological trade-offs of photosynthetic marine organisms along a wave exposure gradient. Diffusion boundary layer (DBL) thickness (left vertical axis) decreases with increasing wave exposure (gray lines). Vulnerability of organisms to physical damage (right vertical axis) increases with increasing wave exposure (black lines). In this model, particular morphological strategies are represented by the intersections of gray and black lines. The intersection space is bounded at the top of the graph by the Maximum Survival Threshold (MST, upper vertical dashed line), which represents both maximum DBL thickness and maximum vulnerability, and at the bottom of the graph by the morphological trade-off limitation (lower vertical dashed 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 gray 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 black 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 black dot-dash line) with a concomitant increase in DBL thickness (slope of gray dot-dash line).



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