

Local variation among rocky subtidal habitats in the San Juan Archipelago: are differences in community structure associated with small-scale changes in abiotic factors?

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Abstract

Previous studies have demonstrated that regional variation in community structure is largely driven by abiotic factors, but that these factors have less influence on community structure at smaller scales. We sought to investigate the potential role of select abiotic factors in regulating benthic communities at spatial scales ranging from 10 to 1000 meters. This was accomplished by comparing benthic point-intercept survey data against measurements of depth, slope, aspect and current flow. Results indicated that substrate depth and slope significantly correlated with observed differences in community composition, while current flow was marginally correlated with community composition. These results suggest that abiotic factors still play an important role in the structuring of biological communities at local scales.

Introduction

Fluctuations in community composition have been assessed at multiple temporal and spatial scales, and are well established in the ecological literature (Dayton and Tegner 1984; Levin 1992). Numerous studies in marine coastal habitats reveal spatial patchiness among benthic communities anywhere from scales of tens of centimeters (Archambault and Bourget 1996; Underwood and Chapman 1996; Benedetti-Cecchi 2001) to hundreds of kilometers (DeForges, Koslow and Poore 2000; Connell and Irving 2008). While some ecological processes are scale specific, others may operate over ranges of spatial and temporal scales. Local-scale heterogeneity has largely been attributed to biotic interactions (e.g., competition, predation; Paine 1966; Underwood et al. 1983; Gaines and Roughgarden 1985; Menge et al. 1994) while regional/global-scale patchiness has generally been attributed to abiotic factors (e.g., current patterns, thermoclines; Menge and Olson 1990; Roy et al. 1998; Menge et al. 2003).

Topography is a common source of spatial heterogeneity that may profoundly influence species distribution and composition of communities at multiple scales. While studied extensively in terrestrial systems, the influence of topography (i.e. bathymetry in marine systems) is just beginning to emerge in marine subtidal systems, largely as a result of multibeam and sidescan sonar technologies (deMoustier and Matsumoto 1993; Clarke et al. 1996; Whitmire et al. 2007; Brown and Blondel 2009). Studies of terrestrial plant communities have shown that

topographic features such as elevation, slope (angle of substrate) and aspect (compass direction a substrate faces) can shape community structure (Whittaker 1960; Ohmann and Spies 1998). Elements of bathymetry have proven important in intertidal systems, largely as a determinant of zonation patterns (Denny 1988; Bertness 1999), but its influence in subtidal systems has historically been relegated to attributes of depth at moderate to large geographic expanses (Choat and Schiel 1982; Vadas and Steneck 1988; Underwood et al. 1991; Goldberg and Kendrick 2004).

The bathymetry of a region can regulate subtidal community composition in many ways, from direct physical influences such as substrate type (rock, sand, etc.) or angle and direction of declination (i.e. slope and aspect), to more indirect influences such as local and global current patterns. In recent years efforts have been made to use bathymetry indices to map, assess and even predict community assemblages, enhancing our understanding of community structure and dynamics from small to large spatial scales (Whitman and Dayton 2001; Beaman and Harris 2007; Greene et al. 2007; Shotwell et al. 2007; Wedding et al. 2008; Miller and Etter 2008).

Qualitative estimates of bathymetric features such as slope have been utilized to assess differences in community structure and organization. Studies in temperate subtidal regions have shown differences in community structure between horizontal and vertical substrates (Baynes 1999; Glasby 2000; Miller and Etter 2011). To the best of our knowledge, no published studies to date have assessed the influence of the aspect of a habitat to community structure, either qualitatively or quantitatively.

Bathymetry can strongly influence current patterns and flow speeds to produce very localized effects (Gaylord et al. 2007). The variation of flow among substrates likely influences community composition and may be an underlying factor in localized patchiness among contiguous habitat. Flow affects organisms at the individual level; from the ability of an organism to settle either via efficacy of settlement cues or arrival of larvae to habitat (Jumars and Nowell 1984; Turner et al. 1994; Wright and Boxshall 1999; Gaylord and Gaines 2000), to an organism's feeding ability and growth (Sebens 1984; Okamura 1992; Arkema 2009), as well as to their morphology (Koehl et al 2008; Ferrier and Carpenter 2009). These effects likely act on multiple species, thereby influencing the community as a whole. It is thus plausible that differences in current flow may play a large role in differences observed among communities, even when in close proximity to one another.

Interest in the community structure and function of invertebrate and fish assemblages has increased steadily among temperate rocky subtidal systems over the past three decades (Whitman and Dayton 2001). These habitats are key structural and ecological components of temperate coastlines, yet our understanding of their importance and function at different spatial scales remains patchy at best (Connell and Irving 2008). We propose to evaluate the contributions of select abiotic factors to explain variation in temperate subtidal benthic

communities at local scales. Observations by divers in San Juan Island, WA noted that areas of contiguous rocky banks in short proximity to one another housed distinctly different communities. We aim to investigate this spatial heterogeneity to determine if observed differences in communities correlate with fluctuations in direct and indirect abiotic factors.

With local and global anthropogenic impacts increasing steadily (Jackson et al. 2001; Halpern et al. 2008) it is imperative to determine both the status of benthic communities as well as the underlying factors responsible for variation in these communities. As climate conditions are changing at unprecedented rates (Bakun 1990; Stachowicz et al. 2002), baseline knowledge of community structure and regulating factors responsible must be understood before these ecosystems are further altered, degraded, or lost completely. Knowledge of these ecosystems will ultimately enhance conservation and management efforts and help to ensure the longevity of these unique and beneficial ecosystems for the foreseeable future.

Study Area

The islands of the San Juan Archipelago, WA are situated within the Salish Sea, lying north of Puget Sound at the intersection of the Strait of Juan de Fuca and the Strait of Georgia (Fig 1). The San Juan Islands are a product of erosional events associated with recent glacial action (Fraser glaciation, 18,500-15,000 years ago). The resulting narrow channels or fjords between islands create strong tidal currents that help to support diverse fish, invertebrate and algal assemblages.

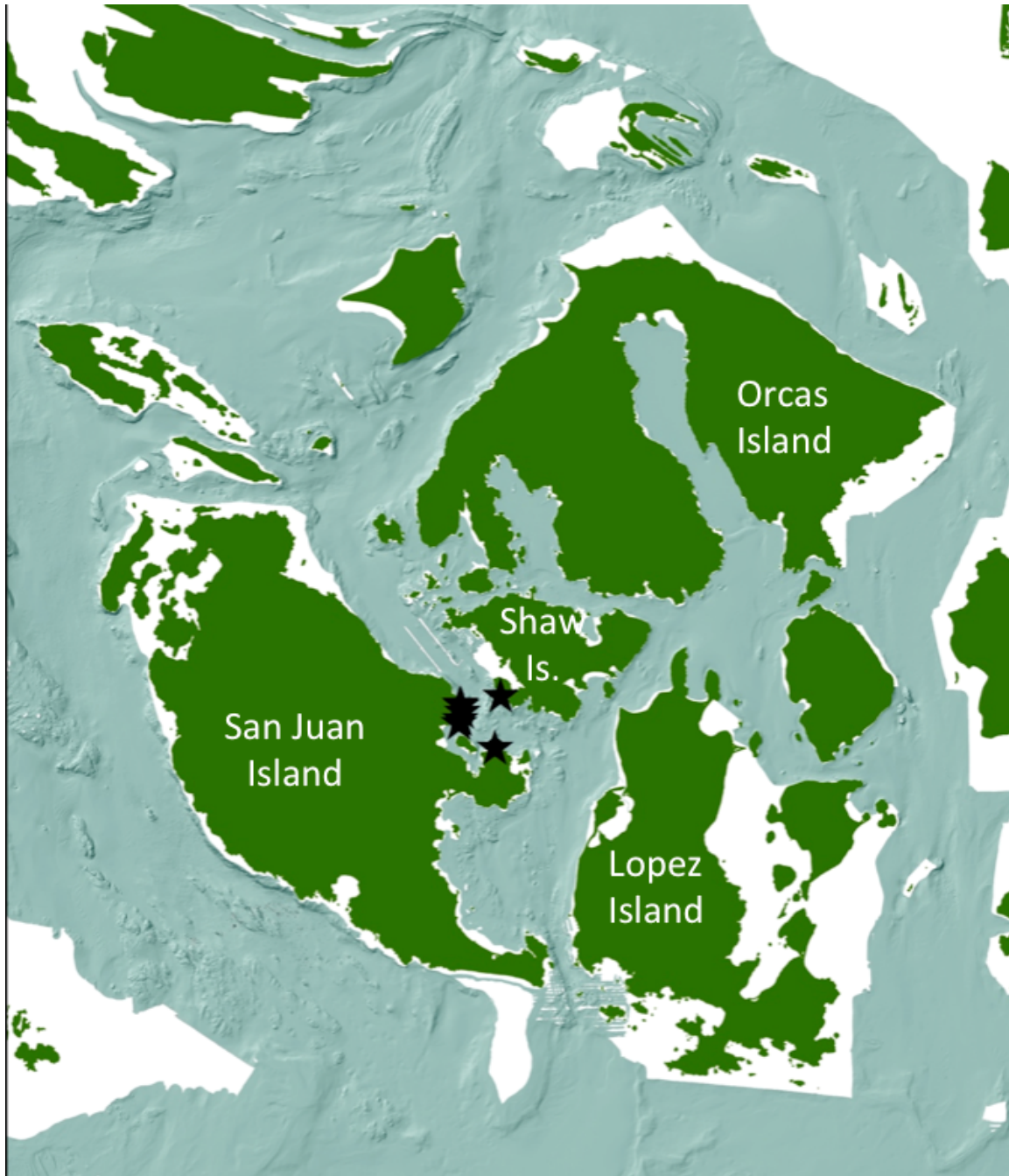


Figure 1: Bathymetry map of San Juan Archipelago. Study sites denoted as black stars. White space indicates areas of no MBES data.

Methods

Benthic community structure

A series of five long-term monitoring sites were established on San Juan Island in 2006. At each site, one 10m long transect is conducted every 3 meters in depth (3-27m) to a depth of approximately 30 meters, for a total of 9 transects per site. Point intercept surveys are conducted along each transect line at 10 cm intervals, totaling

100 points per transect. At each point, the underlying biota is identified to the lowest visually identifiable taxonomic level; if there are no biotic organisms, the substrate is classified by gross habitat type (rubble, bare rock, sediment, etc). All points are then entered and transformed into percent cover estimates (each point representing 1%). The most recent complete dataset for point intercept surveys was collected in 2010 and will be the source for our community structure analysis. Two additional sites were selected due to their close (<1km) proximity to the five long-term monitoring sites; Point George Central on Shaw Island, and 1-mile reef on San Juan Island, for a total of 7 sites (Fig. 2).

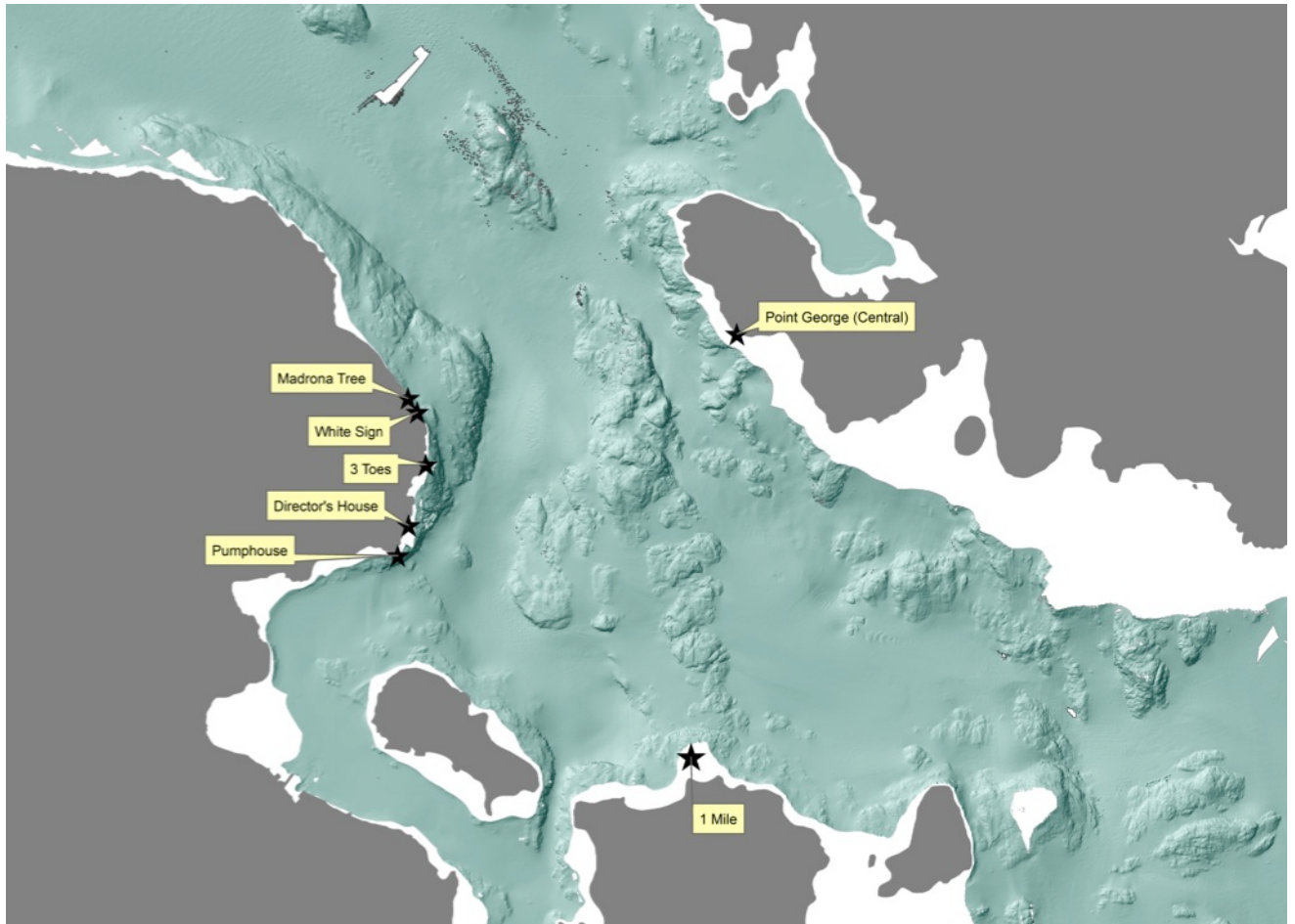


Figure 2: Location of study sites in San Juan Channel. White space indicates areas of no MBES data.

Abiotic factors

Four abiotic factors were chosen for analysis in this paper. These include: depth, slope, aspect, and current flow. Slope (incline or steepness of a surface) and aspect (compass direction that a slope faces) measurements were calculated using multibeam bathymetry maps for the San Juan Archipelago. GPS coordinates for each site were imported into ArcGIS and plotted onto existing MBES data. The direction and location of transects at each site were estimated and subsequently overlaid onto bathymetry maps of the San Juan Channel (Fig. 3).

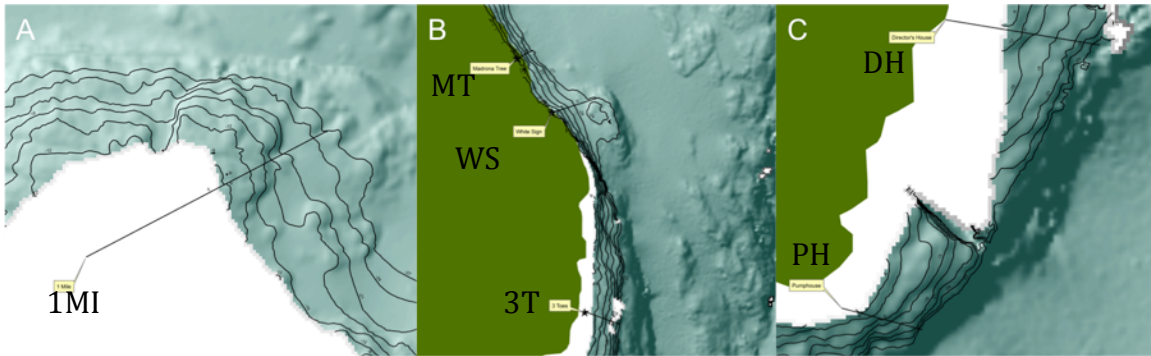


Figure 3: Bathymetry and approximate transect location at A) 1-mile reef (1MI); B) Madrona Tree (MT), White Sign (WS) and 3 Toes (3T); C) Pumphouse (PH) and Director's House (DH) sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data. (See Appendix for full size images)

No bathymetric data was available for the site Point George Central; as such data from this site is included for analysis only for visual estimates of slope and flow. Slope and aspect designations were assigned by evaluating the 2x2 meter bathymetry grid cell at the estimated beginning of each transect (Figs. 4-5).

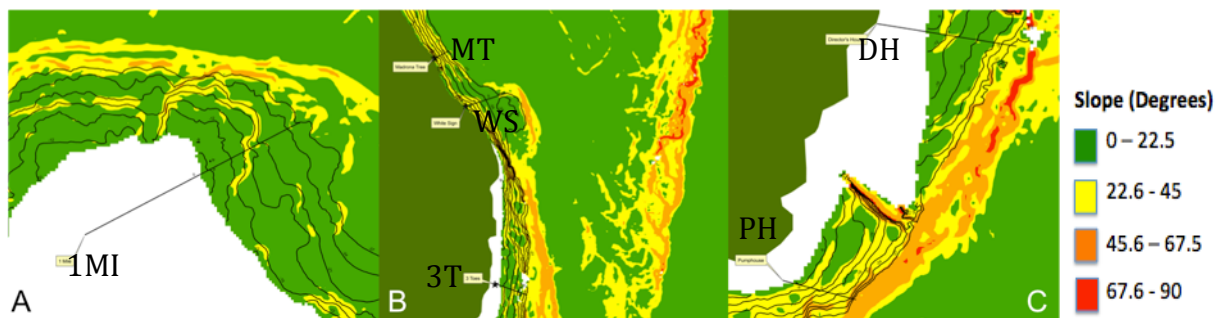


Figure 4: GIS-derived slope and approximate transect location at A) 1-mile reef (1MI); B) Madrona Tree (MT), White Sign (WS) and 3 Toes (3T); C) Pumphouse (PH) and Director's House (DH) sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data. (See Appendix for full size images)

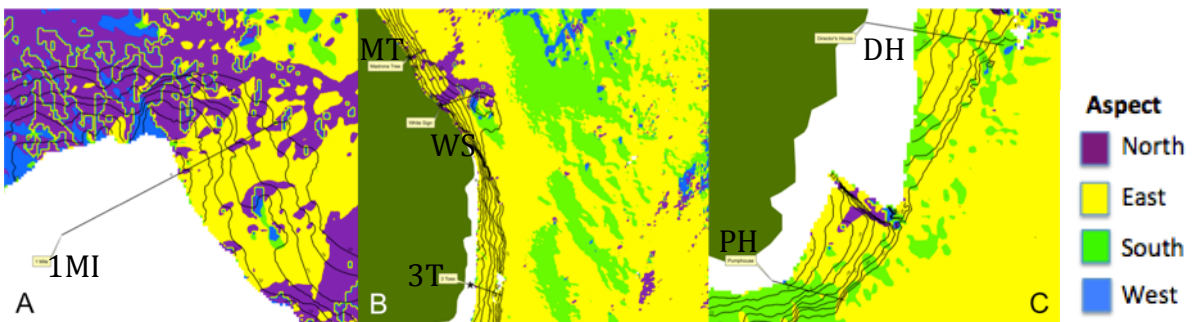


Figure 5: GIS-derived aspect and approximate transect location at A) 1-mile reef (1MI); B) Madrona Tree (MT), White Sign (WS) and 3 Toes (3T); C) Pumphouse (PH)

and Director's House (DH) sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data. (See Appendix for full size images)

Slope estimates were binned into one of four designations: 1) 0 to 22.5 degrees, 2) 22.6 to 45 degrees, 3) 45.1 to 67.5 degrees, and 4) 67.6 to 90 degrees. Aspect estimates were binned into 4 categories by cardinal direction: North) 315.1 to 45 degrees, East) 45.1 to 135 degrees, South) 135.1 to 225 degrees, and West) 225.1 to 315 degrees.

Additionally, qualitative visual estimates for slope were collected at each transect *in situ* by divers. Orientation of the substrate beneath each transect was classified as either horizontal or vertical.

Average flow rates of water at or near the bottom were approximated by measuring the dissolution rates of 5x5x2 cm alabaster blocks (Eckman et al 1989). Dissolution of alabaster in seawater is a transport-limited process (Berner 1978). With proper calibration, alabaster dissolution can be used to approximate average current speed and proves to be a cost-effective way to approximate benthic current flow for multiple sites (Santschi et al. 1991; Porter et al. 2000).

Large slabs of alabaster were cut to create uniform 5x5x2 cm blocks. Each block was then dried in a drying oven at 60°C for 24 hours. Upon cooling, blocks were individually labeled and secured to 7x8 cm plexiglass plates using silicon caulk. The emergent surface area of each block assembly was then measured to the nearest cm to obtain an initial surface area. Each block assembly was then attached to a construction brick via zip-ties. One alabaster block assembly was placed per transect at each site and left for a period of 10 to 12 days. At each transect, all macroalgae was removed in a 1-meter radius around each alabaster block assembly to eliminate potential abrasion of the alabasters by kelps and other macroalgae. Deployment was replicated temporally; as each block assembly was retrieved, another block was placed in the same area and left for another period of 10-12 days. An S4 current meter (InterOcean Systems, Inc.) was deployed at one of the sites to track actual current flow speeds for each of the deployments. Additionally, three alabaster block assemblies were placed alongside the S4 meter to calibrate alabaster dissolution rates with current flow.

Upon collection, alabaster blocks were removed from their substrate location and bagged to ensure no alabaster loss while in transit. Once back in the lab, alabaster blocks were removed from the brick and plexiglass assemblies, rinsed in fresh water and placed back in the drying oven at 60°C for 24 hours. Alabasters were then removed and allowed to cool to room temperature, upon which each alabaster was weighed to obtain a final weight. Dissolution rates were calculated as follows: $[(\text{Initial weight (g)} - \text{final weight (g)}) / \text{surface area (initial; cm}^2)] / \# \text{ days}$ to give a dissolution rate of g/cm²/day.

The deployment sequence was repeated one time for a total number of replicates equaling 2 per transect per site. Dissolution rates were then calculated for each alabaster block and assigned a flow rating. Ratings were obtained by calculating the mean dissolution rate and standard deviation per deployment. Bins were then created for 2 standard deviations above and below the mean and flow ratings assigned (Table 1). Each transect was then assigned to a flow rating category based on the ratings of its corresponding alabaster blocks. If discrepancies of flow ratings arose between deployment periods for an individual transect, the distance was calculated from the next higher or lower designation for each deployment. The deployment with the greater distance to the neighboring bin edge was then selected as the overall rating, yielding one overall rating per transect.

Table 1: Flow categorizations based on Standard Deviations away from mean dissolution rate.

Rating	Dissolution Range
Very Low	Greater than 2 Standard Deviations below mean
Low	1 to 2 Standard Deviations below mean
Medium-Low	1 Standard Deviation below mean to mean
Medium-High	Mean to 1 Standard Deviation above mean
High	1 to 2 Standard Deviations above mean
Very High	Greater than 2 Standard Deviations above mean

Data Analysis

Alabaster dissolution rates were transformed to current flow estimates by calculating the slope between 2 known pairs of dissolution rates and current flow estimates. Three alabaster blocks were placed in a seawater tank to approximate a no-flow environment, while an additional three alabaster blocks were placed next to the S4 meter deployed near one of the long-term monitoring sites. Assuming a linear relationship between alabaster dissolution and flow, the slope and intercept can be calculated to determine a ratio between alabaster dissolution rates and flow speeds.

Comparisons between community structure and individual abiotic factors were analyzed using non-parametric multivariate statistics (PRIMER 6.1.13, PRIMER-E Ltd. Plymouth, UK; Clarke and Warwick 2001). Nonmetric multidimensional scaling (nMDS) was used to determine the significance of spatial trends in community structure between a) depth, b) slope, c) aspect, and d) flow estimates. Tests were based on Bray-Curtis similarity matrices (Kruskal fit scheme 1; restarts=50; minimum stress=0.01), derived from square-root transformed point intercept data. All results were further tested for significance using one-way analysis of similarity (ANOSIM). Similarity percentages (SIMPER) were used to examine individual contributions to any observed differences in community composition.

Results

Thirty-one species were recorded at least once on any given transect during point intercept surveys. An additional 16 categories were created for organisms that could not be visually identified to the species level, but could be uniquely identified by genus or descriptive category (e.g., *Metridium* spp, *Chelysoma* spp, crustose coralline algae, red turf algae) and were included into the species list and used for analysis.

Depth

Community structure appeared to separate in nMDS ordinations when all depths were considered (Fig. 6). One-way ANOSIM highlighted significant differences between depths ($R=0.561$; $p=0.001$). An apparent break between communities occurs at the 15 meter depth – to test this we binned depths into two categories: 1) shallow = 3-15 meter transect depths and 2) deep = 18-27 meter transect depths (Fig. 7). One-way ANOSIM revealed significant differences between deep and shallow bins ($R=0.702$; $p=0.001$).

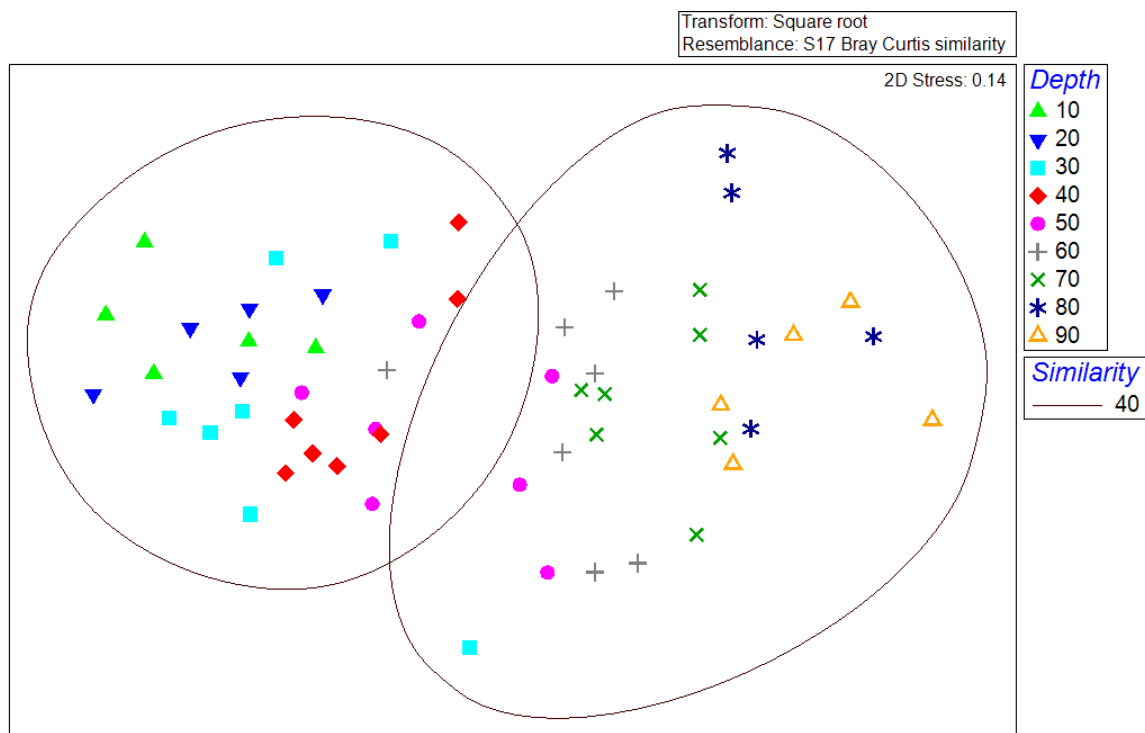


Figure 6: nMDS plot of community structure by transect depth (in feet). Clusters represent 40% similarity within groups.

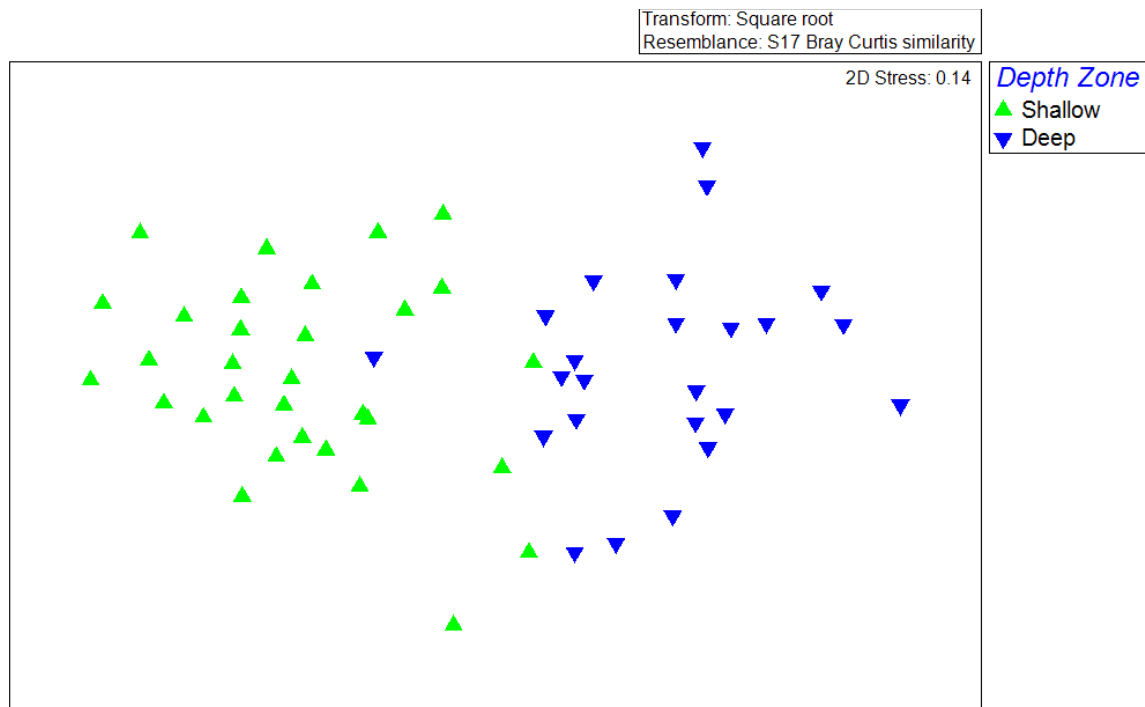


Figure 7: nMDS plot of community structure by binned depth categories.

Macroalgal species are known to be light-limited and may contribute to the observed differences between shallow and deep community structures. To determine the influence of macroalgal species in differences between shallow and deep transect depths, we removed all macroalgal species and re-ran the 1-way ANOSIM between shallow and deep designations. Results indicate that there still remain significant differences in community structure between shallow and deep transects ($R=0.588$; $p=0.001$) and that macroalgae only accounts for approximately 10% of the variation between depth categories.

Slope

Diver-based estimates of slope in the shallow depth bin showed a significant but weak relationship with community structure (Fig. 8; 1-way ANOSIM $R=0.17$; $p=0.025$). More of the variation between communities was explained by diver-based slope in the deep depth bin (Fig. 9; 1-way ANOSIM $R=0.359$; $p=0.001$). Estimates of slope via GIS did not appear to explain variation in community structure at either depth bins (1-way ANOSIM: Shallow, $R=0.065$; $p=0.618$; Deep, $R=0.037$; $p=0.354$).

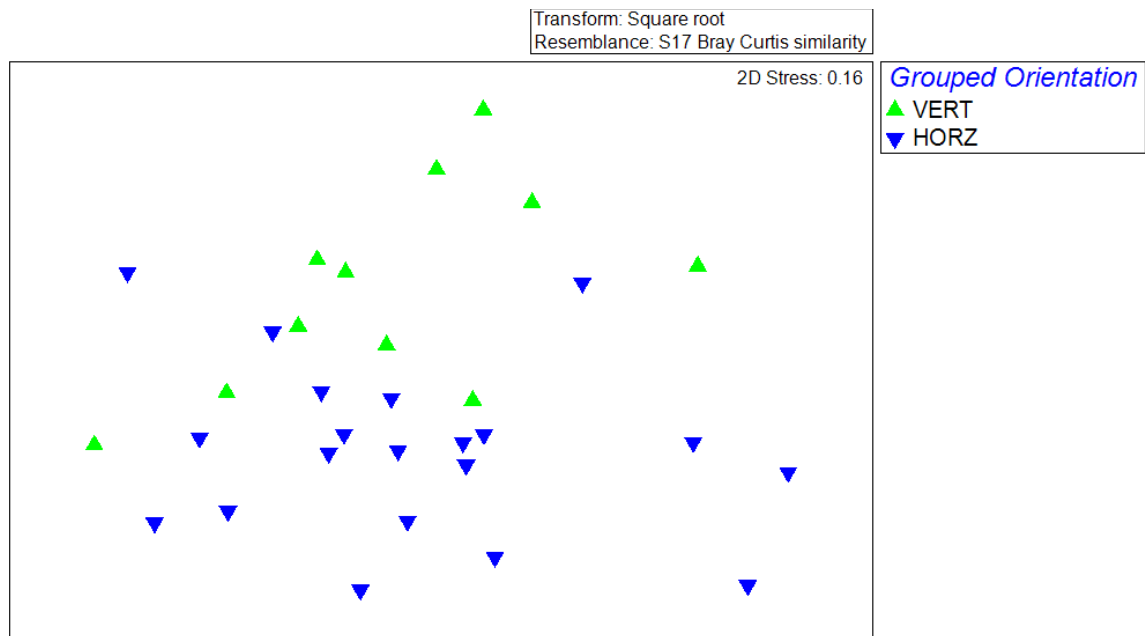


Figure 8: nMDS plot of community structure by diver-based slope estimates in the shallow depth bin.

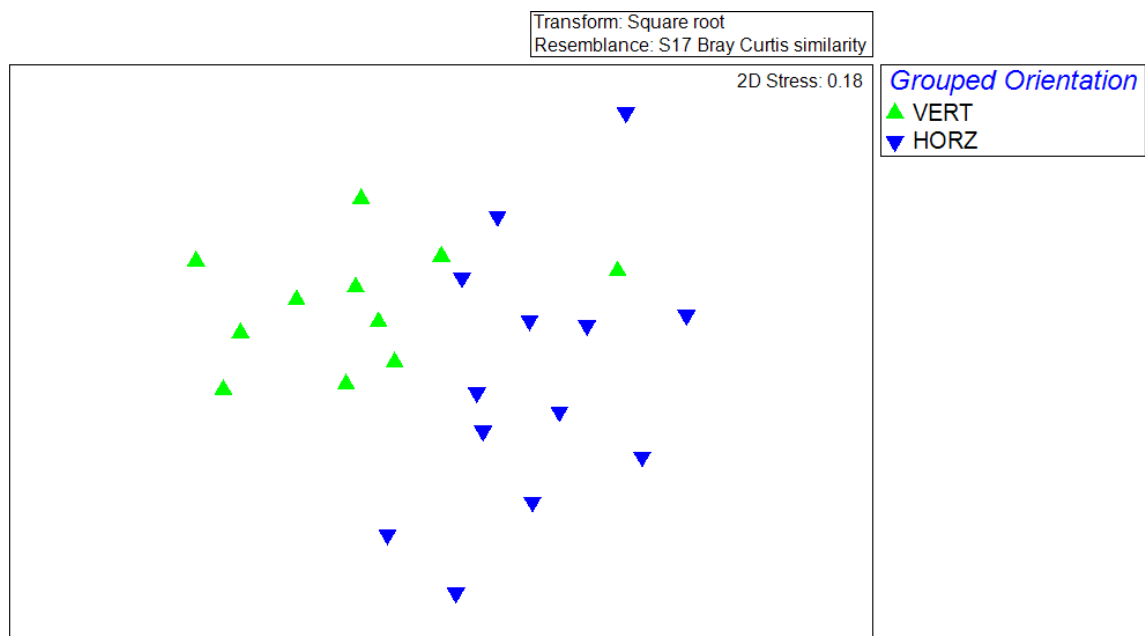


Figure 9: nMDS plot of community structure by diver-based slope estimates in the deep depth bin.

Aspect

Aspect did not appear to explain community structure in either the shallow or deep depth bins (1-way ANOSIM: Shallow, $R=0.054$; $p=0.292$; Deep, $R=0.108$; $p=0.204$), yet there appears to be some indication of southern-facing transects grouping in the shallow depth bin (Fig. 10).

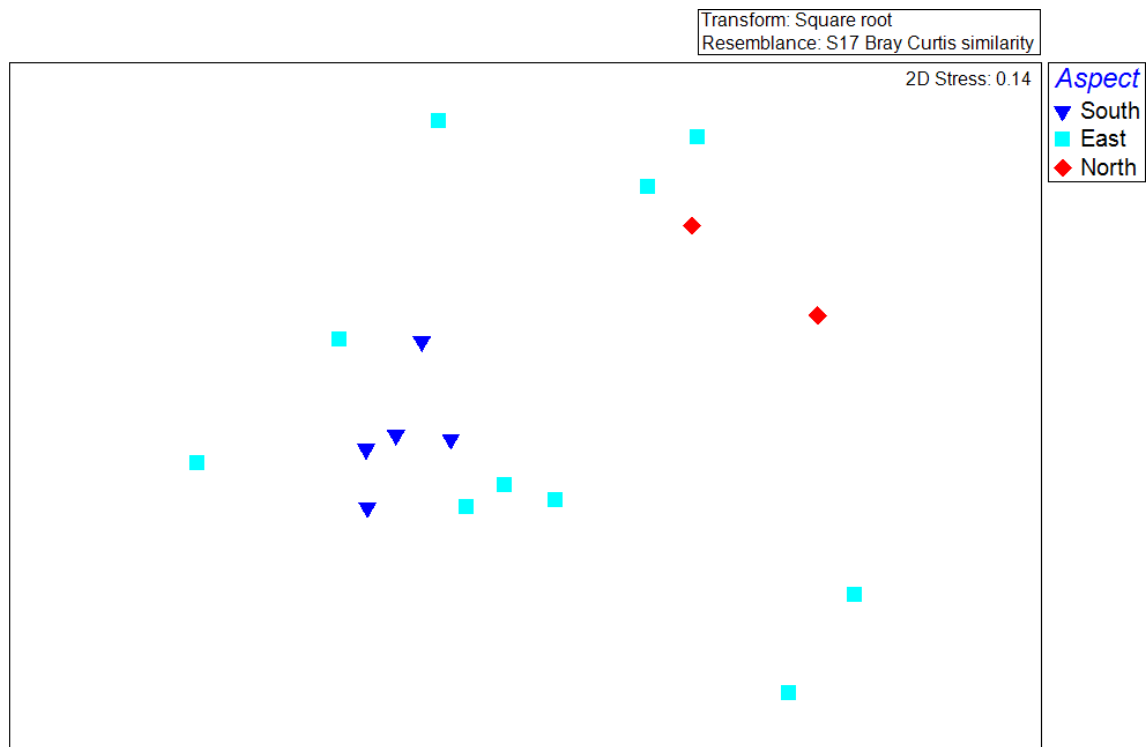


Figure 10: nMDS plot of community structure by aspect in the shallow depth bin.

Flow

The average flow speed recorded by the S4 current meter during the first alabaster deployment was 6.54 cm/second. Plotting dissolution rates of the three alabaster blocks near the S4 meter and 3 alabaster blocks in the no-flow seawater tank yielded the following linear relationship: $y=0.00717x + 0.0217$ (Fig. 11). Using this equation, we were then able to calculate equivalent current speeds for each of the alabaster dissolution rates (Fig. 12).

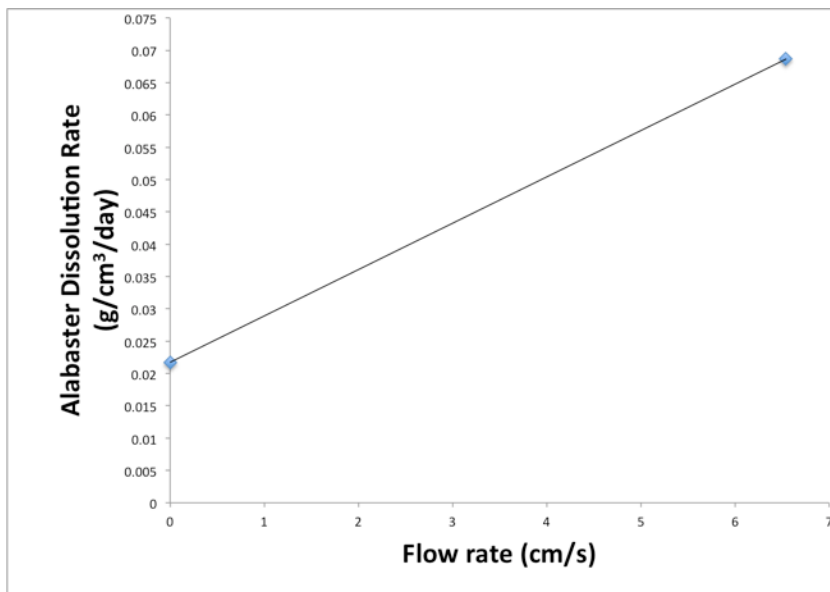


Figure 11: Relationship between observed flow and alabaster dissolution rates.

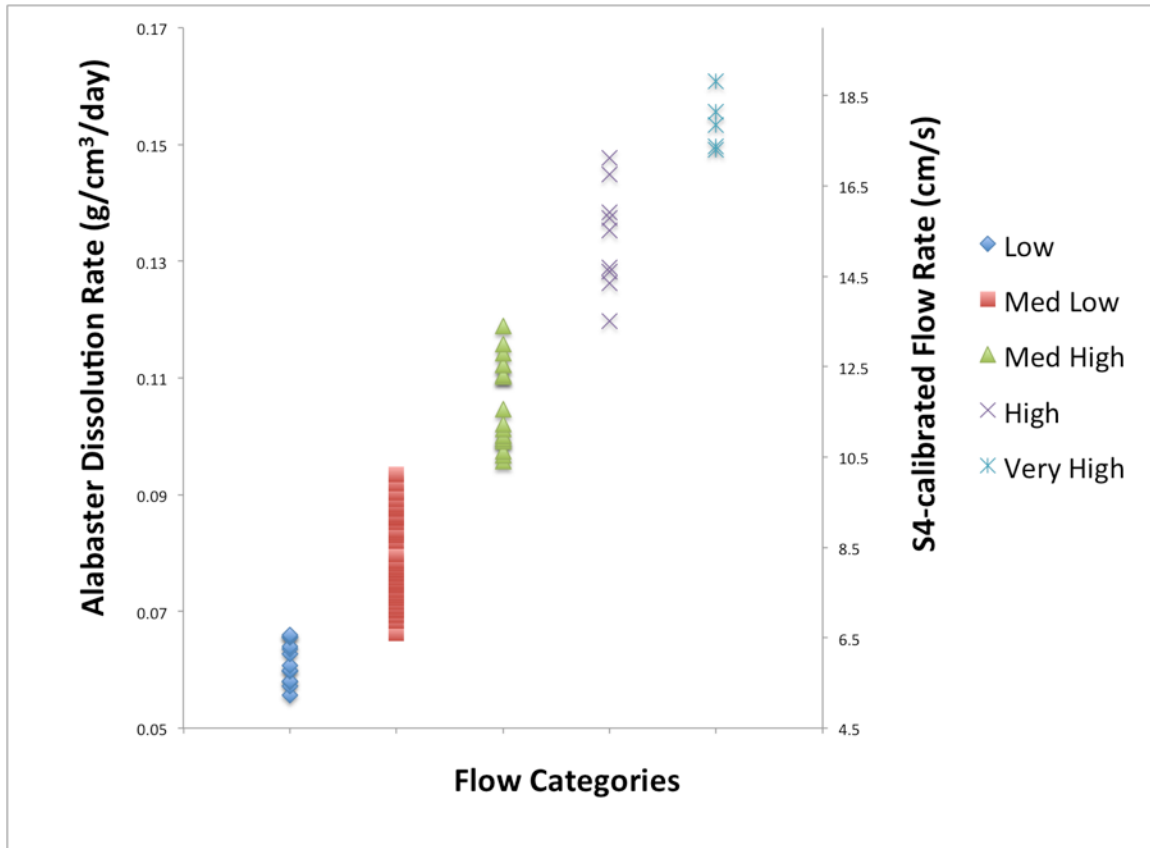


Figure 12: Binned flow categories and their relationship to alabaster dissolution rate and current flow.

Binned flow estimates marginally correlate with community composition at both shallow and deep depth bins (1-way ANOSIM: Shallow, $R=0.165$; $p=0.106$, Fig. 13; Deep, $R=0.116$; $p=0.09$, Fig. 14).

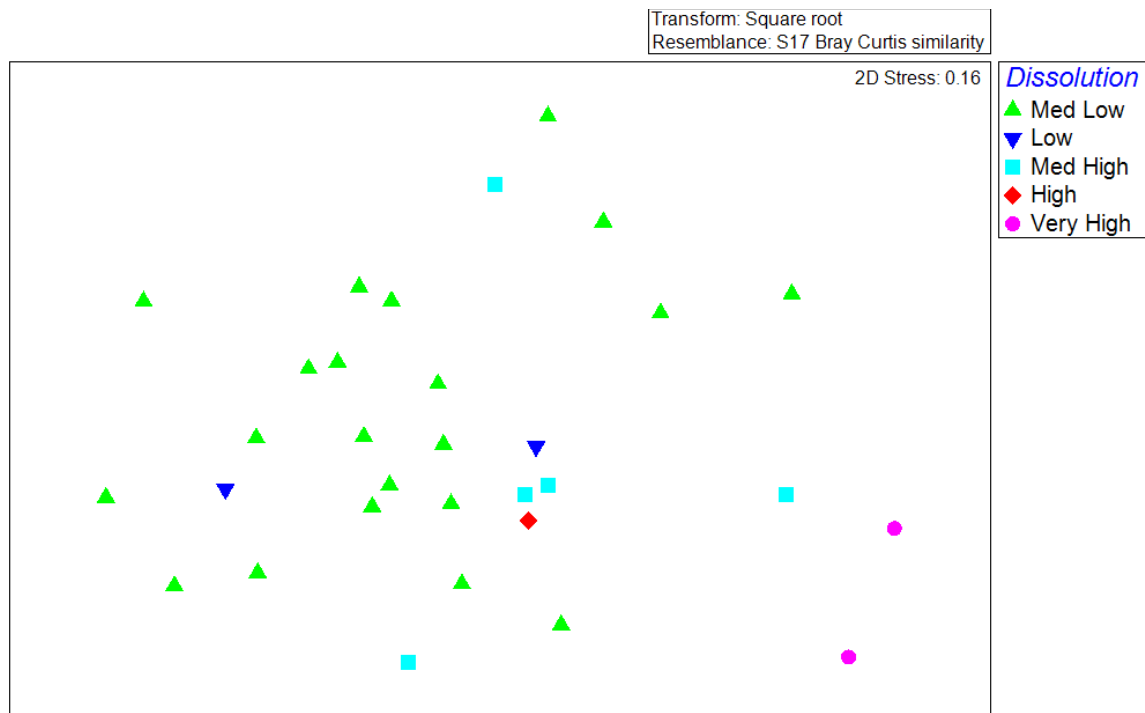


Figure 13: nMDS plot of community composition by alabaster dissolution categories.

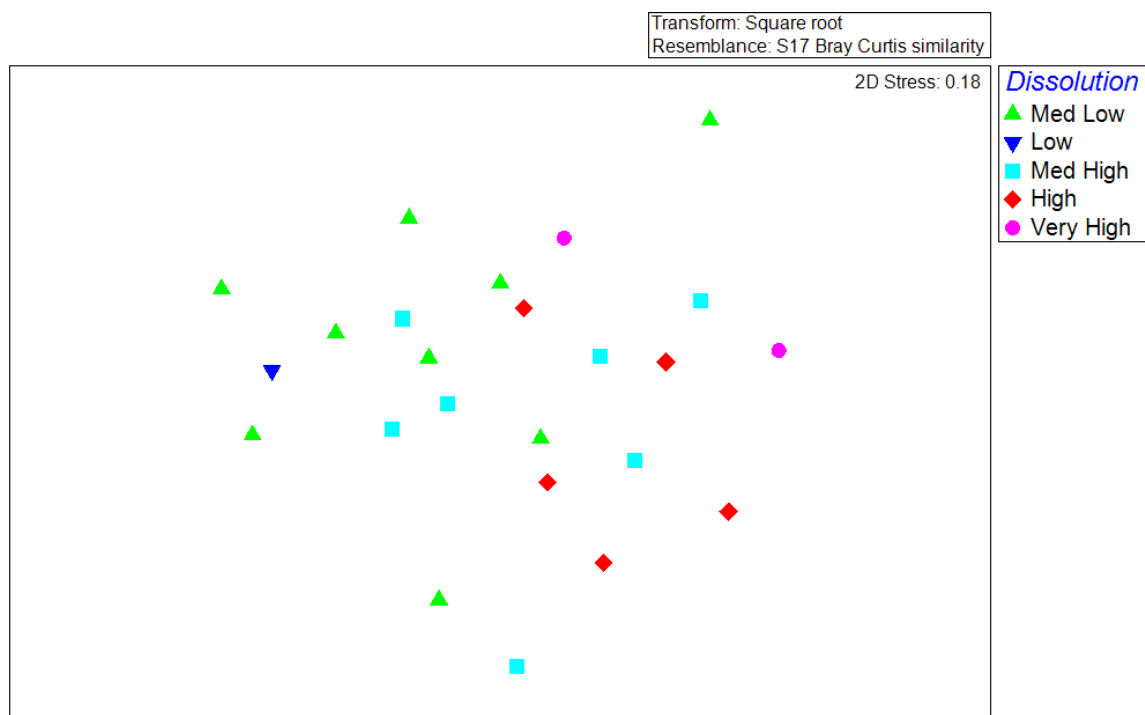


Figure 14: nMDS plot of community composition by alabaster dissolution categories.

Although not significant, there is some evidence of flow-related differences between the low and high flow spectrums at both depth bins. In shallow depths, community structure comparisons between low and high flow bins reveal strong (but not

significant) correlations, largely due to low sample sizes (medium-low to very high: $R=0.844$; $p=0.4$, low to very high: $R=1$, $p=0.33$). SIMPER tests revealed striking differences in species between both medium-low to very high flow categories (Table 2) and low to very high flow categories (Table 3).

Table 2: Species responsible for more than 5% of the dissimilarities between Medium-Low and Very High flow categories at shallow depths. (% Contribution = percent contribution to differences between samples)

Species	Group Med Low	Group Very High	% Contribution
	Avg. Abundance	Avg. Abundance	
Agarum fimbriatum	6.1	0	21.72
Fuzzy Red Algae	0.21	5.37	18.51
Hydro/Bryo confusion	0.42	2.53	7.47
Maroon Encrusting Algae	2.82	1.98	5.73

Table 3: Species responsible for more than 5% of the dissimilarities between Low and Very High flow categories at shallow depths. (% Contribution = percent contribution to differences between samples)

Species	Group Low	Group Very High	% Contribution
	Avg. Abundance	Avg. Abundance	
Agarum fimbriatum	6.45	0	21.83
Fuzzy Red Algae	0	5.37	18.68
Maroon Encrusting Algae	4.08	1.98	8.14
Hydro/Bryo confusion	0.5	2.53	6.98

Similar patterns were found in the deep depth category (low to high: $R=0.76$; $p=0.167$, low to very high: $R=1$, $p=0.33$). SIMPER tests also revealed differences in species between both low to high flow categories (Table 4) and low to very high flow categories (Table 5).

Table 4: Species responsible for more than 5% of the dissimilarities between Low and High flow categories at deep depths. (% Contribution = percent contribution to differences between samples)

Species	Group Low	Group High	% Contribution
	Avg. Abundance	Avg. Abundance	
Didemnum carnulentum	4.24	0	12.4
Hydroids	0	3.98	11.78
Crustose Corallines	0	3.92	11.47
Metandrocarpa taylori	4.24	0.6	10.67
Encrusting Bryo	4.36	1.85	7.39

Table 5: Species responsible for more than 5% of the dissimilarities between Low and Very High flow categories at deep depths. (% Contribution = percent contribution to differences between samples)

Species	Group Low	Group Very High	% Contribution
	Avg. Abundance	Avg. Abundance	
Crustose Corallines	0	4.36	12.28
Didemnum carnulentum	4.24	0	11.95
Metandrocarpa taylori	4.24	0	11.95
Maroon Encrusting Algae	1	4.24	9.06

Discussion

Depth, slope and flow indices all appear to correlate with community structure to varying degrees, indicating that multiple abiotic factors are likely influencing the abundance and distribution of organisms at small geographic ranges (3 to 1000 meters). Correlations between both depth and community structure as well as diver-observed slope and community structure were statistically significant, while correlations between flow and community composition were marginally significant. Correlations between the GIS-based calculations of slope and aspect were not significant, yet there still appears to be trends between these factors and community composition, as noted in the nMDS plots. Correlations between these abiotic factors and community composition support previous studies from the literature (Witman 1987; Gaylord et al. 2007; Miller and Etter 2008, 2011).

The most probable reasoning for lack of significant data lies in the resolution of data analyzed, both biological and geological. The biological data selected for analysis in this study was collected using a point-intercept method where organisms are identified at 100 uniform points along a 10-meter transect line. While this gives an overall estimate of percent cover, it may not adequately reflect the overall community structure or spatial patchiness among organisms. It would be useful to re-run these analyses with a methodology that can more finely depict community structure, such as with photoquadrats. It is promising that trends have already emerged between point-intercept data and multiple abiotic factors. This likely indicates that a more thorough method will highlight these observable but sometimes non-significant trends better and produce more significant results.

Secondly, the categories defined and bins produced from abiotic data were not equally represented in our study sites, largely because we utilized pre-existing sites and data designed for different ecological questions. This was evident when reviewing sample sizes for each of the alabaster dissolution rate categories. Of the 55 transects, 3 were in the low flow bin, 30 in the medium-low bin, 12 in the medium-high bin, 6 in the high bin, and 4 in the very high bin. Interestingly enough, the distribution of alabaster dissolution by transect approximated a normal distribution, indicating that the majority of our sites were placed in similar flow

environments. The low sample sizes in the low and high ends of flow bins were likely responsible for the marginally significant results produced from our statistical analyses. With higher replication within each flow category, we likely would have achieved more statistically significant results. As highlighted above, the marginal significance of analyses utilizing low resolution biological data and small sample sizes among groups is still promising and leads us to think that these trends are valid and would likely emerge more strongly with finer resolution data and wider sampling regimes.

Similar resolution issues arose with GIS-derived factors. GIS-based slope and aspect factors were derived by utilizing pre-existing bathymetric data gridded at 2 meters. While this level of gridded data is satisfactory for discerning geologic features and creating habitat maps, it is likely not fine enough to relate to the types of biological data collected to discern community structure. This was verified by comparing the diver-based estimates of slope at each transect and the GIS-derived calculations of slope at each transect. Overall, the GIS-derived slope estimates gave much shallower (e.g. more horizontal) angle estimates. In areas where there are known vertical walls, GIS-derived slope estimates were still ranging from 20-50 degrees, indicating a predominantly horizontal to sloping orientation.

These discrepancies may have been further confounded by inaccuracies in transect locations. The locations of each site were identified on the bathymetric maps by GPS location, but the exact starting and ending points of transects are presently unknown. As such, we created an arbitrary line that was indicative of the direction the site runs offshore and interpreted the slope and aspect data from the intersection of this site "centerline" with overlaid contours at each transect depth. Additionally, we estimated slope and aspect designations using the 2-meter grid cell that overlapped with this site and transect axis. If we had more resolute starting and ending locations of every transect, we could then make a better designation of slope or aspect, even at a 2 meter grid resolution.

While GIS-based slope did not seem to correlate at all with community structure, a slight trend is apparent with aspect, at least at shallow depths. This is promising and definitely worthy of further investigation. To our best knowledge, the geographic direction in which a substrate faces has never been related to community structure, but may be an important factor. The angle at which a feature protrudes into open water space and the direction it faces with respect to current patterns and sun-angle may be important in structuring communities. For example, if current flow is in a north-to-south direction, those sites that face south may be protected from the direct forcing of currents. As such, these sites may house communities that are more akin to low flow or no flow sites, even though they are in close proximity to high flow. Even though our data did not produce significant results, the aspect of each transect or aspect of sites in general definitely warrants further attention.

Acknowledgements

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Appendix

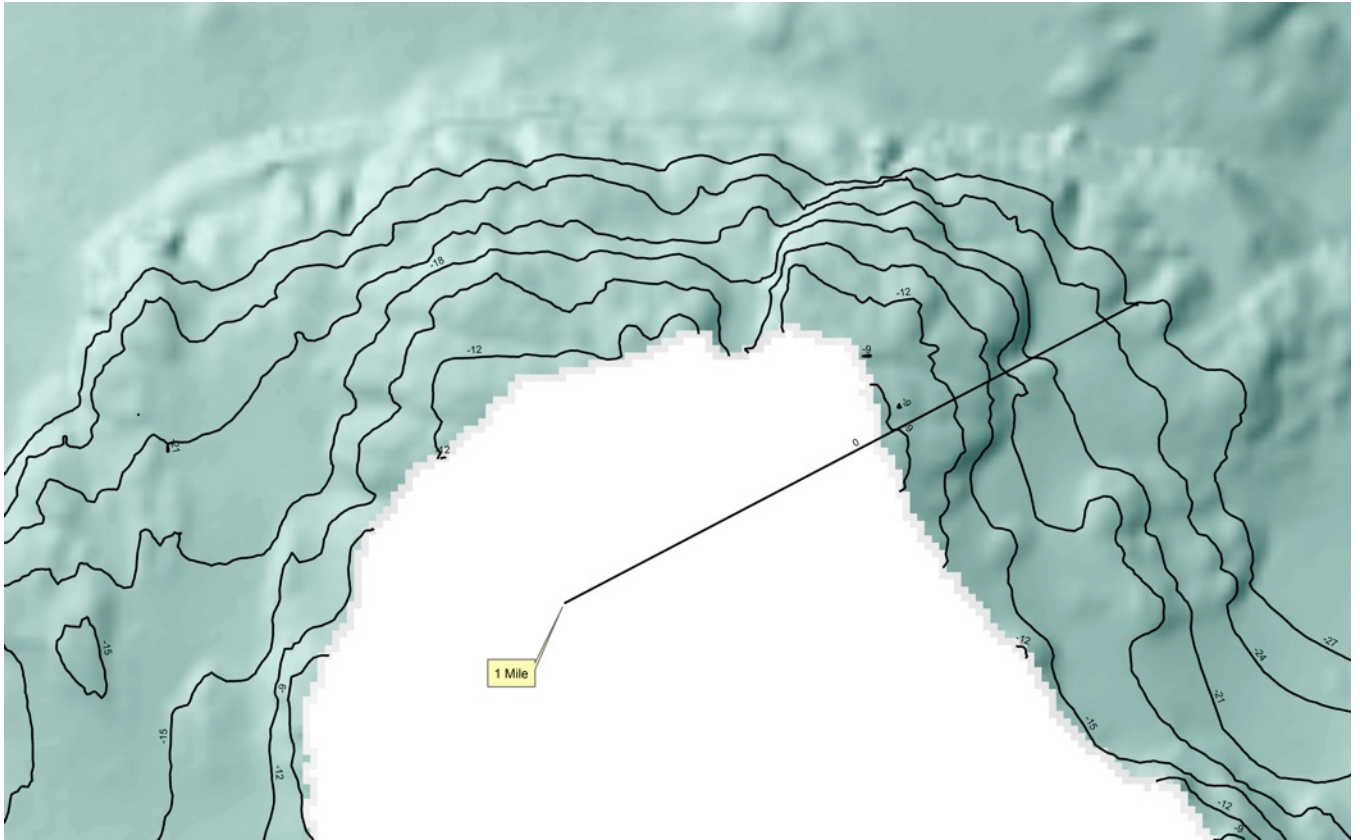


Figure 3A: Bathymetry and approximate transect location at 1-mile reef. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

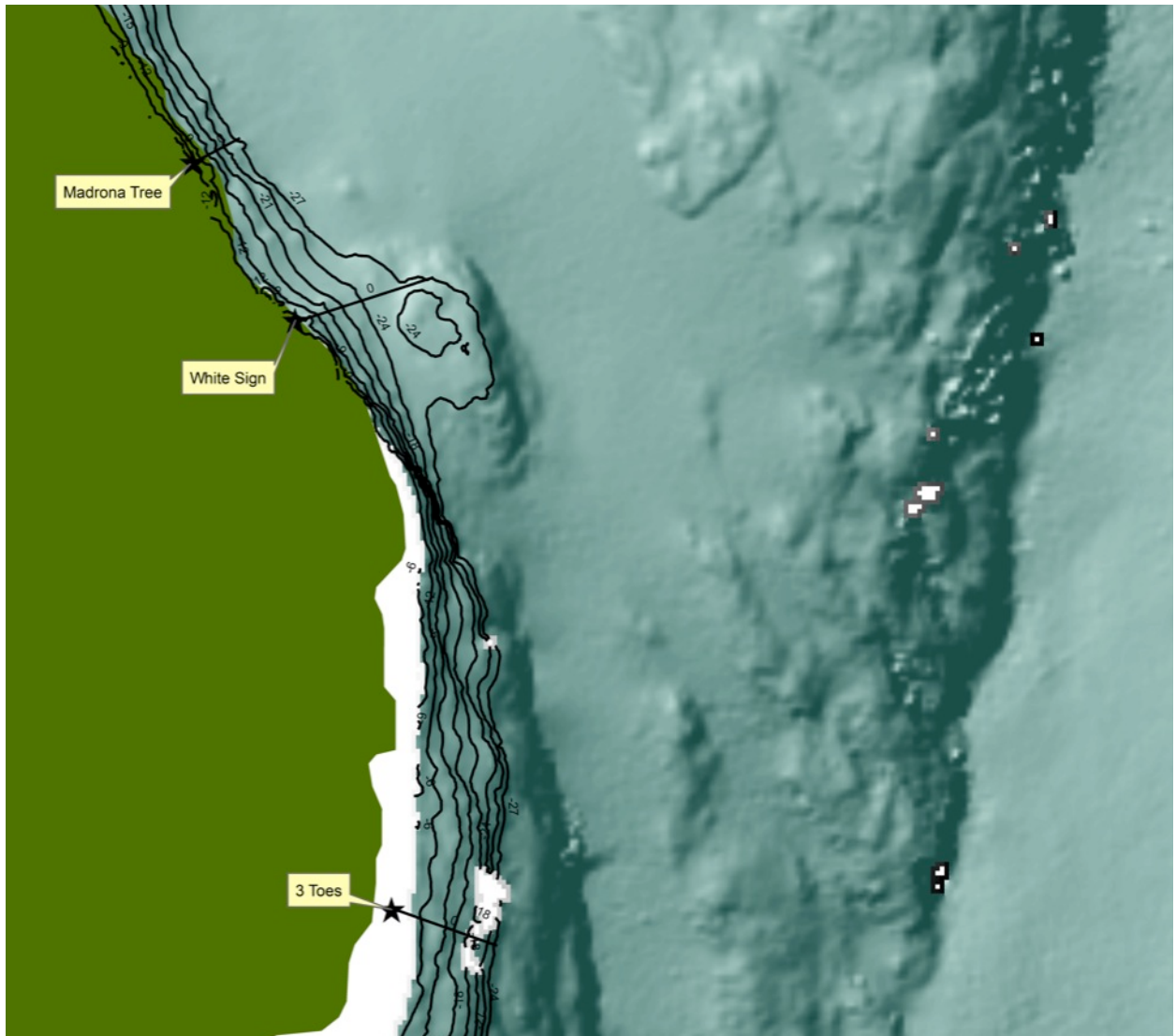


Figure 3C: Bathymetry and approximate transect locations at Madrona Tree, White Sign and 3 Toes sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

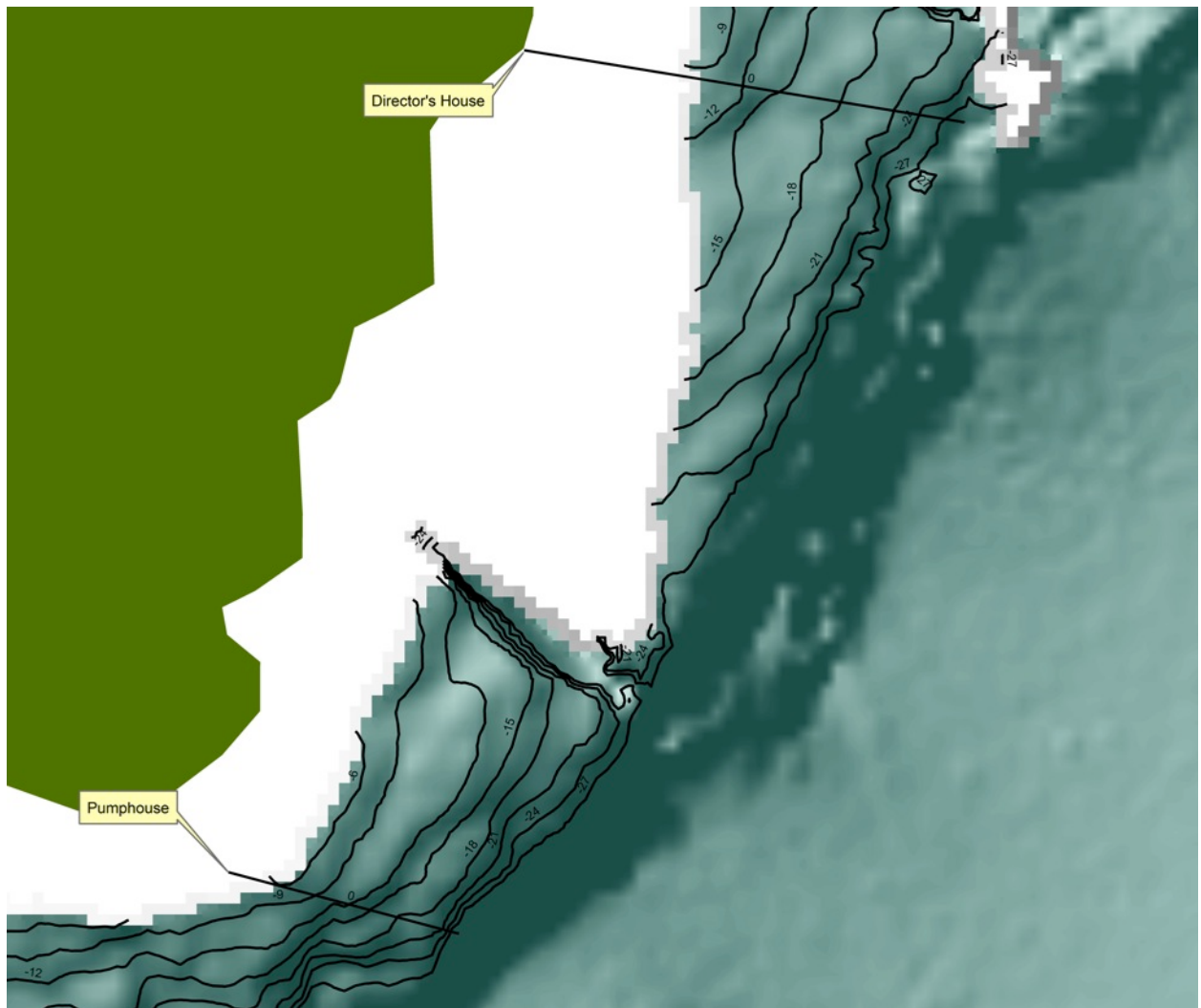


Figure 3C: Bathymetry and approximate transect locations at Director's House and Pumphouse sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

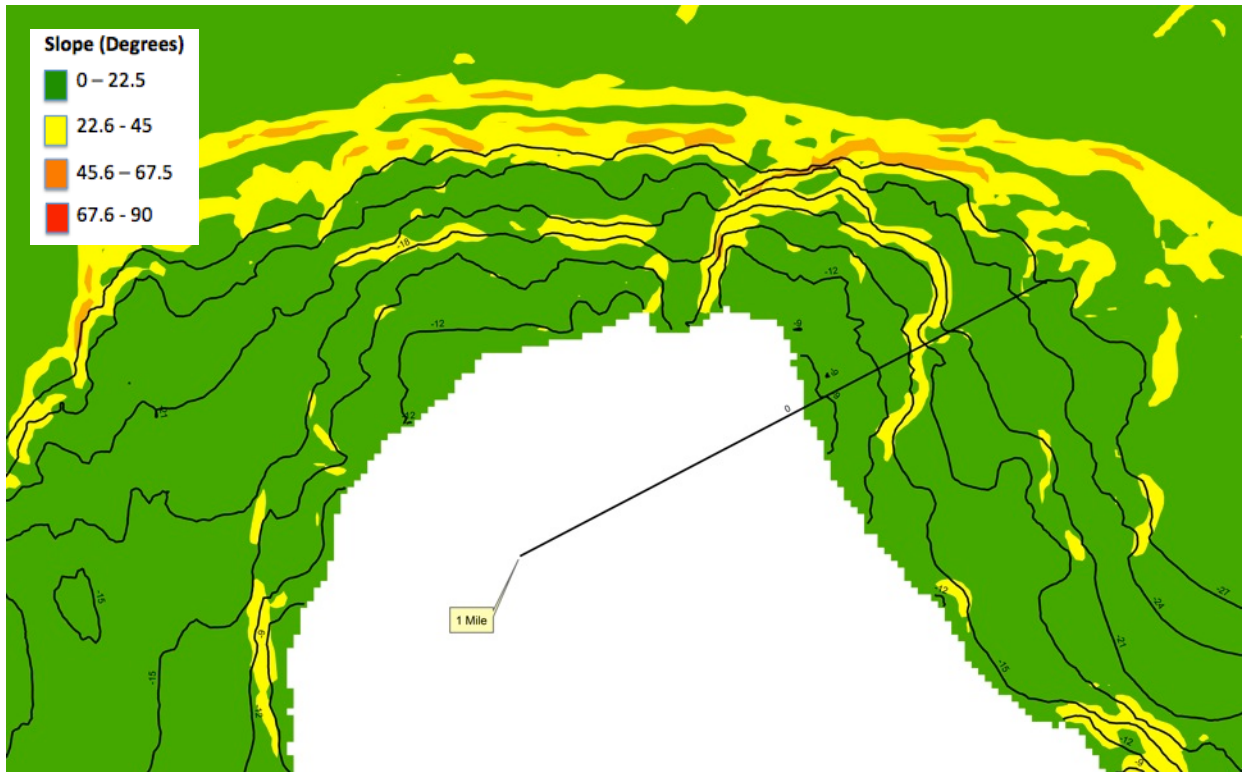


Figure 4A: GIS-derived slope and approximate transect location at 1-mile reef. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

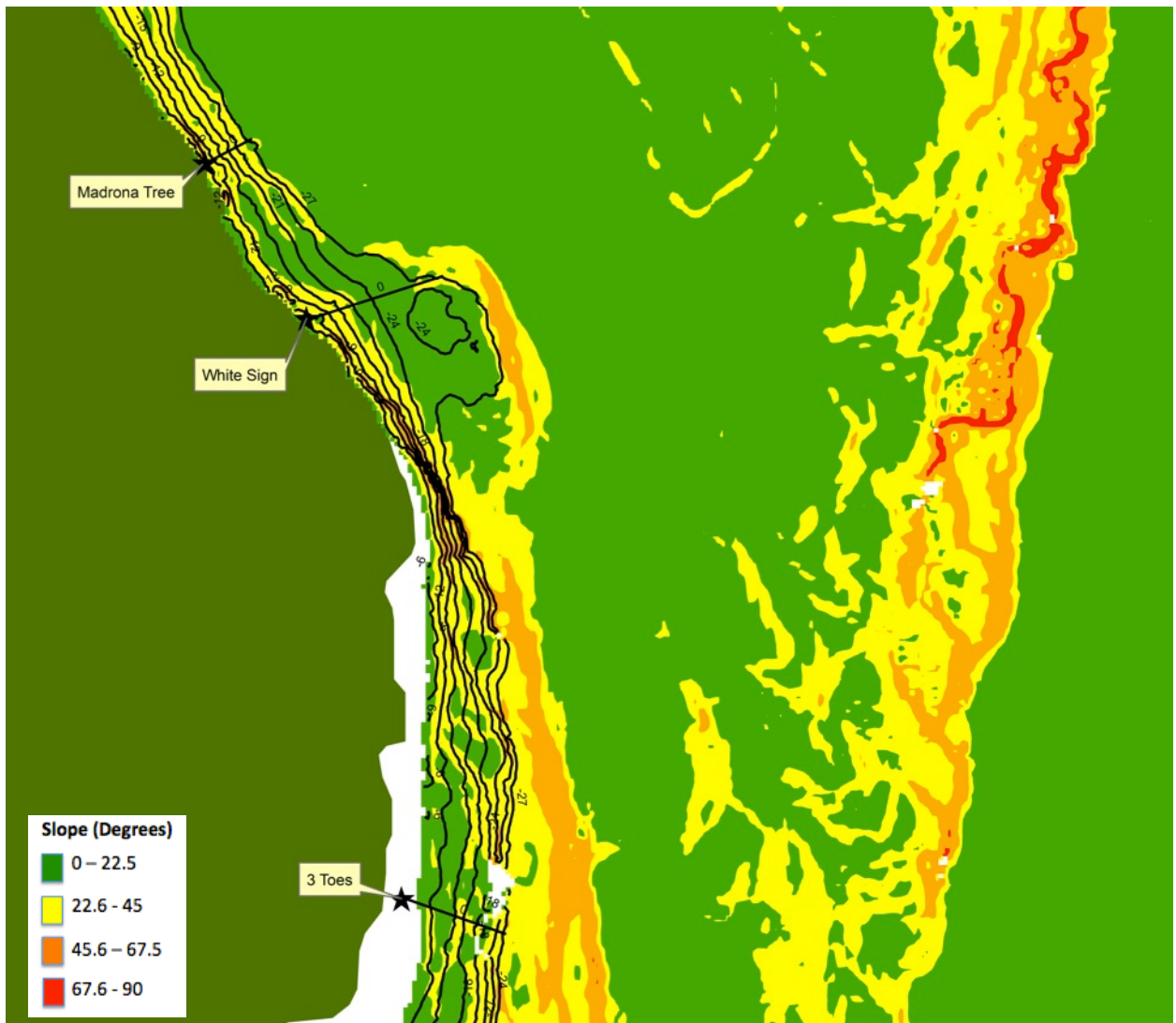


Figure 4B: GIS-derived slope and approximate transect location at Madrona Tree, White Sign, and 3 Toes sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

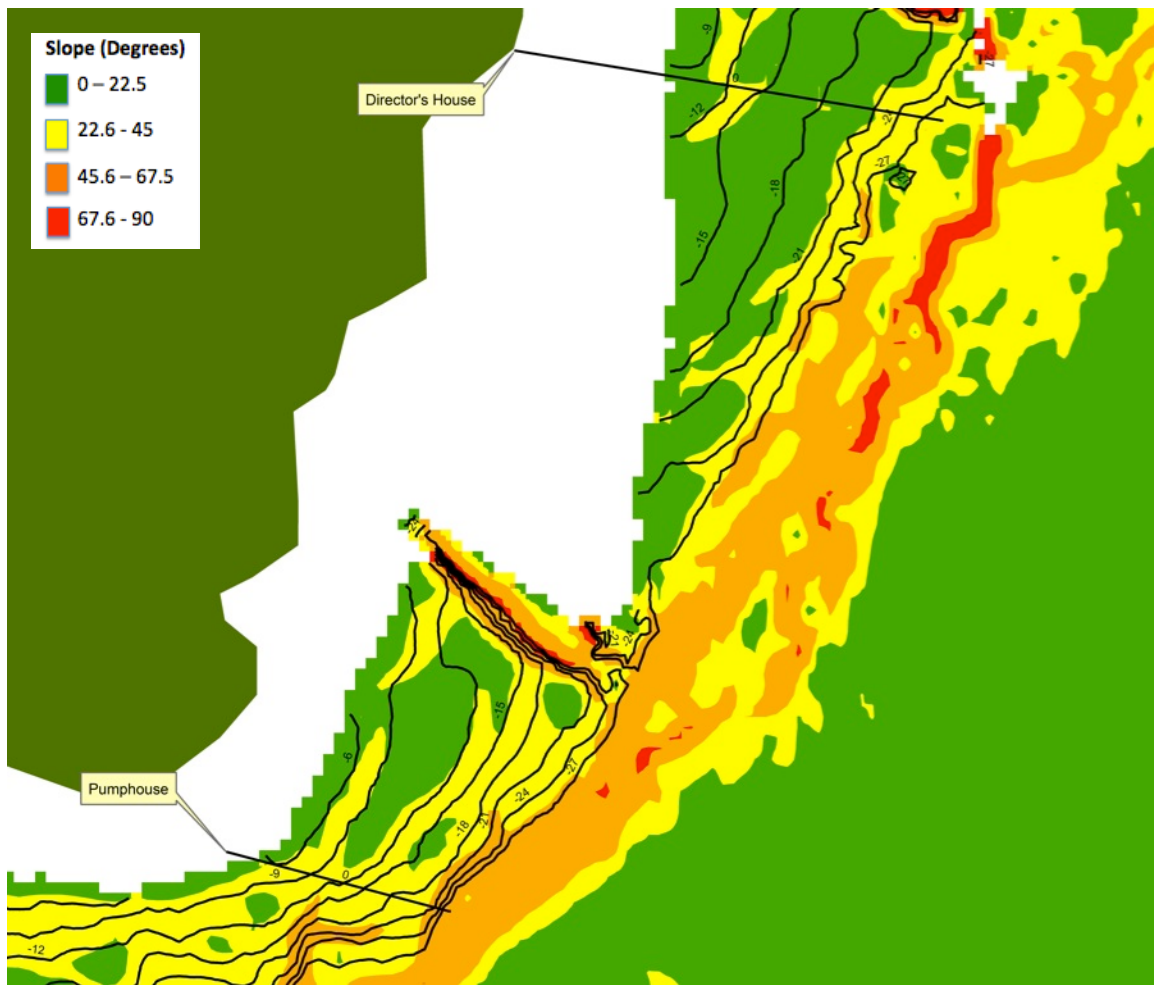


Figure 4C: GIS-derived slope and approximate transect location at Director's House and Pumphouse sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

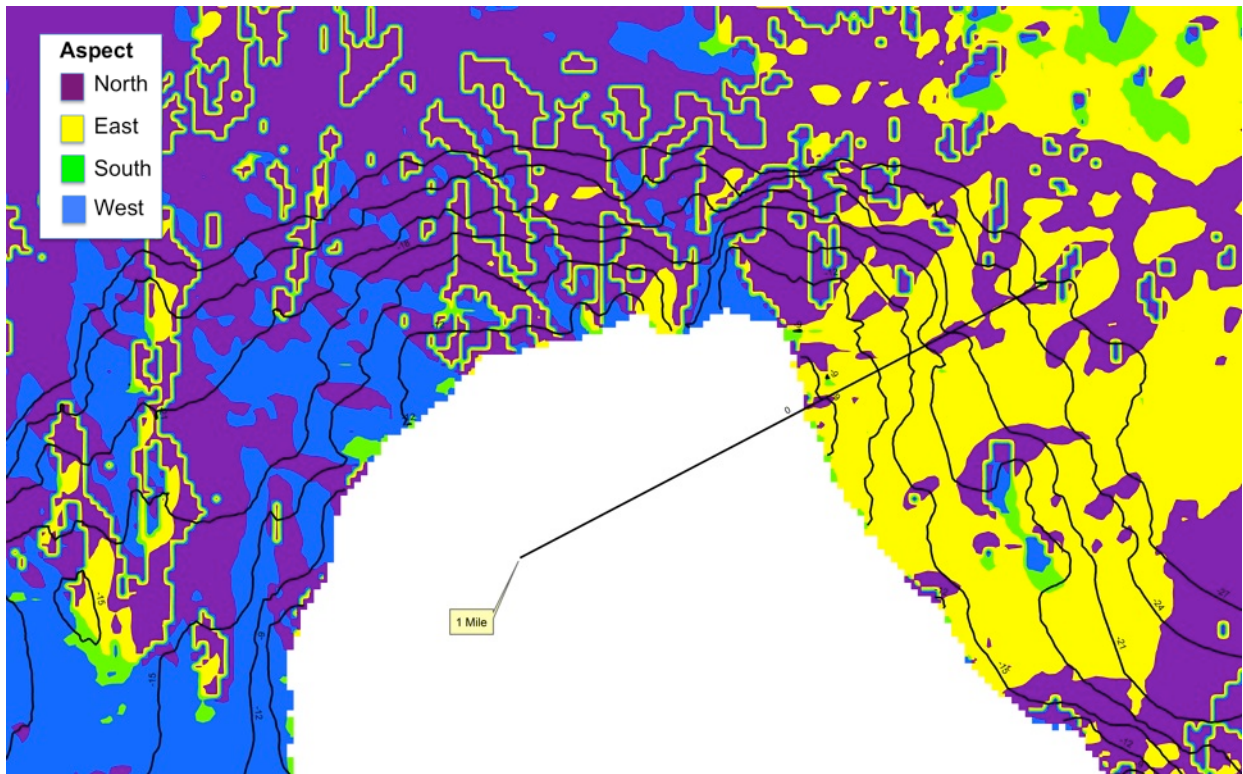


Figure 5A: GIS-derived aspect and approximate transect location at 1-mile reef. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

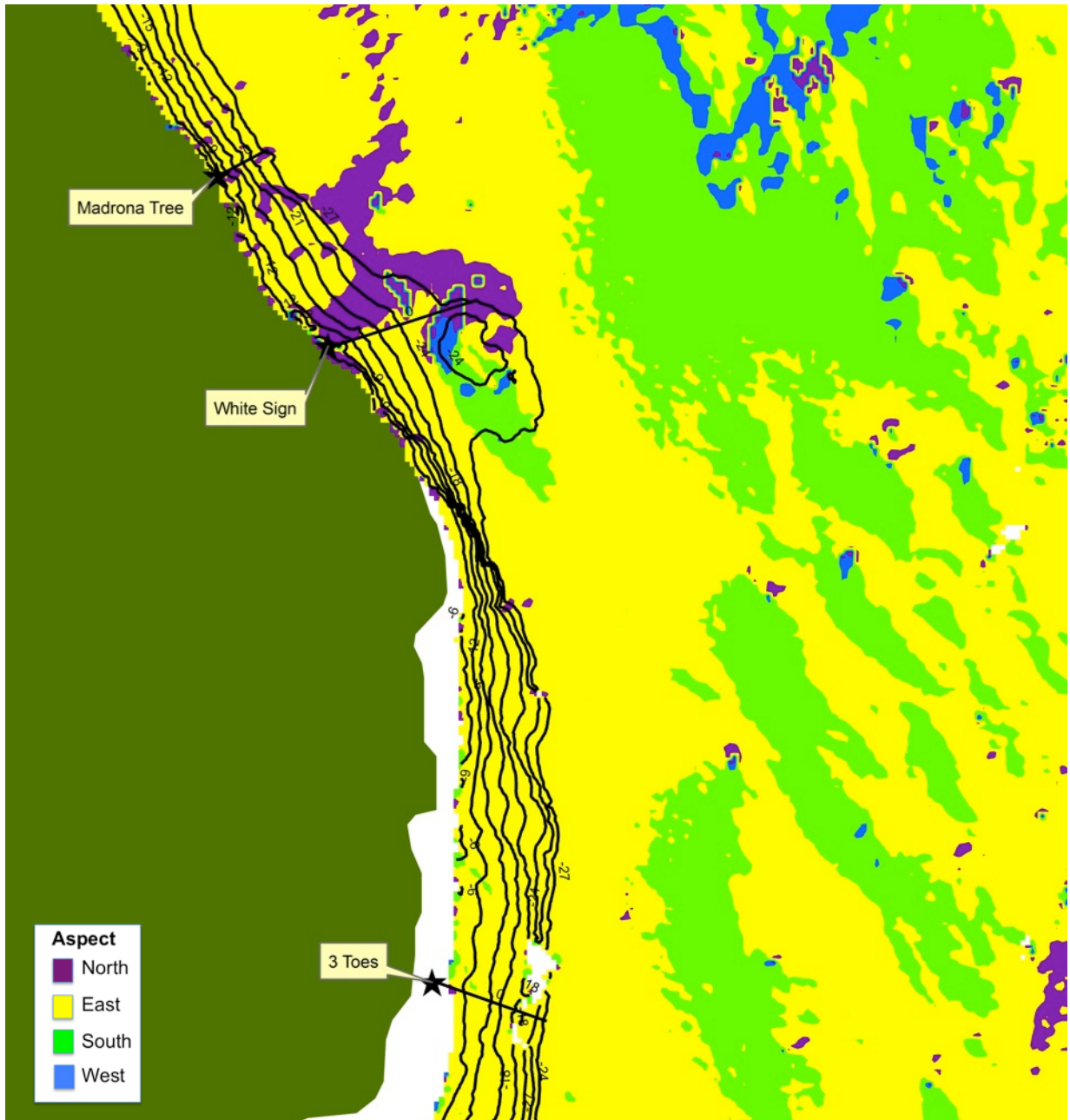


Figure 5B: GIS-derived aspect and approximate transect location at Madrona Tree, White Sign, and 3 Toes sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.

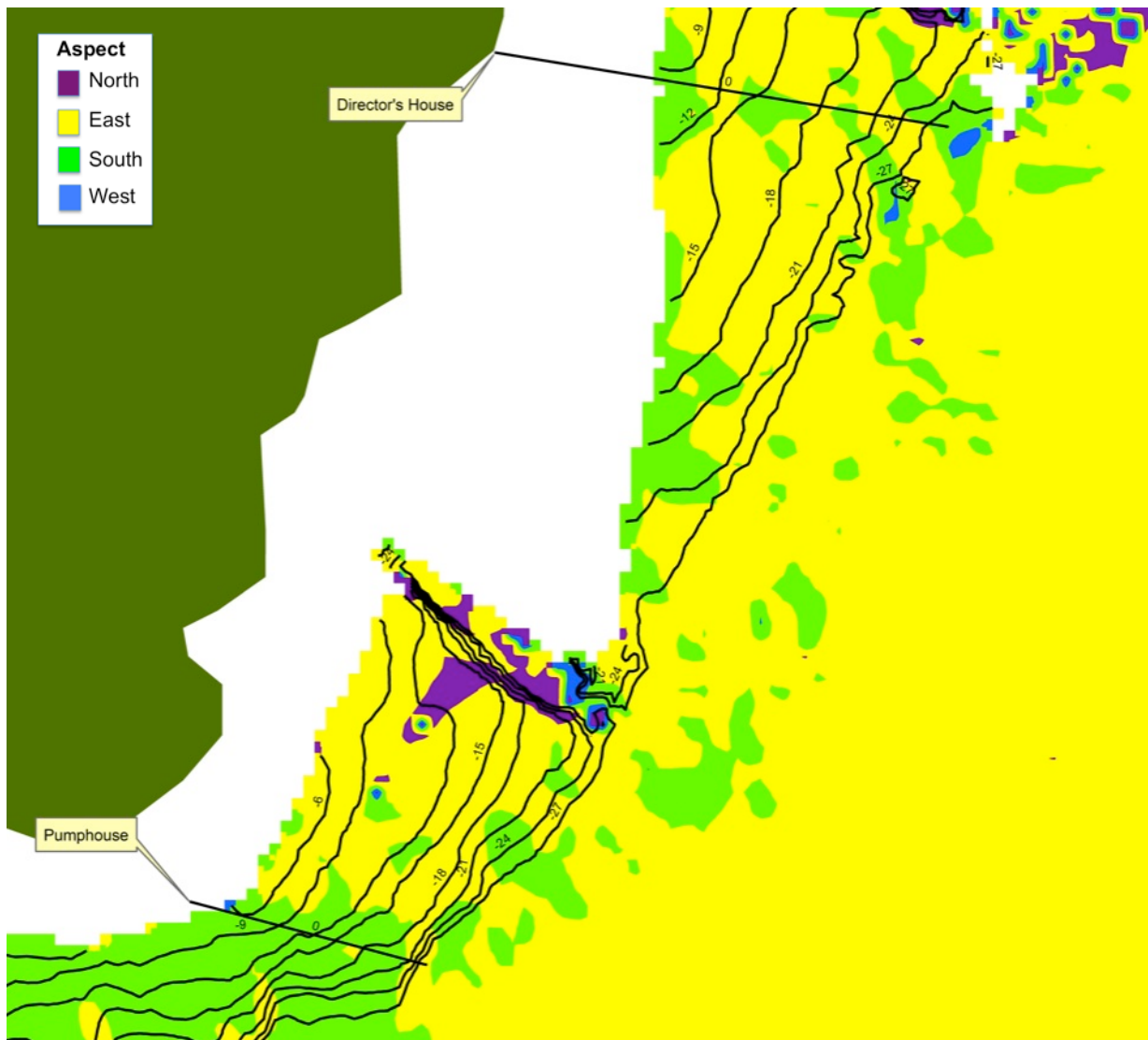


Figure 5C: GIS-derived aspect and approximate transect location at Director's House and Pumphouse sites. Contour lines indicate transect depths from 3 to 27m. White space indicates areas of no MBES data.