

Documenting the effect of substrate angle on invertebrate assembly patterns:
An approach for identifying sessile benthic invertebrate
assemblages in the San Juan Channel rocky subtidal zone

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ABSTRACT

Understanding benthic community distributions, and using such information in marine restoration ecology, requires an understanding of the effect of substrate angle on assembly patterns. To date, there is no information regarding *in situ* identification and remote identification of sessile benthic invertebrate assemblages on substrate angles from 0° to 90°. This study aimed to document the effect of substrate angle on sessile invertebrate assemblages and to both develop and validate an approach for remotely identifying assemblages based on substrate angle. The *in situ* photoquadrat method was used to document invertebrate assemblages at five 15 m deep sites in the San Juan Channel. Substrate angle was recorded for each photo based on six 15° categories. Univariate and multivariate statistical analyses suggested that there are three distinct assemblages of invertebrates: horizontal (0-15°), sloping (15-75°), vertical (75-90°). Crustose coralline algae, non-calcified (maroon) encrusting red algae, encrusting bryozoans, tube complex (amphipods, polychaetes), and porifera contributed more than 5% to assemblage differences due to angle at all sites. These results necessitate a review of factors thought to cause differences in assemblages due to substrate angle. The relationship between species and substrate angle was applied to multibeam echosounder (MBES) bathymetry data, gridded at 2 m, in ArcGISTM. Transect locations were plotted and ArcGIS generated slope values. ArcGIS scale was smaller than the photoquadrat scale; therefore, the scales were not comparable. This technique for remotely identifying assemblages based on substrate angle may be utilized in the future by following a revised protocol that includes the collection of bathymetric and photoquadrat data at the similar

scales. This approach may be used both in the San Juan Channel and internationally for restoration and long-term monitoring efforts.

INTRODUCTION

Marine restoration ecology increasingly involves deployment of artificial structures to serve as fish and invertebrate habitat. Establishing optimal habitat conditions on these artificial structures requires proper design and, thus, valid predictions for how assembly patterns are affected by substrate angle. While current literature addresses locality specific differences in benthic invertebrate distribution as a function of substrate orientation, e.g. horizontal vs. vertical (Pomerat and Reiner, 1942; Sebens, 1985; Connell, 1999; Glasby, 2000; Miller and Etter, 2008, 2011), to date, there is no information regarding the identification and mapping of benthic invertebrate distribution, using MBES bathymetry data, on small features incorporating information on variation in substrate angle.

Previous studies demonstrate that phyla and species distribution vary on horizontal and vertical hard substrate (Pomerat and Reiner, 1942; Harris and Irons, 1982; Sebens, 1985; Connell, 1999; Glasby, 2000; Miller and Etter, 2008, 2011). Despite these globally recognized differences in assembly patterns due to substrate orientation, species-level dynamics vary regionally. In shallow temperate waters, vertical rock wall communities are generally composed of suspension feeding, sessile, encrusting invertebrates while horizontal rocky communities are composed of algae, kelp, and tunicates (Sebens, 1985; Witman and Dayton, 2001; Miller and Etter, 2008, 2011). Previous studies, both in tropical and in temperate waters, address the relationship between horizontal or vertical orientation and invertebrate distribution, yet no prior studies investigate how substrate angles between 0° and 90° affect invertebrate assembly patterns.

Numerous mechanisms, including light, disturbance, sedimentation, predation, and other hydrographic factors, such as water flow and larval dispersal, are proposed explanations for these assembly differences due to substrate orientation (Connell, 1999; reviewed in Witman and Dayton, 2001; Knott et al., 2004; Miller and Etter, 2008, 2011). Light levels may be higher on horizontal than vertical surfaces due to shading (Witman and Cooper, 1983), perhaps explaining macroalgae abundance on shallow horizontal substrate (Harris and Irons, 1982; Miller and Etter, 2011). Sedimentation rates may be higher on horizontal than vertical surfaces, justifying the distribution of filter-feeding organisms on vertical surfaces (Irving and Connell, 2002). Physical and biological disturbances may be greater on horizontal than vertical substrate (Witman and Cooper, 1983). Biological species interactions, such as competition and predation, may also play major roles in structuring invertebrate assemblages on vertical and horizontal substrate through processes, such as grazing (Sebens, 1986). Current literature suggests that while all of these factors may contribute to assembly patterns on differently oriented substrate, competition and light may be dominant influences (Miller and Etter, 2008, 2011). Furthermore, these differences in assemblages decrease with depth due to the “depth emergence” phenomenon (Witman and Cooper, 1983) in which coverage of sessile invertebrates on horizontal surfaces increases while coverage of algae decreases. This argues for a strong light effect because deeper horizontal substrate is likely to receive more sedimentation than vertical walls. However, this is also dependent upon current flow and sediment source.

Despite the marked differences in assemblages on vertical and horizontal rocky substrate, no habitat maps have been compiled to facilitate prediction of these

assemblages in new areas based on substrate angle. Historically, habitat mapping has been conducted for fisheries management of overexploited groundfish (Greene et al., 2007). In the past decade, habitat mapping efforts have shifted towards subtidal regional classifications and present efforts include mapping of large-scale small features in shallow habitats (Greene et al., 2007). There are no habitat maps, however, for large-scale differentiation of epibiotic assemblage patterns due to substrate angle (Kostylev et al., 2001) for the Salish Sea or similar regions.

This study examines sessile invertebrate assembly patterns from underwater transects in the San Juan Channel (Fig. 1) to develop an approach for remote

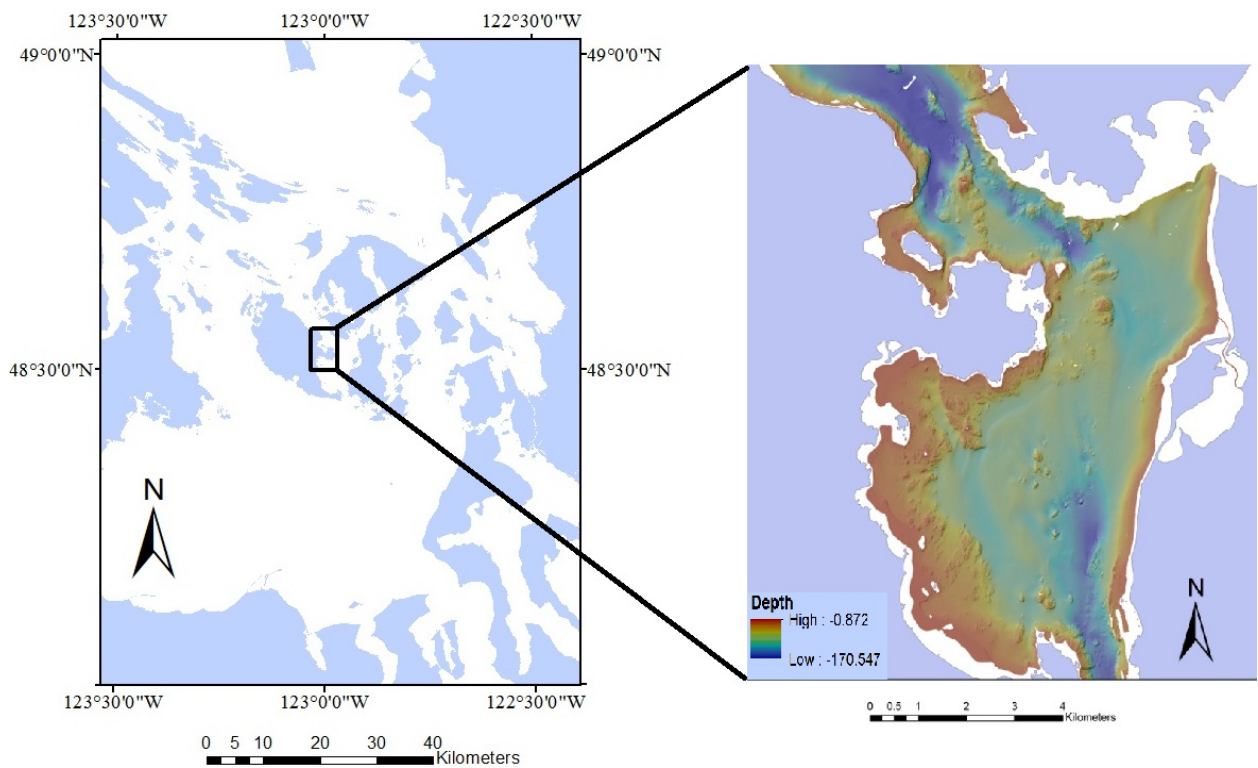


Figure 1: Study area in San Juan Channel. (Left) San Juan Archipelago. (Right) San Juan Channel bathymetry, in which purple is land and white is areas without bathymetric data.

identification of invertebrate assemblages based on depth and substrate angle. The San Juan Islands are located in Washington State, USA in the Salish Sea. The San Juan Channel, which separates San Juan Island from Orcas, Shaw, and Lopez Islands, is a glacially scoured area characterized by fiords and thus nearshore rocky substrate that rapidly drops off to depths of approximately 150 m. The shallow, subtidal rocky substrate along the edges of San Juan Channel formed from past ice carving and is typically oriented in three manners: horizontally, vertically, or sloping at various angles.

Biota associated with the San Juans' large tidal fluctuations and nutrient-rich water include demersal and pelagic fishes, as well as, mobile and sessile benthic invertebrates. This study will focus on predominantly sessile invertebrates. The hypothesis is that sessile invertebrate percent cover, and hence, assembly patterns, are affected by substrate angle, and as substrate angle increases from horizontal and decreases from vertical, assemblages will converge.

This study in the San Juan Archipelago, therefore, has three objectives: First, document and analyze how substrate angle affects sessile benthic invertebrate assembly patterns. Second, develop an approach to identify species assemblages in the rocky subtidal, based upon substrate angle, using SCUBA and MBES bathymetry. Third, assess the validity of this model by comparing data from *in situ* SCUBA and remote sensing techniques. This approach for documenting assembly patterns and identifying species assemblages may be used to improve restoration efforts, especially those involving hard substrate.

METHODS

The first component of this study was conducted at five sites, designated: Pumphouse, Three Toes, Mardrona, Yonder, and Slump, located on the east side of San Juan Island (Fig. 2). Three sites, Pumphouse, Three Toes, and Madrona were selected because they are part of a long-term monitoring study. Two previously undocumented sites, Yonder and Slump, were selected based on criteria including water depth, presence of a variety of slope categories, and geologic characteristics.

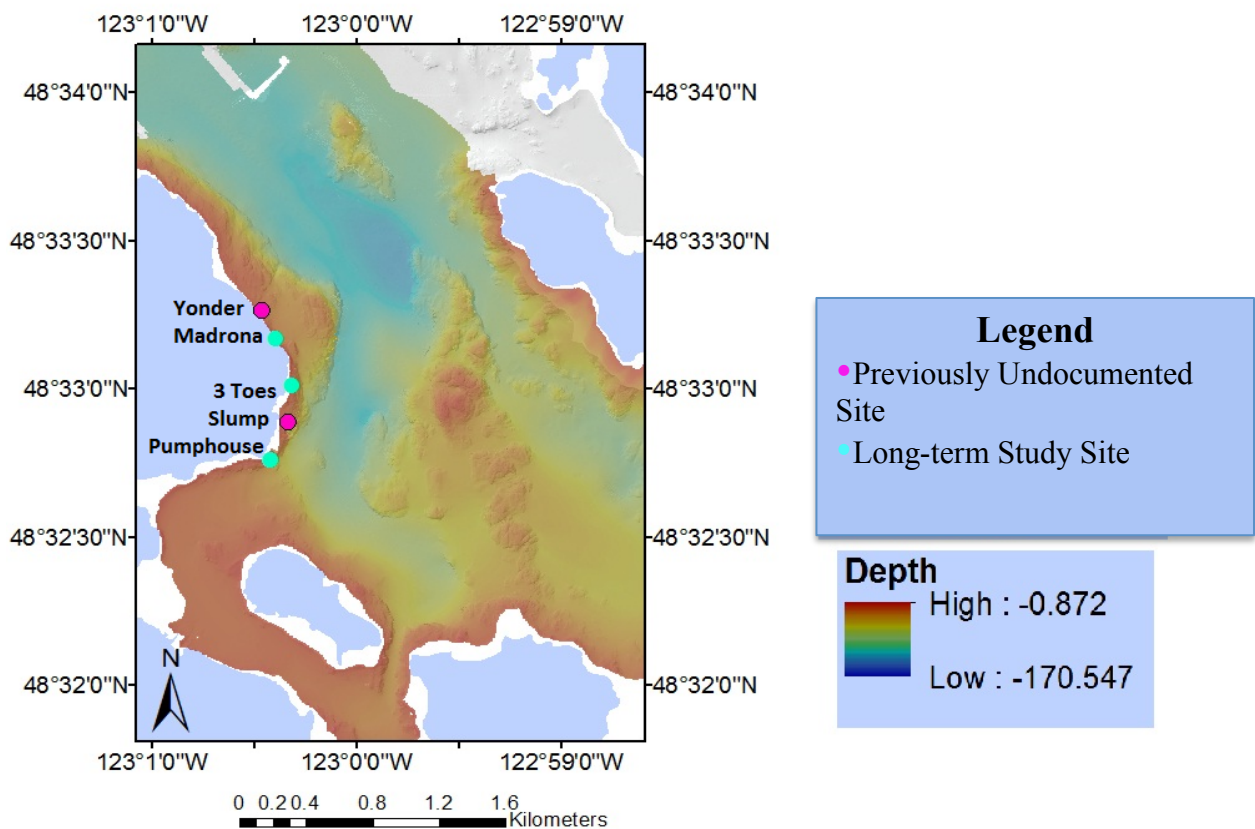


Figure 2: Five study bathymetric map. Five study sites shown along San Juan Channel. Madrona, 3 Toes, and Pumphouse are long-term monitoring sites. Yonder and Slump are previously undocumented sites.

At each of the five sites, one depth, 15 m, was surveyed with the photoquadrat method (Bohnsack, 1979). Ten random 36 x 24 photoquadrat images were obtained along a 10 m horizontal transect at each transect with an 8 MP Olympus digital camera, Ikelite strobe, and aluminum framer. Substrate angle was estimated in six 15⁰ categories:

- 1: 0⁰-15⁰
- 2: 15⁰-30⁰
- 3: 30⁰-45⁰
- 4: 45⁰-60⁰
- 5: 60⁰-75⁰
- 6: 75⁰-90⁰

Where category ‘1’ was approximately horizontal and category ‘6’ was approximately vertical. From this we obtained four angle classification schemes: 1) six 15° categories, 2) three 30° categories, 3) two 45° categories, 4) three orientation categories in which horizontal is 0-15°, sloping 15-75°, and vertical 75-90°.

Photoquadrat images were cropped and analyzed using ImageJ software (Rasband, 1997). A 6 x 4 rectangular grid was superimposed over each image with ImageJ. Percent cover of each species was estimated in seven percent cover categories for each of the 24 rectangles (Dethier, 1984; Reese and Tomich, 1992; Dethier, 1993):

- 1: <1%
- 2: 1-19%
- 3: 20-39%
- 4: 40-59%
- 5: 60-79%
- 6: 80-99%
- 7: >99%

All organisms were documented to the lowest taxonomic level possible using taxonomic reference sources.

Percent cover was calculated for each species in all 24 rectangles. This raw percent cover value was summed for one photoquadrat and divided by the sum to generate a rescaled percent cover value. Canopy, sediment, and rubble were removed from the dataset and the remaining values were rescaled by the useable area to generate final percent cover values for both species and phyla.

Data were analyzed with univariate and multivariate statistics to examine the effect of substrate angle on invertebrate assemblages and to determine which species drive these patterns. A two-way nested analysis of variance (ANOVA) was performed in JMP 9.0 (JMP, 2011). Site was the main independent variable while angle was the random effect, nested within site. Percent cover by species and phyla were dependent variables. The ANOVA was run for each angle categorization scheme.

Multivariate analyses were conducted with PRIMER Software (Clarke and Gorley, 2006) for each angle categorization scheme. Percent cover data were square-root transformed. Nonmetric multidimensional scaling (nMDS), based on Bray-Curtis Similarity with 50 runs, examined angle and species patterns. A two-factor nested analysis of similarity (ANOSIM) was conducted for angle, and a one-factor ANOSIM was used for site, to determine the degree of similarity among sites and between angles, in each nMDS. Similarity percentage analysis (SIMPER) determined the similarity and difference indices for communities due to angle, as well as which species contributed to these differences. Species accumulation curves were generated with Chao2 and S_{obs} metrics.

The MBES data, with 200% bottom coverage, collected with a Simrad EM1002 and EM3000 by the Canadian Hydrographic Office in cooperation with the Geological

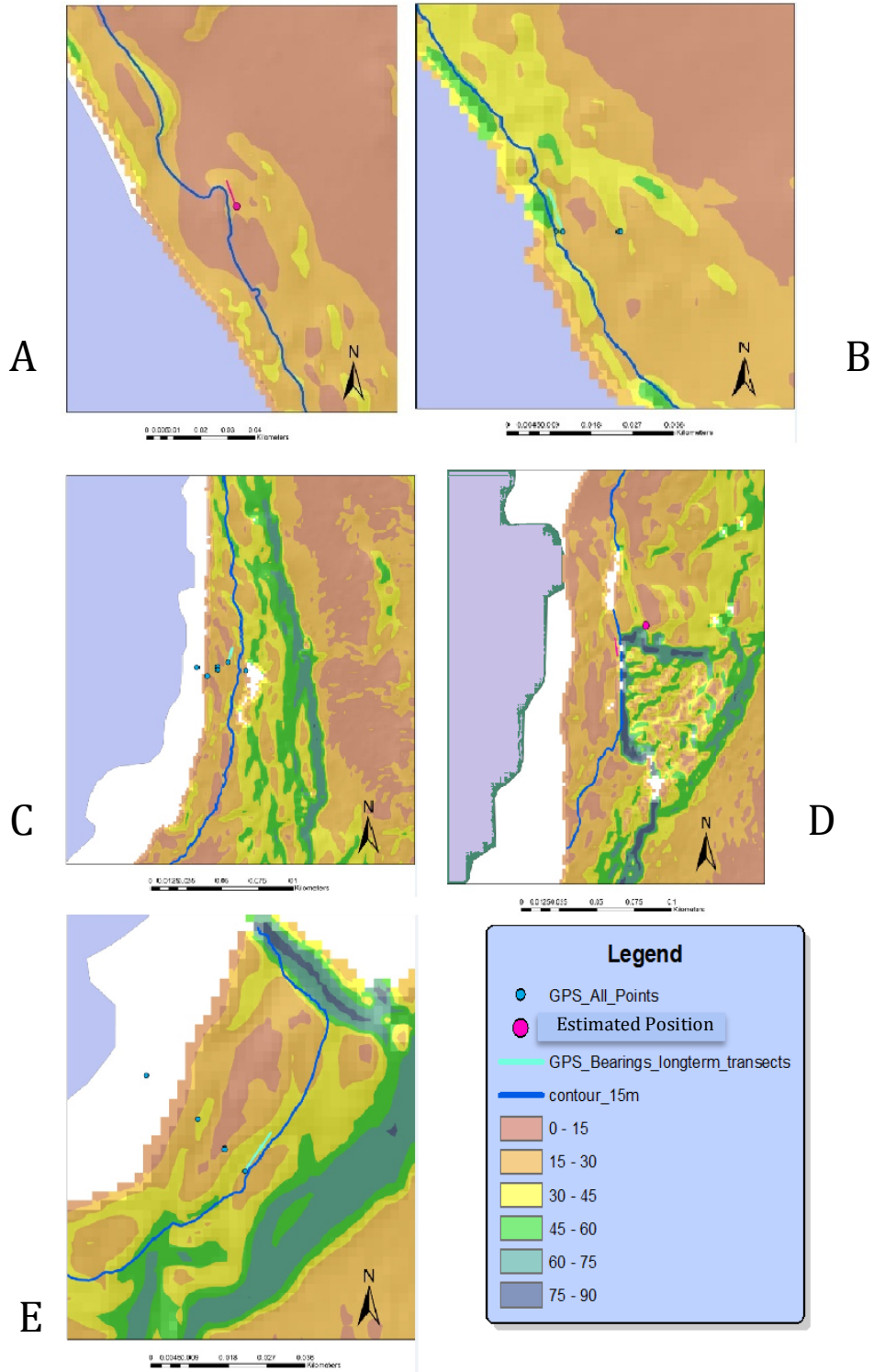


Figure 3: Slope for five study sites. A) Yonder. B) Madrona, C) 3Toes. D) Slump. E) Pumphouse. Colors denote inclination in degrees.

Survey of Canada and the Tombolo/SeaDoc Society, gridded at 2 meters, (Greene et al., 2006) and corresponding backscatter, gridded at 1 m, were interpreted with ArcGIS (ESRI, 2011) for the San Juan Channel to distinguish substrate angle. Substrate angle was classified with the ArcGIS 'Slope' tool, and contours were created corresponding to each of the six 15° angle categories and transect depths (Fig. 3). GPS points for transects were superimposed over the bathymetry data and angle was recorded for each site. Assembly types and species distribution predictions were created for each angle category using the species percent cover and substrate angle statistical relationship.

RESULTS

Forty-four different species and groups of organisms (Fig. 4, Appendix 1) were identified in fifty photoquadrat images obtained from five sites on hard rocky substrate ranging from horizontal to vertical. Chao2 species accumulation reached an asymptote at approximately 20 photoquadrat images while S_{obs} did not reach an asymptote (Fig. 3).

Effect of Angle on Assemblages: Univariate Analyses

Substrate angle affected percent cover of sessile benthic invertebrates at both the phyla and species level. Percent cover of three phyla: porifera, mollusca, and annelida varied due to site, but not due to angle (Table 1). Substrate angle, at both the 15° and 30° levels, impacted Bryozoa percent cover. Substrate angle, at the 30° level, affected percent cover of crustose algae and bare space, a proxy for space available, as well as mollusca. Cover of crustose algae and bare space was higher on sloping substrate than

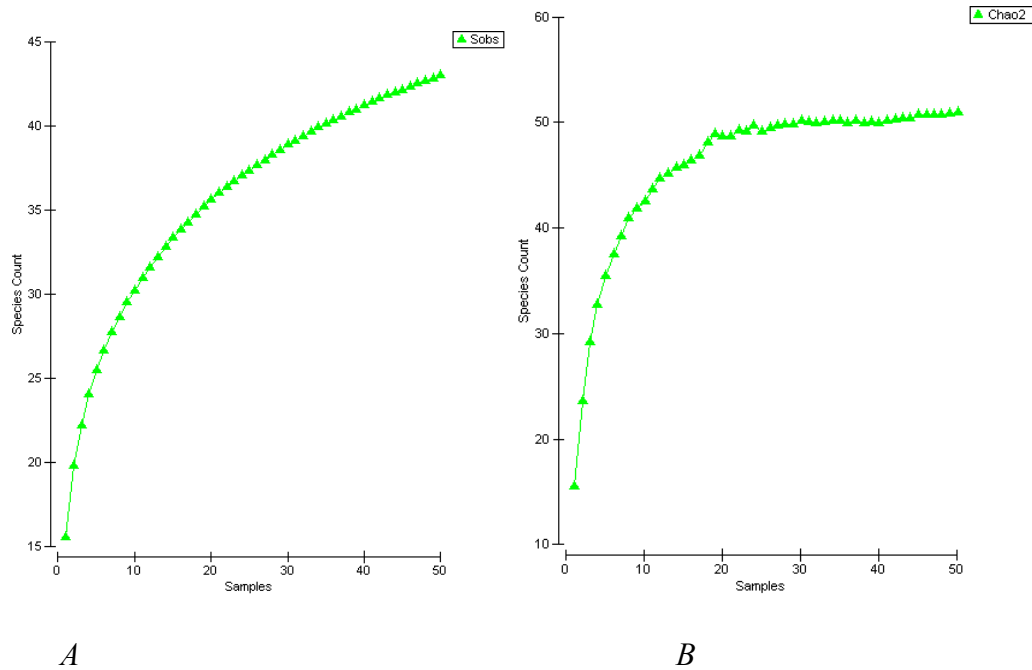


Figure 4: Species accumulation curves. A) S_{obs} species accumulation curve. B) Chao2 species accumulation curve.

Table 1: Two-way nested ANOVA p-values by phyla. 'X' indicates no statistical significance. Bare space and crustose algae combined as proxy for space available.

Phyla	Site Significance	15° Angle (Site) Significance	30° Angle (Site) Significance
Crustose Algae & Bare Space	X	X	0.012
Chordata	X	X	X
Bryozoa	X	0.025	0.001
Porifera	0.048	X	X
Mollusca	0.001	X	X
Annelida	<0.001	x	0.001
Algae	X	X	X

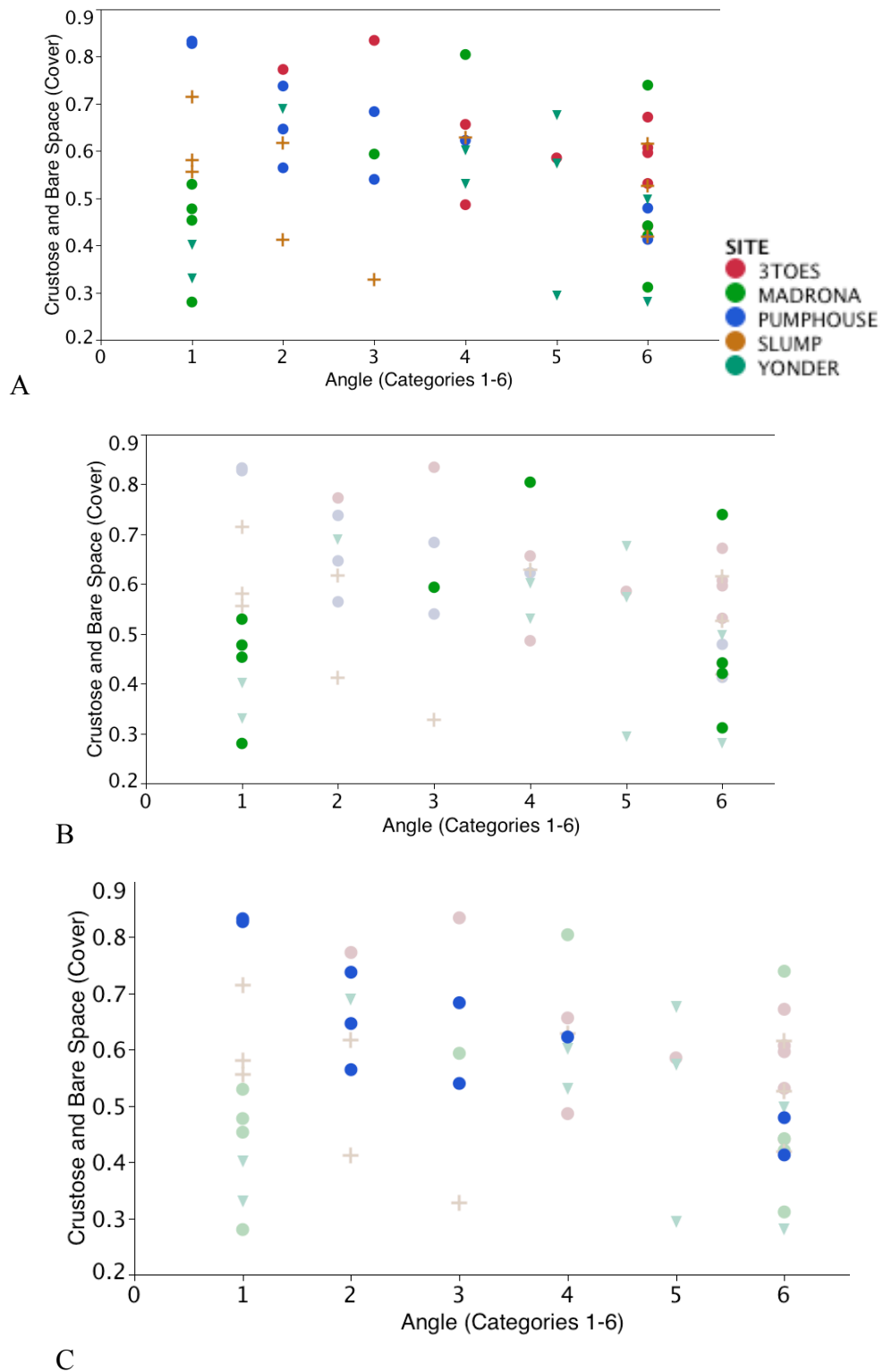
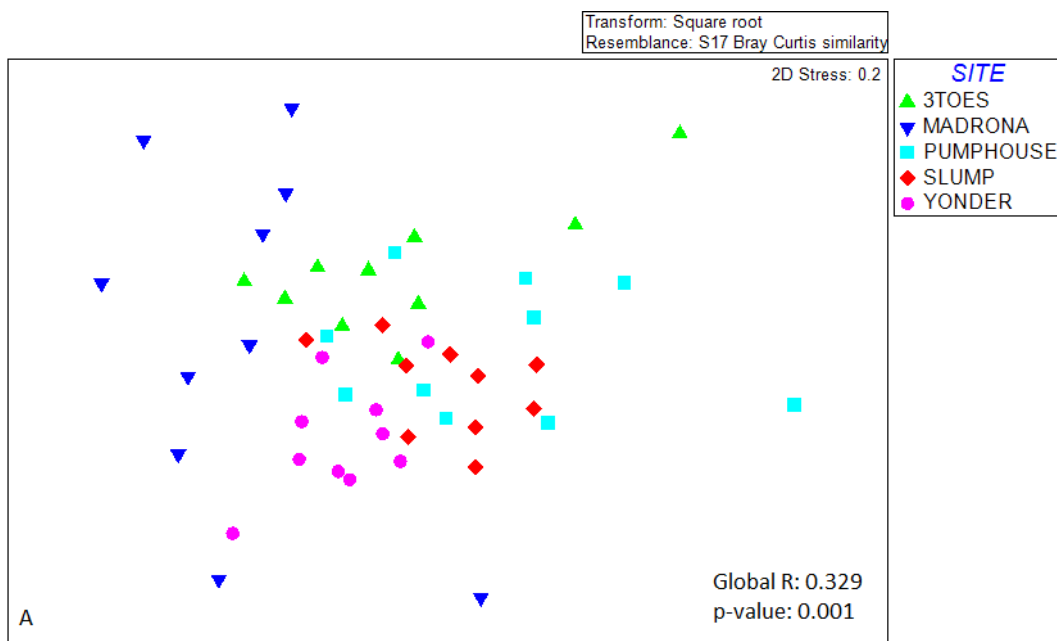


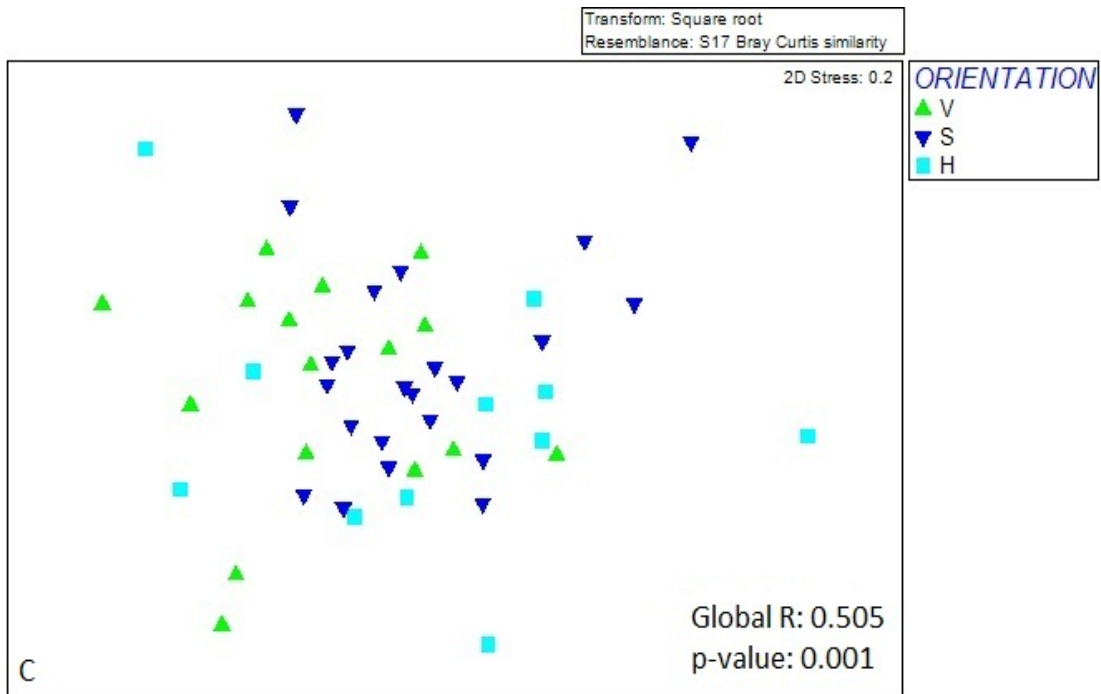
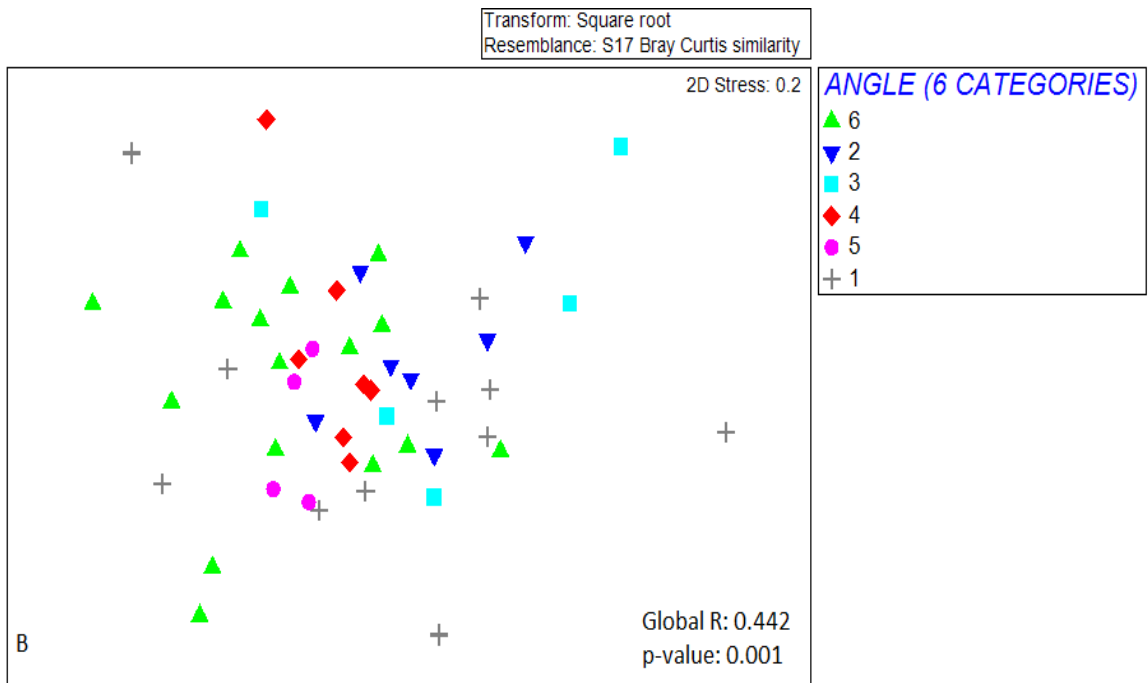
Figure 5: Effect of substrate angle (15°) on crustose algae and bare space percent cover. A) All sites. B) Madrona. C) Pumphouse.

horizontal and vertical surfaces (Fig 5). There was no significant difference in sediment cover between angles.

Effect of Angle on Assemblages: Multivariate Analyses

Both nMDS and ANOSIM analyses indicated that assemblages separate by substrate angle. Site based nMDS ordinations demonstrated that assemblages are different between site (Fig. 6A). Those within Slump and Yonder appeared to be most similar within the individual site. Assemblages separation was more pronounced at broader angle categories than at six 15° categories according to 2-dimensional nMDS plots (Fig. 6B-E). ANOSIM indicated that assemblages are statistically different between substrate angles for site and all four angle classification schemes, the later of which were nested within site suggesting that assemblages are influenced by angle (Fig. 6). As the angle classifications decreased from six categories to two categories, the global R values increased from 0.44 to 0.83 (Fig. 6).





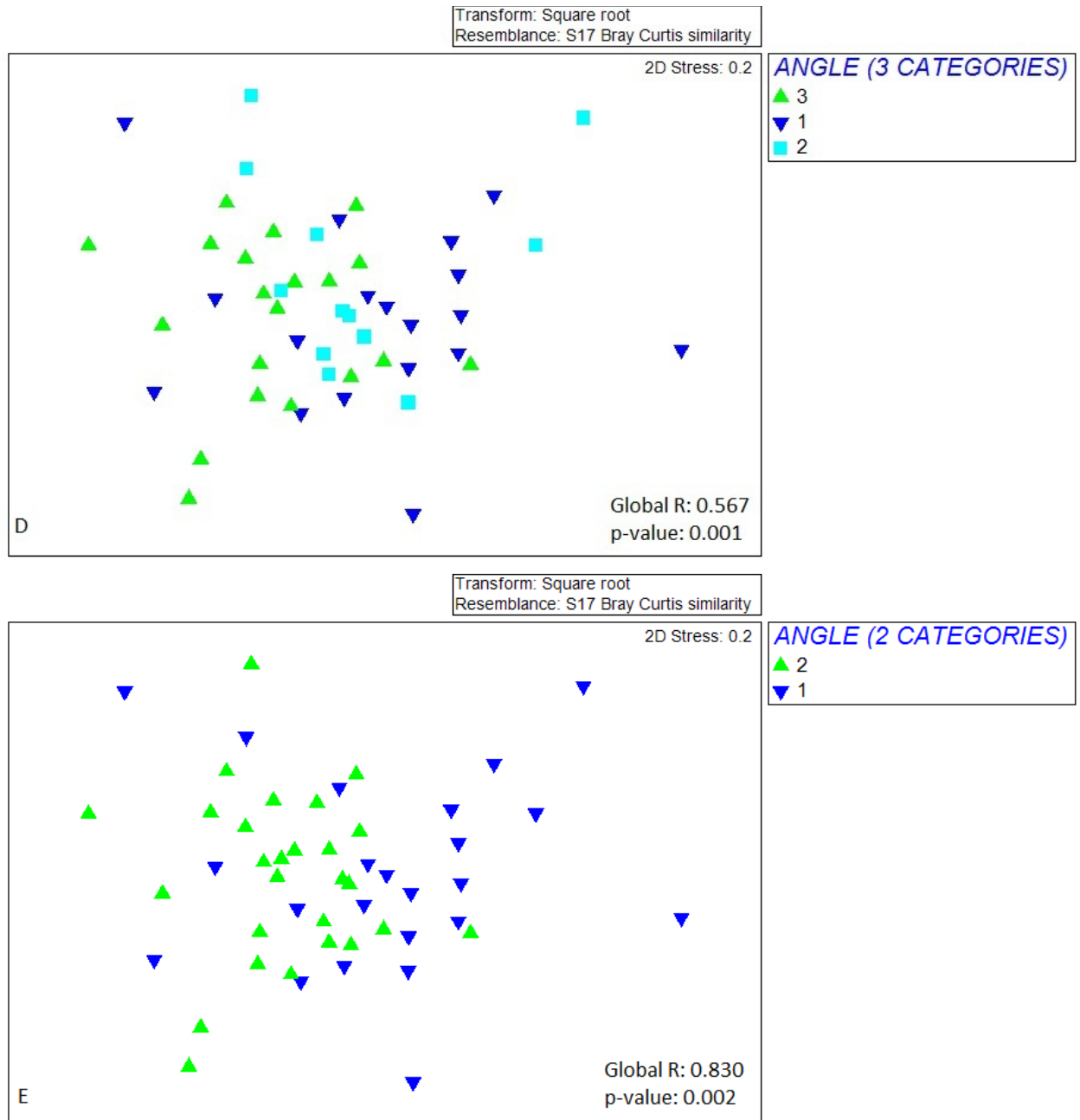


Figure 6: nMDS plots and ANOSIM global R and p-values for site and angles. A) Site. B) Six 15° angles. C) Angle orientation (horizontal, sloping, vertical). D) Three 30° angles where 1 is 0-30°, 2 is 30-60°, and 3 is 60-90°. E) Two 45° angles.

SIMPER indicated that certain species and groups of species contributed to assemblage differences between angles. Crustose coralline pink algae, encrusting maroon algae, bare space, tube complexes, hydroid-bryozoan complexes, encrusting bryozoans,

and porifera contributed to more than 5% of dissimilarity for all four angle categories. Similarity values for all angles ranged from 69 to 80 while difference values ranged from 20 to 31.

Dissimilarity and similarity values for the three 30° angles and three orientation angles indicated differences between horizontal, vertical, and sloping assemblages. The similarity values for horizontal, sloping, and vertical substrate were 72, 74, and 70, respectively. Similarity values for 0-30°, 30-60°, and 60-90° were 73, 69, and 73 respectively. These relationships suggest that sloping substrate is similar between 15° and 75°.

Approach for Identifying Assemblages

Angles measured *in situ* for each transect were different than those indicated by ArcGIS (Table 2). For Yonder, ArcGIS indicated that the transect covered 15-30° while *in situ* qualitative measurements indicated that substrate angle ranged from 0-90° (Table 4). For Madrona, Slump, and Pumphouse, ArcGIS indicated that transects covered a 30° range while actual measurements ranged from 0-90°. GIS indicated that the slope of 3 Toes ranged from 0-30° while measurements actually ranged from 15-90°.

Table 2: Comparison of substrate angle as provided by ArcGIS for bathymetric data and as measured in situ. Number for measured angles for each site is frequency of occurrence along transect. Numbers across measured rows sum to 10, representing ten photoquadrats.

Site	ArcGIS Angle	Measured					
		0-15°	15-30°	30-45°	45-60°	60-75°	75-90°
Yonder	15-30°	2	1	0	2	3	2
Madrona	15-30°, 30-45°	4	0	1	1	0	4
3 Toes	0-15°, 15-30°	0	1	1	2	1	5
Slump	0-15°, 15-30°	3	2	1	1	0	3
Pumphouse	15-30°, 30-45°	2	3	2	1	0	2

DISCUSSION

Effect of Angle on Assemblages

This study confirms findings from previous studies that organism distribution is different on horizontal and vertical surfaces (Pomerat and Reiner, 1942; Harris and Irons, 1982; Sebens, 1985; Connell 1999; Glasby, 2000; Miller and Etter, 2008, 2011). Unlike previous studies which grouped horizontal and sloping assemblages together (Sebens, 1985), this study examined horizontal, vertical, and sloping substrate separately, with up to 15° resolution. Assemblages on sloping substrate were distinct from those on horizontal and vertical surfaces. Moreover, results from SIMPER analysis suggested that

there are no significant differences between assemblages on 15-75° slopes. There are thus, three distinct communities: horizontal, sloping, and vertical.

Cover of organisms by angle was different than in previous studies. The present study suggests that assemblage differences are mainly attributed to crustose algae, bare space, and hydroid-bryozoan complexes. Previous studies suggested that vertical surfaces would have greater cover of filter feeders than horizontal slopes. Contribution of chordata and porifera to these differences were less than expected on vertical walls. Algae usually dominate horizontal surfaces (Harris and Irons, 1982), yet there was no erect macroalgae effect in this study (Table 1), perhaps due to constant transect depth and the exclusion of algal canopy from percent cover calculations. Irving and Connell (2002) state sediment cover was greater on horizontal substrate than vertical, yet in this study sediment cover was not related to substrate angle.

The relationship between substrate angle and percent cover of crustose algae and bare space was different than expected. Knott et al. (2004) and Baynes (1999) document that bare space and crustose algae, respectively, are greater on vertical than horizontal surfaces. This study indicated that percent cover of crustose algae and bare space was higher on sloping surfaces than either vertical or horizontal (Table 1, Fig. 5A-B). This relationship was observed across four sites. The fifth site, 3 Toes, did not show this trend, perhaps because there were no horizontal photoquadrats from 3 Toes (Fig. 5C). Crustose coralline algae is usually outcompeted by bare space (Knott et al., 2004). There was low algal cover on horizontal surfaces. This may explain the high cover of crustose coralline algae on horizontal surfaces.

This study utilized four different angle classification schemes. Results from statistical analysis indicated that while there are differences between six 15° angles, there are statistically stronger relationships for angle classification schemes with broader categories. Based on these results, it is acceptable to document assemblages on the scale of horizontal, sloping, and vertical. Perhaps with a larger number of photos, there would be more specific assemblage differences between 15° angle categories, even despite the conclusions of this study that three distinct assemblages may exist.

The addition of a third orientation category, sloping, to previous literature challenges proposed factors that influence species distribution based on substrate angle. Sediment cover was similar on all surfaces arguing against a sedimentation effect. Distinct horizontal and sloping communities argues against a light effect because light would be similar on horizontal and sloping surfaces. Crustose algae and bare space are a proxy for bare space and thus indicator of grazing. Similar cover of crustose algae and bare space on horizontal and vertical surfaces argues against biological disturbances as controllers of assembly patterns due to substrate orientation. However, all three surfaces may have high grazing rates due to the high percent cover of crustose algae. This study calls for a re-evaluation of factors historically proposed to contribute to assemblage differences.

This study raises numerous questions. How distinct are horizontal assemblages from sloping assemblages? How distinct are sloping assemblages from vertical? Why are there similar accumulation on horizontal, sloping, and vertical surfaces? Do different mobile invertebrate grazers exert pressure on differently oriented substrate? Are these results constant seasonally? Are these results upheld at multiple depths?

Future research should strive to further understand the effect of substrate angle on assemblages of both sessile and mobile invertebrates across multiple depths, seasons, and locations. Angle should be measured with an inclinometer and sample size should be increased. The contribution of additional variables, such as aspect and rugosity, to assembly patterns should be examined.

Approach for Identifying Assemblages

Differences in scale complicated the developed approach for identifying assemblages. The MBES bathymetry data were gridded to 2 m while photoquadrats were 36 x 25 cm snapshots. The multibeam bathymetry data, when converted to slope data in ArcGIS, provided the broad substrate angle, rather than angles for small features. Bathymetric data were applicable to large features while photoquadrats were applicable to small features. ArcGIS substrate angles did not match photoquadrat angles because of this scale difference. Accurate identification of assemblages remotely, based upon slope, was not effective due to this incongruence.

Particular ArcGIS tools were more relevant for this approach than others. Slope calculations, especially with either the bilinear or cubic methods, were necessary to approximate substrate angle. Contours, both regular and listed, were used to document the position of each transect on the bathymetry maps. The ability to create polygons was useful at a small scale but would have been more useful at a large scale applicable to photoquadrats.

In the future, identification of assemblages based upon substrate angle may be achieved with three changes to this protocol. First, multibeam bathymetry data must be

gridded on large scale to apply to small features. The current grid scale was two meters. The technology exists to collect bathymetric data on the scale of centimeters, but at the expense of increased sampling time. In the future, if possible, data should be gridded at the same scale as photographic data collected *in situ*. Second, accurate GPS coordinates for the beginning and end of each initial transect must be obtained. Without the correct coordinates, species slope relationships will be referenced incorrectly. Third, the results of remote species identification should always be verified with *in situ* surveys.

The revised protocol for remotely identifying assemblages based on substrate angle is as follows:

1. Collect *in situ* photographic data.
 - a. Conduct *in situ* photoquadrat survey at multiple depths across sites.
 - b. Analyze photoquadrats to determine percent cover to lowest taxonomic level possible and which species are present at particular angles.
2. Collect bathymetric data.
 - a. Collect bathymetric data at same scale of previously collected photographs and to highest sampling density possible.
 - b. Calculate slope of study area with ArcGIS 'Slope' tool.
3. Use species-slope relationship determined from photoquadrats to identify which species are present on bathymetric data overlaid by substrate slope.
4. Verify predictive identification with additional *in situ* photoquadrat surveys at undocumented sites.

This study documented three different assemblages due to substrate angle: horizontal, sloping, and vertical as a means to develop and test an approach for remotely identifying assemblages. Although scale issues complicated the approach, with few modifications, this approach is suitable for large-scale differentiation of invertebrate assemblages in the rocky subtidal. This approach is valuable for long-term monitoring studies and restoration ecology because it would not only identify assemblages due to substrate angle but would also serve to track changes over time.

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APPENDIX 1

Appendix 1: Species code and list. List is inclusive of all sites.

Code	Species
AGFI	Agarum fimbriatum
ALGA	Unidentified algae
ASPT	Ascidia paratropa
BAEL	Balanophyllia elegans
BASP	Bare space
BOVI	Boltenia villosa
BRBR	Branching bryozoan
CCAP	Crustose coralline pink alga
CHEL	Chelyosoma
CNFI	Cnemidocarpa finmarkiensis
CORE	Corella spp.
COST	Costaria costata
CRAN	Craniella spp.
CRDO	Crassadoma gigantea
CRIS	Crisia spp.
DICL	Diapoeroecia californica
EALM	Encrusting maroon alga
ENBR	Enrusting bryozoan
EUBI	Eudistoma purpuropunctatum
HBCO	Hydrozoa-bryozoa confusion
HEPA	Heteropora pacifica
LEUC	Leucosolenia spp.
META	Metandrocarpa taylori
PDMC	Pododesmus machrochisma
PHPA	Phidolopora pacifica
PSCH	Psolus chitonodes
PYRH	Pyura haustor
RED2	Red alga, filamentous
RED3	Red alga, branching
RED4	Red alga, bladed
SCUN	Schizoporella unicornis
SERP	Serpulid worms
SPUN	Sponge unidentified
STCL	Styela clava
SYPA	Synoicum parfustis

TCUN	Tunicate colonial unidentified
TETR	Terebratalia transversa
TEUG	Terebratalia unguicula
TSUN	Tunicate solitary unidentified
TUBC	Tube complex
TUBE	Tube builders, unidentified
ULVA	Ulva spp.