Title

The Use of Large-Area Imaging to Study Rocky Intertidal Dynamics with a Focus on the Surfgrass Phyllospadix

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The Use of Large-Area Imaging to Study Rocky Intertidal Dynamics with a Focus on the Surfgrass *Phyllospadix*

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Isabella Doohan

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Professor Jennifer Smith, Chair
Professor Sarah Giddings
Professor Stuart Sandin

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The Thesis of Isabella Doohan is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

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DEDICATION

I would like to dedicate my thesis to my parents, Mimi and Jim and my partner Killian. Their constant support and encouragement has carried me through this Master's while also navigating a global pandemic. Mom, thank you for always being there for me when I need someone to talk to. Dad, Thank you for being one of my best friends. Killian, Thank you for always believing in me more than I believe in myself. And to my brother Matthew, we may be hundreds of miles apart, but knowing you are always proud of me is the best feeling. Your kindness inspires me to be a better person. I love you all with my whole heart.

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ABSTRACT OF THE THESIS

The Use of Large-Area Imaging to Study Rocky Intertidal Dynamics with a Focus on the Surfgrass *Phyllospadix*

by

Isabella Doohan

Master of Science in Marine Biology

University of California San Diego, 2022

Professor Jennifer Smith, Chair

Rocky intertidal habitats are highly diverse coastal ecosystems that may be disproportionately affected by climate change due to their susceptibility to marine and terrestrial heat waves and sea level rise. It is important to enhance understanding of community dynamics as well as habitat preferences for canopy forming taxa in order to better inform conservation efforts in the face of climate change. This study investigates variation in community composition with a focus on the role that elevation and structural complexity measured as rugosity plays on the presence of the functionally important surfgrass, *Phyllospadix* at Cabrillo National Monument in San Diego, California. Three long term monitoring sites were analyzed using large area imaging and 3D models across 3 timepoints from 2019-2020. We found that community composition varied between all sites with the most abundant taxa across sites being turf algae and the functionally important surfgrass *Phyllospadix.* Elevation and structural complexity both proved to be significant factors in determining the presence of *Phyllospadix* with it generally being found between the lowest elevation measured and 0.4 m tidal heights and in areas of relatively low structural complexity. The results from the elevation analysis of *Phyllospadix* align with conclusions from previous studies, while there is no comparison for the results showing the dependence of *Phyllospadix* on structural complexity as no previous research has investigated this relationship. It is likely that habitat heterogeneity affects *Phyllospadix* abundance in a variety of ways but further research is needed to understand these patterns.

INTRODUCTION

The rocky intertidal zone is one of the most iconic marine ecosystems and has been a focal area for research for over a century (Baker 1909) due to the habitat's cultural significance, ecological importance and general accessibility. These habitats have generated fundamental and foundational principles in ecology specifically regarding the role of competition and predation in influencing species distributions and community structure (Paine 1966, Connell 1961). However, now with climate change, sea level rise and ocean acidification these habitats may be changing at an unprecedented rate (Helmuth et al. 2006, Kaplanis et al. 2020). As such it is important to develop a better understanding of community dynamics across space and time, as well as species habitat preferences in order to develop effective conservation and management strategies.

The rocky intertidal habitat is defined as the area of a rocky shore that exists between the high and low tidal ranges, determined by features of the environment such as elevation, slope, and distance from shore. The rocky intertidal includes the low, mid and high zones which are characterized by the amount of time they are exposed to the air. The high zone is flooded only during high tides and spends the most time exposed to air, while the low zone is directly adjacent to the sublittoral zone and is only exposed to air during low tides. A defining feature of the rocky intertidal environment is vertical zonation; the distributional pattern of species occupying space on rocks that creates distinct horizontal bands moving from the high to low zones (Connell 1972, Lubchenco 1980). These bands are formed due to species being constrained to certain zones by physical and biological controls (Dayton 1971). In general, a species' lower limits are thought to be bounded by competition and predation. This was definitively shown by Paine (1966), who discovered that mussels have a lower limit that corresponds directly with the upper limit of the predatory *Pisaster* sea star. A species' upper limits are bounded by exposure to air and lack of water, which lead to desiccation and heat stress. This was made clear by Connell (1961), who conducted field experiments that proved that desiccation sets the upper limit for two competing barnacle species. This fundamental view of the dynamics of rocky intertidal ecology is now considered an oversimplification and there are many complex mechanisms still being discovered and elucidated (Tomanek & Helmuth 2002).

Rocky intertidal research has expanded upon this foundational knowledge in an attempt to further understand drivers of community composition at larger spatial scales. Studies have shown that community composition is strongly determined by large scale regional external factors (Hacker et al. 2019, Bagur et al. 2022). These factors include upwelling, primary production inputs, nutrient availability (Menge & Menge 2013, Nielsen & Navarrete 2004), wave action (McQuaid & Branch 1985, Heaven & Scrosati 2008), land temperature (Helmuth et al. 2002), sea temperature (Bolton & Anderson 1990, Blanchette et al. 2009) and seasonality of day-time low tides (Helmuth et al. 2002). Historically missing from these large scale studies is an adequate description of how benthic structural complexity (e.g., rugosity) contributes to variations in community composition. Schoch et al. (2006) attempted to include structural complexity as a factor in a large-scale study of community composition but found that complexity was difficult to control and compare. For example, they found that selecting sites with homogeneous rock structures in a 1km region was not always possible, thus confounding such comparisons (Schoch et al. 2006). While structural complexity has been investigated at smaller (cm) scales to determine the importance of microhabitats on species distributions (Menge 1976, Beck 2000), large (m-km) scale relevance across sites has not been well studied.

Modern technology and the use of high resolution photography has led to an increasing ability to study the large scale community dynamics including the effects of habitat heterogeneity and complexity on rocky intertidal community composition (Bryson et al. 2013, Murfitt et al. 2017, Meager et al. 2011, Guichard et al. 2000). In particular, the use of photogrammetry to study community structure involves taking hundreds to thousands of images of study sites in order to build 3-dimensional (3D) models in which spatial and biological data can be extracted (Gomes et al. 2018). With these models, the physical structure of the habitat can also be analyzed quantitatively with measures such as rugosity and fractal dimensions, and qualitatively with categorical descriptors of the varying structures (Meager & Schlacher 2013). Results have shown that topographic features can be detected with low margins of error and that they affect community composition in varying ways depending on scale (Guichard et al. 2000, Meager et al. 2011). When considering biological data, large scale imagery has proven most effective when quantifying canopy forming macrophytes as they can easily be identified in images and are not obscured by other species (Murfitt et al. 2017). Using high resolution imagery and photogrammetry is an efficient and cost effective method that has been used widely in many coastal ecosystems from coral reefs (Burns et al. 2015, Edwards et al. 2017) to sand dunes (Gonçalves & Henriques 2015), but research in the rocky intertidal has been minimal, and there is thus a need for further investigation (Kaplanis et al. 2020, Garza 2019).

Large canopy-forming seaweeds and seagrasses are commonly found in the rocky intertidal and play a significant role in shaping overall community composition (Jonsson et al. 2006). They influence the local environment as a source of food for herbivores, provide shade and moisture for other species, increase structural complexity and are an important source of primary production (Dijkstra et al. 2012, Chemello et al. 2018). Arguably the most significant way that these taxa influence intertidal communities is by creating understory habitat as ecosystem engineers (Leonard 2000). Canopy-forming macrophytes create a shaded habitat with significantly lower temperatures and prevent desiccation of sub-canopy species during low tide exposures (Ørberg et al. 2018, Bertness et al. 1999). As temperatures increase and extreme heat events become more frequent and severe due to climate change (Projected Climate Change, 2018), the importance of canopy forming macroalgae is being magnified.

Research has shown that the presence of canopy forming macroalgae mitigates climate-driven disturbances for understory species (Bertocci et al. 2010, Pocklington et al. 2018). The presence of canopy forming species has been shown to reduce temperatures in the rocky intertidal, which is a large source of stress for many organisms. The seagrass *Phyllospadix* has been shown to reduce temperature in an intertidal pool by up to 10 degrees Celsius (Shelton 2010), while the brown algae *Fucus* reduced rock surface temperatures by up 16 degrees Celsius (Cimon & Cusson 2018). While providing protection for other species, canopy forming macrophytes are susceptible to the impacts of climate change, primarily heat waves, and their loss is particularly damaging due to their role as foundational species (Román et al. 2020, Serrano et al. 2021). This has been seen around the globe as canopy forming macroalgae and seagrasses have been in decline worldwide, often due to anthropogenic warming (Kendrick et al. 2019, Lewis 2020). When these foundational species are lost, there can be a transition to an alternate stable state dominated by turf algae which are much less structurally complex and do not provide the same habitat or ecosystem services that the foundation species provide (Strain et al. 2014, Álvarez-Losada et al. 2020).

Phyllospadix is an important genus of seagrass commonly found in rocky intertidal habitats along the west coast of North America from Southern Alaska to Baja California (Phillips 1979). *Phyllospadix* is referred to as a surfgrass because it anchors directly onto rocks in the wave swept low to sublittoral intertidal zones, unlike most seagrasses, which are found occupying sandy substrates (Cooper & McRoy 1988). It has been occasionally referenced that *Phyllospadix* is found on rock benches or in mid-low zone rock pools (Shelton 2010), but no evidence of rock habitat preference has ever been studied. Once established, surfgrasses have been shown to preclude other species from occupying space, with the exception of invertebrates and shade tolerant algae that live below the canopy (Turner 1985). However, surfgrasses are susceptible to removal during times of heightened disturbance-especially wave action, and once removed, the space they fill can be quickly recolonized by opportunistic algae. This was observed in San Diego when two years of heavy disturbances led to removal of surfgrass canopy, which was subsequently replaced by turfing algae species (Stewart 1989). Once removed, *Phyllospadix* has been shown to be slow to recover, taking up to 3 years or more to return to pre-disturbance levels (Turner & Lucas 1985).

There are two species of surfgrass commonly found in Southern California, *Phyllospadix torreyi* and *Phyllospadix scouleri* (Hartog & Kuo 2007). They are morphologically distinct, with *P. torreyi* having longer and thinner leaves than *P. scouleri*, but they are functionally very similar (Stewart, 1991). When cohabitating, *P. torreyi* will shift about 40cm lower than *P. scouleri*, suggesting that *P. scouleri* has a slight competitive advantage when resisting desiccation (Ramírez-García et al. 1998). These North American species of *Phyllospadix,* along with *Phyllospadix serrulatus* found in the Pacific Northwest, were studied extensively in the late 1900's (as reviewed in Phillips 1979), but little recent research has been conducted.

The purpose of this thesis and the body of research it represents is to investigate rocky intertidal community composition across space and over time in Cabrillo National Monument (Cabrillo), San Diego, California between 2019 and 2020. Specifically, I will explore: 1) if and how algal and seagrass community composition varies significantly across three sites in Cabrillo and if so, does this trend persist through time? and, 2) the factors that influence the abundance and distribution of *Phyllospadix* across these sites at Cabrillo including tidal elevation, habitat availability, substrate type and structural complexity. To address these questions, large-scale imagery from three long term monitoring sites at Cabrillo was used to create 3D models of the rocky intertidal.

METHODS

Study Location

Cabrillo National Monument is a protected natural area located at the southern tip of Point Loma in San Diego, California that operates under the management of the US National Parks Service. Within Cabrillo there is a rocky intertidal area that spans about 1.7km of open ocean coastline (Pandori et al. 2020). The rocky intertidal area is protected from human foraging as a state marine reserve. The rocky intertidal community present at Cabrillo has been considered to be the most diverse of all rocky intertidal areas in San Diego County (Engle & Davis 2000). Given the proximity to a large urban population, the easy accessibility and the thriving intertidal environment, Cabrillo is a popular destination for both tourists and locals alike. In 2011, the rocky intertidal area of Cabrillo received over 213,000 visitors, with the daily maximum being almost 1,800 people (Phillips et al., 2013). Within the rocky intertidal area at Cabrillo, there are three distinct zones (Zone 1, Zone 2 and Zone 3) that have been established for long-term monitoring purposes. Zone 1 is located at the entrance to the rocky intertidal area, Zone 2 is south of Zone 1, and Zone 3 is the farthest south, extending to the tip of Point Loma. There is a gradient of human visitation between the three zones, with Zone 1 receiving the highest degree of visitation and Zone 3 being closed to public access since 1996.

Study Sites

In 2016, three long term monitoring sites were established with the purpose of collecting images for a large-scale photogrammetry study of the rocky intertidal community. The sites are referred to as CNM1, CNM2 and CNM3 and they reside within the pre-established Zones 1, 2 and 3, respectively. Each site is 30 meters (m) long from shoreline to ocean and 6 m wide swath, spanning a region of the intertidal area that encompasses the low, mid and upper intertidal zones. A detailed explanation of the site selection process is described in Kaplanis et al. (2020).

CNM1 (Figure 1a) can be characterized as having a dense boulder field in the lower and mid intertidal zones which abruptly transitions to a sloping rock bench in the mid to high intertidal zone. This rock bench steepens significantly and reaches an elevation of >3m, with one persistent rock pool found in the upper intertidal zone. There is generally little to no sand present in this site.

CNM2 (Figure 1b) can be characterized as having a medium to intermittently dense boulder field interspersed with patches of sand and flat rock. CNM2 is the most homogenous in elevation with most of the plot falling in the low and mid zones. There is a large patch of sand that experiences seasonal deposition and removal in the upper half of the plot. In early March of 2020, there was a disturbance in which a large rock tower bordering the northern edge of the site collapsed into the site. This created a massive pile of rock rubble and altered the topography of the benthic habitat.

CNM3 (Figure 1c) can be characterized as dominated by rock bench structures, with upper intertidal rock pools and very few large boulders exceeding 0.5m in height. There is a large trench bisecting two large rock continuous benches which creates a perennial pool of water. The lower intertidal rock benches are less continuous and are interspersed with medium sized flattened boulders.

Field Survey Methods

For this research, imagery was collected bi-annually from 2018 to 2020, between late fall and early summer to encompass the lowest daytime tides of the year. Site boundaries were replicated using photomosaic maps produced from previous field surveys to ensure the same area was being captured by the imagery during each survey. Four 0.5m scale bars (Figure 2a) were randomly placed throughout the site to accurately scale the models in the post processing stage. Ground control points were placed at random flat surfaces throughout the site to collect spatial and elevation data using an iG8 RTK GNSS (Real Time Kinematic Global Navigation Satellite Systems) receiver mounted on a tripod base (Figure 2b). Carbon fiber poles (Ron Thompson Gangster Carp Poles) were fitted together to form an approximately 8 meter long pole, a reel was attached to each end of the pole and a custom sliding camera mount was placed in the middle of the pole (Figure 2c). Images were collected by mounting a Nikon D7000 16.2-megapixel DSLR camera to the pole and programming it to take an image every ~1 second. With one person on each side of the pole, the camera was positioned about one meter above the benthos then slowly reeled across the site whilst continuously capturing images. This was repeated horizontally across the width of the site and vertically up and down the length of the site to create a gridded pattern that ensured all areas were sufficiently captured. This process produced about 10,000 images per site with ample overlap that allows for a 3D model to be rendered without large gaps.

3D model processing

The technical process of converting raw images into 3D models and photomosaics used in this study have been described in detail previously (Sandin et al. 2020, Westoby et al. 2012). Raw images from the field surveys were uploaded to the commercially available software: structure from motion (SfM) program *Metashape (Agisoft LLC., St. Petersburg, Russia). Metashape* identifies overlapping areas in the images in order to stitch the images together into a 3D model of the site in the form of a dense point cloud. From *Metashape*, the dense point cloud was exported into a custom-built software called *Viscore* that allows for visualization and ecological data extraction (Petrovic et al. 2014). In *Viscore*, models were scaled and oriented to accurately represent the physical environment being replicated (Figure 3). Scale was assigned by identifying the scale bars in the model and manually inputting the known distance of 0.5m from end to end. Spatial orientation was assigned by identifying ground control points in the model and manually inputting the correct elevation based on RTK data and field notes. The process for orienting the model based on RTK data was only utilized for one time point per site, known as the “reference model” due to the time constraints of utilizing the GPS for each survey. Given the prevalence of static structures in the rocky intertidal environment such as large boulders and rock benches, further models were oriented based on the elevation data of the reference model. This was done by dropping markers on static structures throughout the reference model and recording the elevation of each point. The same points were then located in the other models and the elevation was manually inputted to match that of the reference model. Finally, the models were spatially aligned so that multiple time points for each site were layered on top of each other to track change over time.

Data extraction

All ecological data extraction was conducted in *Viscore* using raw images to quantify the benthic community composition of each model. This was done using the “Virtual Point Intercept” (VPI) tool in *Viscore* that uses randomly stratified points to determine percent cover in a predefined rectangular area. For each model, approximately 9,600 points were dropped onto the plot, resulting in approximately 50 points per m^2, with each point being identified to the finest taxonomic level possible (Figure 4). Using raw images, points were manually identified to the species or genus level for morphologically distinct species, such as *Sargassum muticum*, *Phyllospadix* spp., *Stephanocystis* spp., *Ulva* spp. and certain invertebrates. Inconspicuous species that could not be accurately identified using images alone were identified to the functional group level such as articulated coralline algae, turf algae, red fleshy algae, fleshy encrusting algae, crustose coralline algae and certain invertebrates. All brown algae species other than *Sargassum muticum* and *Stephanocystis* spp. were grouped as “brown algae other” because they are functionally similar and were rarely present. Abiotic benthic structures were identified as either rock or sand. VPI data extraction resulted in comprehensive percent cover estimates for each model as well as the spatial positioning and elevation associated with each identified point (X, Y, Z coordinates). Structural complexity data was extracted using the virtual profile gauge tool in *Viscore*. This tool is designed to interrogate structural complexity along a transect line in a manner analogous to a profile gauge *in situ* (McCormick 1994; McCarthy et al., in prep). This tool exports the position of virtual profile gauge rod termini as spatial points, and the distance between these points along a transect line can be used to calculate the structural complexity of the reef contour across multiple scales, depending on the chosen settings of the tool. For this study, the scale was set to a 1cm distance between profile gauges and a 5 cm distance between transect lines across the plot.

Statistical analysis

To determine if benthic community structure varied significantly across sites, first it was necessary to create replication by sub setting the data. For each model, 30 replicates were created with each replicate representing the points identified in a 1 by 6 meter swath, with swaths moving from the low to high end of the plot. The count of identified points was converted to proportion and abiotic features were removed from the dataset to focus on biotic interactions. Next, Bray Curtis Similarity values were calculated on the raw percent cover data and these were used in a multifactorial permutation based multivariate analysis of variance (PERMANOVA) with 999 permutations with both site and time treated as fixed effects. Algal community composition was visualized with a stacked bar plot to highlight the taxa responsible for the greatest variation between sites. To determine if the presence of *Phyllospadix* is dependent on elevation, a Chi Squared test of independence was used. Elevation values were grouped into 0.1m bins and identified points were grouped into “phyllospadix” or “other”. Counts of “phyllospadix” and “other” occurrences for each bin were summed to determine the total amount of each group in each elevation bin. To account for a large quantity of zeros in certain elevation bins, all points with an elevation of 0.5m and above were grouped into one elevation bin called “>0.5”. The relationship between the amount of available habitat in each elevation bin and across substrate type and the amount of *Phyllospadix* in each site was investigated using descriptive statistics. For each site, the total percent cover of points that fall within the preferred range for *Phyllospadix* was calculated, excluding all points identified as sand. This value was compared to the total percent cover of *Phyllospadix* present and then these percent cover values were compared between sites and timepoints to determine if a consistent spatial or temporal trend existed.

Structural complexity was analyzed using outputs from the virtual profile gauge tool in *Viscore*. The diameter of virtual profile gauge rods was set to 1 cm, and structural complexity was assessed continuously along virtual transects oriented perpendicular to shore. This data was used to calculate linear rugosity, the ratio of the contour distance of the substrate to the horizontal linear distance traversed by the measurement instrument. Linear rugosity is scale dependent, and values can vary depending on the scale that is chosen (Friedman et al. 2012). Regardless of scale, linear rugosity increases from a minimum of 1 (i.e., a completely flat surface) toward infinity (infinitely complex surface). The 1 cm scale was chosen because it is a small enough distance to allow for the 3D profile of fine scale benthic structures to be adequately resolved (McCarthy et al., in prep). It was also found that this scale provided a more accurate visual representation of the benthic structure than a scale of 5cm based on structural complexity maps created for each site. Using the spatial point data created via the virtual profile gauge tool, rasterized maps of each site were created, with 25x25cm grid cells. Using a bootstrapping approach, virtual profile gauge points were randomly sampled 100 times to calculate rugosity for each raster cell across the study site. Spatial data for *Phyllospadix* identified in each plot was overlaid onto the corresponding rugosity maps to identify the rugosity values associated with each *Phyllospadix* point. The same method of Chi squared analysis used for elevation was used to determine if *Phyllospadix* distribution is dependent on linear rugosity. Rugosity values were grouped into 0.1 (unitless) bins, with all bins above 2 grouped into one bin called “>2” to reduce an excess of zeros. All statistical tests were performed using R Statistical Software (R Core Team 2022) and elevation maps were created using Surface Modeling Software.

RESULTS

Community composition

There was greater similarity in rocky intertidal community composition within sites than among sites for all three timepoints with PERMANOVA resulting in p < .001 (figure 5). Algal turf, red algae and *Phyllospadix* were the most commonly identified taxa across all sites and times, with the exception of CNM1, which had lower cover of *Phyllospadix* ranging from 3.4%-4.4% (Figure 6). CNM2 and CNM3 had similar amounts of *Sargassum muticum* ranging from 3.4%-4.6% and 2.4%-3.5% respectively, while CNM1 had an almost complete absence of *Sargassum muticum.* CNM1 however had similar values, 2.5%- 6.7%, of *Stephanocystis spp*., while CNM2 and CNM3 had total or near total absence of *Stephanocystis spp.* The greatest overall variation between sites in a given time point comes from *Phyllospadix*, which had a maximum coverage of 29.8% at CNM2 and a minimum coverage of 4.4% in October 2019.

Elevational trends

Maps based on elevation data for CNM1, CNM2 and CNM3 (Figure 7) show an accurate visual representation of the topography of each site. From these maps and the associated elevation data (Table 1), it is clear that there are very different elevational profiles at these three sites. CNM1 is the most heterogeneous site containing both the highest (3.3 m) and the lowest (-0.3 m) elevation of all three sites. CNM2 is the most homogenous with 98.7% of the site at an elevation between 0 m and 1.0 m. CNM3 represents an intermediate between CNM1 and CNM3 in terms of representation of tidal zones. Mid and low tidal zones have strong representation at all sites, while habitat in the high intertidal zone is the most variable across sites.

To explore vertical distribution in taxa across intertidal habitat, algae and seagrass were plotted by proportion of identified points per elevational bin for each site and time (Figure 8). Some taxa were observed in all zones within the elevations measured, while others were only found in distinct elevation bands. Across all sites and times, turf algae was found in every bin from -0.3m to 3.3m, *Ulva* species were found in every bin from -0.2 m to 2.9 m and fleshy encrusting algae was found in every bin from -0.2 m to 2.9 m, with only a few exceptions. Most other taxa displayed habitat preferences based on elevation. Of the most abundant taxa identified, red algae displayed an elevational preference between -0.3 m to 0.9 m, with only 4 out of 8,803 points falling above this range. *Phyllospadix* displayed an elevation preference from -0.3 m to 0.4 m, with the exception of presence in an upper intertidal rock pool found in CNM3.

Phyllospadix and Elevation

Results from Chi Squared analysis show that the proportion of *Phyllospadix* present is dependent on elevation for all sites and time points (CNM1: Feb 2019 $\chi2 = 1236.2$ p-value < 2.2e-16, Oct 2019 $\chi2 = 1763.8$ p-value < 2.2e-16, March 2020 $\chi2 = 1444.6$ p-value < 2.2e-16, CNM2: Feb 2019 $\chi2 =1836$ p-value < 2.2e-16, Oct 2019 $\chi2 =2547$ p-value < 2.2e-16, March 2020 $\chi2 =2893.2$ p-value < 2.2e-16, CNM3: Feb 2019 $\chi2 =1818.7$ p-value < 2.2e-16, Oct 2019 $\chi2 =2286.1$ p-value < 2.2e-16, March 2020 $\chi2 =2713.1$ p-value < 2.2e-16). This shows that *Phyllospadix* is capable of growing at Cabrillo National Monument at elevations from the lowest range measured in the plots up to 0.4m, excluding the case of the presence of higher elevation intertidal pools.

The overall abundance of *Phyllospadix* varies greatly between sites. CNM1 has the least amount of *Phyllospadix*, CNM2 has the largest amount, and CNM3 is in the middle, with this trend persisting across all times surveyed (Figure 9). Between February and October 2019, all sites saw an increase in *Phyllospadix* percent cover, and between Oct 2019 to March 2020, all sites saw a small reduction, or no change. The percent cover of *Phyllospadix* was compared to the percent cover of available habitat, with available habitat being defined as substrate excluding sand within the optimal elevation range for *Phyllospadix* of -0.3m to 0.2m. The average amount of available habitat occupied by *Phyllospadix* was 11.7% for CNM1, 49.6% for CNM2 and 34.2% for CNM3. (Table 2.) This shows considerable variation in the amount of *Phyllospadix* present when compared to normalized amounts of available habitat based on elevation and substrate type.

Structural Complexity and Phyllospadix

Structural complexity maps overlaid with points identified as *Phyllospadix* show a trend of *Phyllospadix* being present in less complex areas with lower rugosity (Figure 10). Chi Squared analysis of *Phyllospadix* and rugosity resulted in significant p values for all sites and times, therefore we can conclude that *Phyllospadix* presence is dependent on rugosity (CNM1: Feb 2019 $\chi2$ =81.4 p-value < 2.18e-13, Oct 2019 $\chi2$ = 84.5 p-value < 6.47e-14, March 2020 $\chi2$ =70.9 p-value < 2.88e-13, CNM2: Feb 2019 $\chi2$ =202.61 p-value < 2.2e-16, Oct 2019 $\chi2$ =280.1 p-value < 2.2e-16, March 2020 $\chi2$ =292.8 p-value < 2.2e-16, CNM3: Feb 2019 $\chi2$ =39.693 p-value < 1.91e-05, Oct 2019 $\chi2$ =135.8 p-value < 2.2e-16, March 2020 $\chi2$ =68.4 p-value < 8.86e-11).

DISCUSSION

The goals of this study were to explore intertidal community dynamics on the rocky shore of Cabrillo National Monument in San Diego, CA across three sites between 2019-2020. Using large-area imaging and structure from motion technology we were able to survey the intertidal at scales not typically feasible during a given low tide due to time and access to habitat. Specifically, we were able to survey a 540 m^2 area across three sites over three time points. Further we were able to use this technology and the subsequent 3D models that were generated to explore how intertidal communities were structured and how they varied over time. The 3-dimensional nature of these models allowed for an exploration of how key taxa were distributed with respect to a) intertidal height and b) structural complexity measured by rugosity. These tools provide an incredibly unique opportunity to study the intertidal (and many other habitats) at scales not previously studied and allow for repeat surveys of the exact same site over time with sub mm level resolution. With advances in remote vehicles such as drones these types of surveys will only become more accessible. Further with artificial intelligence and advances in image analysis and computer processing, post processing of these types of data will also become more efficient. Of course, there are limitations to this workflow which largely include complexities associated with canopy forming species obscuring understory species and the finer details of the underlying structure, thus making these types of surveys inappropriate for some research questions.

Here we show that intertidal community composition varied between sites and this trend was consistent across time. While most of the same taxa were present across the sites their absolute abundance varied. For 8 out of the 9 surveys, the most abundant taxa present was either algal turf or *Phyllospadix*. While collectively algal turf and *Phyllospadix* were the most abundant, these taxa showed the greatest variation in percent cover between sites. Seasonal and spatial variation in algal turf versus *Phyllospadix* dominance is important to track given the alternate stable state that these two species can represent. In the most recent Natural Resource Condition Assessment for Cabrillo National Monument, the biggest knowledge gap was identifying the mechanisms that drive intertidal population dynamics (Hudgens et al. 2019). When considering characteristics often investigated as drivers of community composition, these sites are very similar due to their physical proximity to one another. Other studies have found that external inputs can significantly influence rocky intertidal community dynamics. Specifically, upwelling can influence the community as a source of primary production and nutrients (Menge & Menge 2013, Bosman 1987), extreme sea temperatures can cause thermal stress and mortality to organisms (Suryan et al. 2021), seasonal patterns of day-time low tides can affect desiccation rates (Helmuth et al. 2002) and intensity and frequency of wave action can preclude organisms from certain areas (McQuaid & Branch 1985). The sites at Cabrillo all experience comparable exposure to these factors as well as other regional scale factors including but not limited to weather patterns, invasive species, pollution, pH, salinity and aerial predation. The two main factors, not including biotic interactions, which are different between the three sites are human influence in terms of trampling, and the topography of the benthic structure. It is likely that these two factors are influencing the community composition of the varying zones at Cabrillo, but to what degree is largely unknown.

The location of the three sites within Cabrillo results in a gradient of visitor presence and subsequently human impact from trampling. CNM1 is located nearest to the entrance of the rocky intertidal area, beginning directly under the public accessway. As the most accessible zone, it receives the highest degree of direct human impact with up to 1,000 people or more walking through the site in a single day (Phillips et al. 2013). CNM2 is located at a ~5-10 minute walk south from CNM1 and it is only accessible during negative low tides. Walking to CNM2 requires traversing a rocky terrain covered in often slippery algae and interspersed with pools of water. This creates a barrier to access for many people and reduces visitor numbers by an order of magnitude below CNM1. CNM3 is located directly below the Point Loma Lighthouse at a ~5 minute walk south of CNM2. CNM3 receives minimal direct human impact as it has been restricted to the public since 1996 with access granted solely to national park service personnel and outside agencies conducting research. Prior to being protected, CNM3 still received the lowest visitation rates due to its distance from the entrance to the intertidal area.

It is important to consider the possible effects of trampling as a factor contributing to the variation in percent cover of the two most abundant and variable taxa identified at Cabrillo: *Phyllospadix* and turfing algae. The effects of trampling on intertidal turfing algae at Cabrillo were studied by Huff (2006) with a 17 month manipulative field experiment. Results showed that trampling of turf algae led to significantly more bare rock and changed the community of meiofauna living within the turf, however recovery following disturbance was rapid (Huff 2006). The effects of trampling on seagrasses have been studied with various sand anchored species, but never on surfgrasses. For seagrasses, there has been a general consensus in the literature that human trampling causes a reduction in biomass and leaf density, but recovery can be rapid (Eckrich & Holmquist 2000, Nurdin et al. 2019, Travaille et al. 2015). Given that CNM1 has the highest amounts of trampling and the lowest amounts of *Phyllospadix*, it is possible that trampling is exerting a negative influence on surfgrass abundance. However, without a better understanding of *Phyllospadix's* response to being trampled to varying degrees, it is not possible to fully know the effects that human visitation may be having at Cabrillo. The most recent natural resource assessment for Cabrillo calls for further experimental research to investigate the long term effects that the gradient of visitation has on community composition (Hudgens et al. 2019).

When exploring the distribution of *Phyllospadix* across the intertidal at Cabrillo, we found that it's abundance is related to vertical elevation with a height limit of 0.4 m above MLLW in the absence of rock pools. These findings are expected based on the overwhelming consensus that the two species of *Phyllospadix* that are present in Southern California (*P. torreyi* and *P. scouleri*) inhabit the low intertidal to shallow subtidal zones of the rocky shores with an upper limit set by desiccation. Very few studies on surfgrass have sought to determine an elevational range more specific than the generalized low to subtidal zone characterization. Research in the Pacific Northwest showed that *P. scouleri* had a maximum elevation at the MLLW level, however there were no methods beyond anecdotal observations explaining the measurements used to obtain this value (Phillips 1979). *Phyllospadix in* Baja California has been recorded to have a maximum elevation of -0.3 m below MLLW, while *Phyllospadix* in Southern California was found at an elevation of +0.3m above MLLW (Ramírez-García et al. 1998, Littler 1983). These studies similarly had very minimal explanation of methods in terms of determining MLLW and measuring elevation. Given a lack of clear methods, as well as unexplored confounding site specific differences that can extend upward ranges such as wave action and tidepools, it is not currently possible to compare *Phyllospadix* ranges found in the literature to the results of this study. Despite this, it is still useful to establish location specific elevation ranges of *Phyllospadix* in areas where conservation and restoration efforts may one day be implemented. This will prove particularly important when investigating the effects of sea level rise on rocky intertidal community structure as species may be forced to shift out of their current intertidal zones to survive (Kaplanis et al. 2020).

Using rugosity as a measure of structural complexity we found that *Phyllospadix* was more commonly located on less structurally complex substrates, being most common in areas with rugosity values of 1.2 or less. This is a result that has not been previously described given that *Phyllospadix* and habitat heterogeneity (beyond elevation) have never been directly compared. However, there are clues from past research that suggest that habitat structure and substrate type may play a key role in the life history of *Phyllospadix*.

Topographic heterogeneity can exert local influence on a rocky intertidal community by modifying the hydrodynamics of the area (Breitburg et al. 1995, Cusson & Bourget 1997). Specifically, the presence of boulders can significantly reduce the flow velocity of water, with larger boulders causing greater reductions in flow velocity (Guichard and Bourget 1998). Water flow velocity has been shown to have a direct impact on *Phyllospadix* abundance as a determining factor in seed attachment. As a marine angiosperm, *Phyllospadix* produces flowers and releases seeds, which are negatively buoyant and drift along the bottom until they find a host alga to attach to (Williams 1995). The seeds are small with a U-shaped hook ~1 mm in width - that is used to anchor on to the branches of typically a red algal host (Turner 1983). Lab experiments conducted by Blanchette et al. (1999) tested the effect of low (45 cm/s), intermediate (85 cm/1) and high (180 cm/s) flow velocities on *P. torreyi* seed attachment to a variety of known host species. The results showed that *P. torreyi* seeds have a higher likelihood of attachment in intermediate flow velocities than low or high flow velocities. This suggests that the topography of an intertidal area can affect the flow rates of water passing through, and subsequently enhance or prevent *Phyllospadix* recruitment.

Based on the assumption that an intermediate amount of large boulders leads to intermediate water flow velocity and optimized conditions for *Phyllospadix* seed recruitment, it could be expected that the greatest amount of *Phyllospadix* would be at sites that meet this topographic criterion. Of the sites studied at Cabrillo, CNM2 has an intermediate amount of large boulders, with CNM1 having a comparatively high amount and CNM3 having a comparatively low amount. This aligns with the results which show CNM2 having significantly greater amounts of *Phyllospadix* than the other two sites. However, no measurements of flow velocity have been recorded for Cabrillo so it is not possible to make conclusions on the effect that hydrodynamics has on *Phyllospadix* abundances at these 3 sites.

Given that *Phyllospadix* is a perennial marine plant, it is likely that the large variation in *Phyllospadix* cover between sites may be partially due to patch dynamics rather than seed dispersal and recruitment. *Phyllospadix* has been observed to form continuous meadows at the lower end of its elevational range, whereas in the upper end of its range it grows in patches of varying size (Ramírez-García et al. 1998). Patch dynamics have been studied in many species of seagrasses, but there has never been research focused on the patch dynamics of surfgrasses. Other studies exploring seagrass patch dynamics have shown that over the course of a year seasonal shrinking and growth occurs but overall patch sizes stay relatively similar to starting values (Ramage & Schiel 1999, Jenson & Bell 2001). This aligns with our data on *Phyllospadix* percent cover measured at Cabrillo, which shows seasonal fluctuations but a subsequent return to near baseline values after a year.

Studies investigating patch dynamics of the seagrass *Zostera* have shown that patch mortality is generally higher for smaller patch sizes (Ramage & Schiel 1999, Olesen & Sand-Jensen 1994). Patch mortality may be lower in larger sized patches due to the ability of seagrass to self protect during exposure to disturbances such as strong wave action and increased temperature events (Ruiz-Montoya 2021). These patterns may help to explain the persistence of high percent cover of *Phyllospadix* in CNM2 where large perennial patches are seen, and low percent cover in CNM1, where patches are much smaller in size. Based on research from other seagrass species, large patches experience minimal size change year over year, whereas smaller patches are likely to experience mortality with limited replacement due to low success rates of recruitment (Blanchette et al. 1999).With comparatively little information available on patch dynamics of *Phyllospadix*, future research should focus on life history traits including growth rates, seasonality, mortality and recruitment preferences to help inform management of this habitat forming species.

Sand movement is also a key component of habitat heterogeneity that may influence space availability and subsequently the presence of *Phyllospadix* in the rocky intertidal. *Phyllospadix* is considered to be a sand tolerant plant due to its large size and the morphology of the rhizomes by which they attach to rocks (Littler 1983). This ability to tolerate seasonal fluctuations of sand in an otherwise rock dominated environment may provide a competitive advantage for *Phyllospadix* over smaller algal species that would be smothered under the sand. *Phyllospadix* has been observed persisting in sand depths up to 10 cm in Southern California (Stewart 1980) and up to 15 cm in controlled lab experiments (Craig et al. 2008). In fact, a study exploring the growth and carbohydrate reserves of *Phyllospadix* during sedimentation events found that while buried under 12 cm of sand, photosynthesis and growth decreased, but the plants were able to survive (Plechner 1996). Distance to sand patches and exposure to seasonal fluxes of sand also likely affect the abundance of *Phyllospadix* at Cabrillo in this study. CNM2 is the only site that experiences considerable seasonal fluctuations of sand, with the highest percent cover of sand reaching almost 40% during one survey. During periods of increased sand inundation at CNM2, *Phyllospadix* can be seen seemingly growing out of the sand, while the rocky substrate it is attached to is submerged under an unknown depth of sediment. Without tracking specific patches of *Phyllospadix*, it will remain unknown if sand inundation at Cabrillo is causing any level of mortality or providing a competitive advantage for *Phyllospadix* over other taxa.

Future research

The purpose of this study was to investigate the rocky intertidal community structure and dynamics at Cabrillo National Monument using large-area imaging methods not widely used in this habitat. Given the capacity of these methods to collect vast amounts of high resolution imagery in a short period of time, allowing for extensive post-field time data collection, we strongly urge other intertidal monitoring programs to consider integrating these approaches into existing efforts. The 3D models serve as repositories of long term spatial and ecological data, allowing change over time to be tracked. Maintaining this record of seasonal variation may prove invaluable as the environment adapts to the impacts of climate change and sea level rise.

Surprisingly little research has been conducted on the habitat forming surfgrass species *Phyllospadix* that was studied here. Future research efforts at Cabrillo should be aligned with the Cabrillo 2019 assessment which recommends that future management includes increasing the scope of surfgrass surveys and understanding mechanisms underlying community structure. Future studies should substantially expand the size of the study area while narrowing the scope of data processing to focus on *Phyllospadix* presence, due to its importance as an ecosystem engineer. Novel methods should be developed and adopted in order to minimize sources of error from the methods used in this study as well as to increase the analytical power of the results.

The rocky intertidal area at Cabrillo has been estimated to cover about 130 acres in total across a 1 km length of coastline. Given that the current methods of this study utilized three 180m^2 plots, only 0.03% of the entire rocky intertidal zone at Cabrillo was captured using large scale imagery. The sub-km scale of the current plots may be confounding the metrics of elevation and structural complexity measured in this study. The low and mid intertidal zones of the three sites at Cabrillo are occupied by broad and gradually sloping rock bench, as described by Kaplanis (2020). Therefore, it is possible that *Phyllospadix* was generally found in areas with rugosity values of 1.2 or below because the elevation of these areas was within Phyllospadix's elevational range. Expanding the size of the study sites will lead to the presence of a greater variety of structures and elevations. This will allow for further analysis to determine if the factors of elevation and structural complexity are co-dependent or if they excerpt separate influence on *Phyllospadix* abundance. In order to have a more comprehensive understanding of how *Phyllospadix* interacts with the physical environment at Cabrillo, future methods should expand the size of the field sites considerably.

To collect data at this larger scale, it would be necessary to adapt the current methods to account for limitations in resources, specifically time and person power. Past research has shown that drones are efficient and effective tools capable of collecting rocky intertidal images for scientific purposes (Barbosa et al. 2022, Murfitt et al. 2017). A sample model created in *Viscore* using images collected from a drone survey conducted at Scripps Coastal Reserve in La Jolla, CA provided a comprehensive representation of the entire rocky intertidal area. While the image resolution was not high enough to confidently identify cryptic or small species of algae, canopy forming taxa such as *Phyllospadix* were easily identifiable. To streamline post processing of large models built from drone surveys, *Phyllospadix* aerial extent could be virtually traced in place of the time intensive random point intercept method used in this study. Tracing *Phyllospadix* in the models would allow for patches to be tracked through time as well as provide a more accurate estimation of percent cover in the sites.

Adapting field methods related to collecting spatial metadata will allow for better accuracy in the elevation values associated with the 3D models. Current methods rely on collecting GPS data only once for each site and then virtually overlaying those values onto all timepoints. The 3D models are subject to imperfections during construction in *Metashape,* which subsequently leads to small inaccuracies in alignment and subsequently elevational values. Incorporating GPS data collection into each field survey will allow for accurate elevation points to be recorded and mapped on to each model, regardless of how it aligns with other timepoints. This method was not possible in past surveys due to the time constraints, however, with the use of drones it will be possible to collect images and spatial data simultaneously.

Incorporating additional field methods for measuring habitat characteristics would allow for more robust analysis of benthic structure and *Phyllospadix* specifically. While rugosity is a commonly used measurement of benthic structural complexity, there have been warnings throughout the literature of the scale dependency of this metric (Kostylev et al. 2005). Analyzing habitat structure in multiple ways will allow for stronger conclusions to be drawn regarding the role structural complexity plays in shaping population dynamics.

CONCLUSION

This study sought to analyze rocky intertidal community composition using large area imaging and 3D model analysis- a modern research method that has been rarely used in this dynamic environment. These methods have proven to be an effective means to evaluate spatial and temporal trends in community composition, particularly for highly distinguishable taxa that form patches or canopies. For the three long term monitoring sites analyzed at Cabrillo National Monument, community composition varied between all sites, despite being subject to highly similar conditions. The most abundant of the taxa found within the study sites at Cabrillo were turfing algae species and the functionally important surfgrass *Phyllospadix.* The relative abundance of these two groups has important ecological implications as dominance of one versus the other can present two alternative stable states in the rocky intertidal. Between the three sites at Cabrillo, there were vastly different percent cover values of *Phyllospadix*, with CNM2 having significantly more than any other site. Results from this study show that the proportion of *Phyllospadix* present at a given site is related to both elevation and structural complexity. Specifically, Phyllospadix was generally found between the lowest elevation measured and 0.4 m tidal heights and in areas of relatively low structural complexity with rugosity values of 1.2 or less. There are many aspects of *Phyllospadix* that may relate to other habitat features but further research is needed to understand these patterns.

Phyllospadix was studied extensively in the late 1900’s, but research has dwindled in recent years, especially in comparison to other seagrass species. Given the functional importance, as well as the worldwide trend of decline in seagrasses, it is important to continue studying *Phyllospadix* to better understand its life history and its spatial and temporal dynamics especially in relation to global change stressors such as warming and sea level rise. Adapting methods and expanding the scale of this study to incorporate larger areas of the rocky intertidal zone at Cabrillo will allow for a more in-depth analysis of *Phyllospadix* and benthic structural composition. Future research should consider adapting methods to incorporate the use of drones to efficiently capture images of large areas, collect more frequent GPS data to improve accuracy, and include other physical and environmental data such as temperature, pH and sea level variability to better understand how global change may be impacting these iconic ecosystems and the species that characterize them.

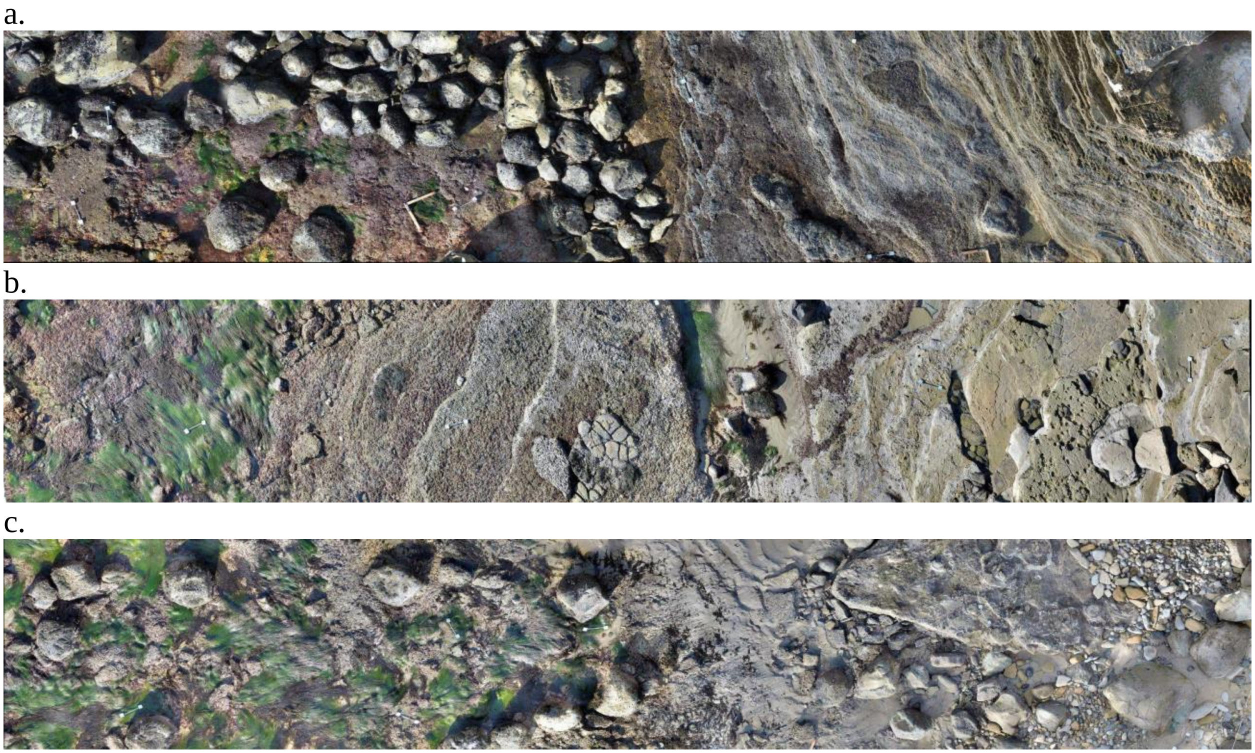


Figure 1: Aerial photomosaics of the three 180m^2 study sites at Cabrillo National Monument. The photos represent site a. CNM1 b. CNM2, and c. CNM3.

Figure 2: A. A 0.5m scale bar placed in a plot during a field survey. B. The tripod legs of an iG8 RTK GNSS instrument used to collect GPS data of identifiable points in the plot. C. An ~8m pole being held above the survey plot while an attached camera continually captures photos.

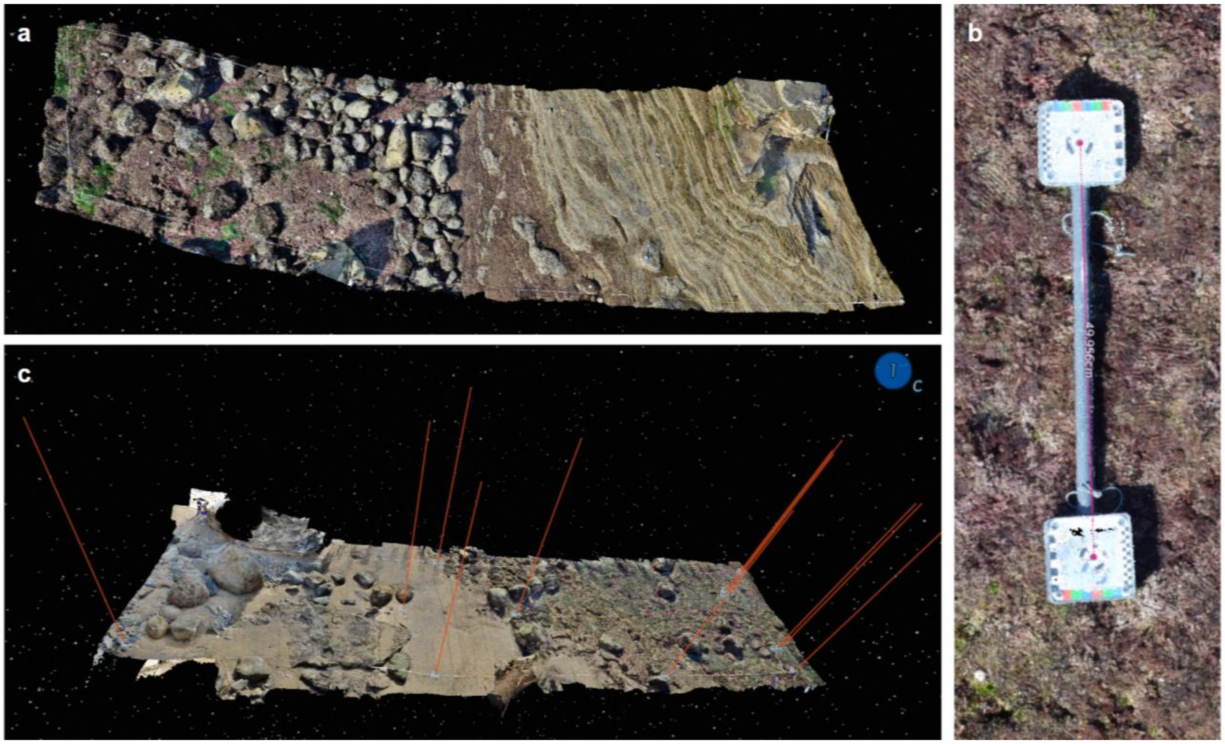


Figure 3: a. A 3D model of site CNM1 in *Viscore*. b. A scale bar in *Viscore* with manually inputted length values. c. A 3D model of site CNM2 being oriented with manually inputted elevation points in *Viscore.*

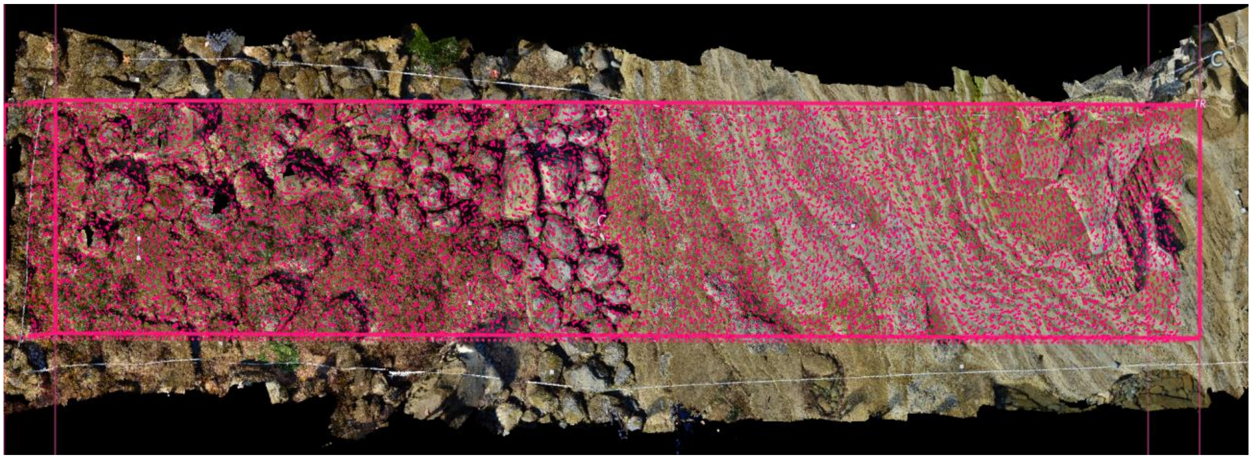
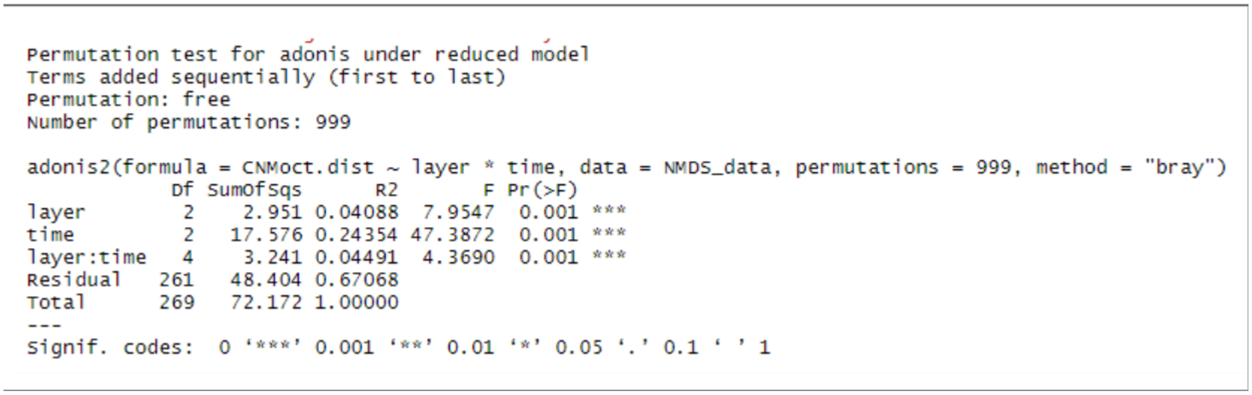


Figure 4: Approximately 9,600 dots randomly on the 3D model in *Viscore.* With the virtual point intercept tool, each pink dot gets identified to the finest taxonomic level possible using the raw images.



```
Permutation test for adonis under reduced model
Terms added sequentially (first to last)
Permutation: free
Number of permutations: 999

adonis2(formula = CNMoct.dist ~ layer * time, data = NMDS_data, permutations = 999, method = "bray")
            Df SumOfSqs      R2       F Pr(>F)    
layer        2    2.951 0.04088  7.9547  0.001 ***
time         2   17.576 0.24354 47.3872  0.001 ***
layer:time   4    3.241 0.04491  4.3690  0.001 ***
Residual   261   48.404 0.67068                  
Total      269   72.172 1.00000                  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
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Figure 5: PERMANOVA results for variation of community composition with layer (site) and time as factors.

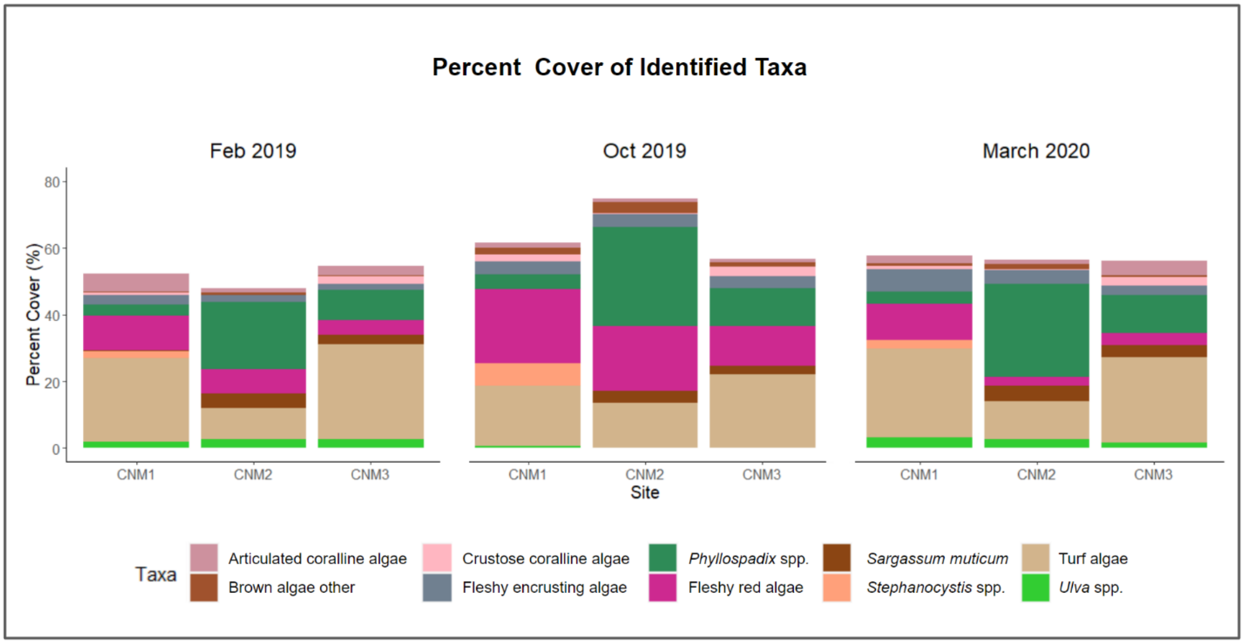

Figure 6: Percent cover of algae and seagrass taxa identified at each site for three time points. Total percent cover varies for each site and time point due to the removal of abiotic features and invertebrates, which were not of interest to the study.

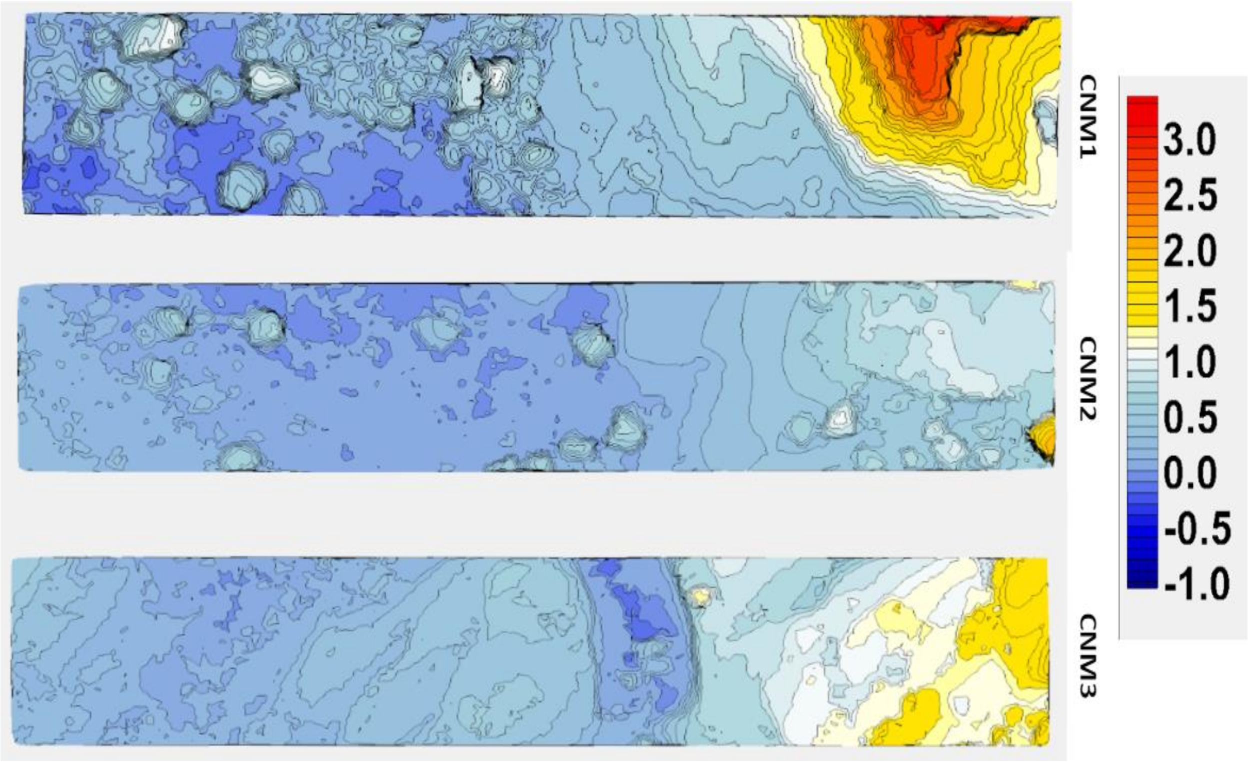

Figure 7: Topographic map of site CNM1, CNM2, and CNM3 showing variation in elevation using 0.1m bins. These maps are an accurate representation of the topography present in each site, including distinguishing features. These features include; the dense boulder field and step wise elevational gain of the rock bench in CNM1, the sparse boulder field and the side of a rock tower entering the plot in the southwest corner of CNM2, and the deep trench and the gradual rock benches that occupy the majority of CNM3.

Table 1: A summary of the elevation values of the sites in relation to MLLW. The low zone ranges from the lowest point in the plot to 0.4 m, the mid zone ranges from 0.5 m - 1.1 m and the high zone is 1.2 m and above. The maximum and minimum elevation values represent the highest and lowest point in each plot.

Site	Low Zone	Mid Zone	High Zone	Max Elevation	Min Elevation
CNM1	49.4%	31.9	18.7%	3.3 m	- 0.3 m
CNM2	68.9%	30.7%	0.6%	2.0 m	- 0.1 m
CNM3	51.8	33%	11.8%	1.7 m	- 0.1 m

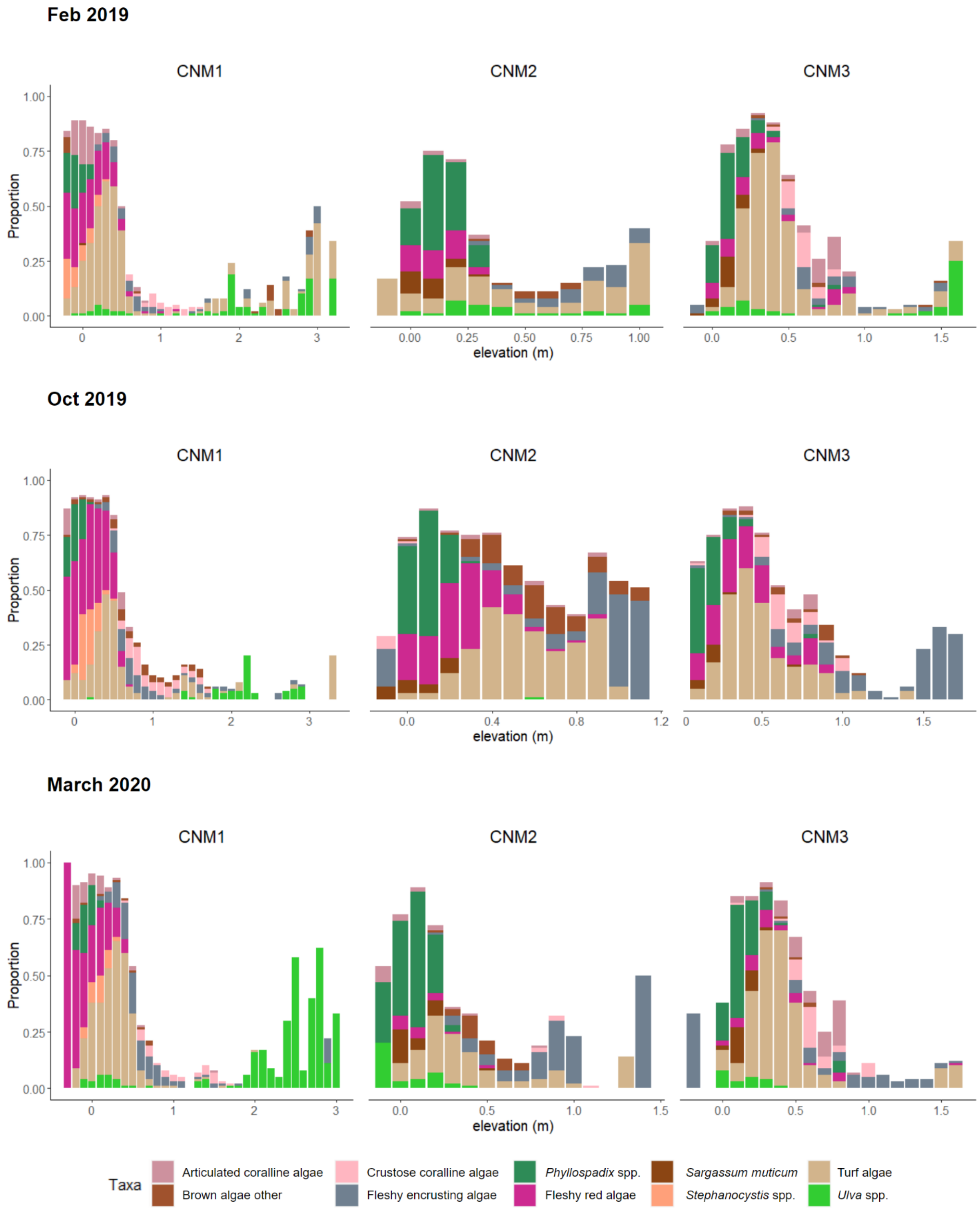

Figure 8: Proportion of algae and seagrass present in each 0.1 m elevation bin for CNM1, CNM2 and CNM3, through three time points. The number of points in each bin varies greatly as this figure is investigating elevational trends rather than abundance. CNM1 has a greater elevational range leading to more bins than CNM2 and CNM3.

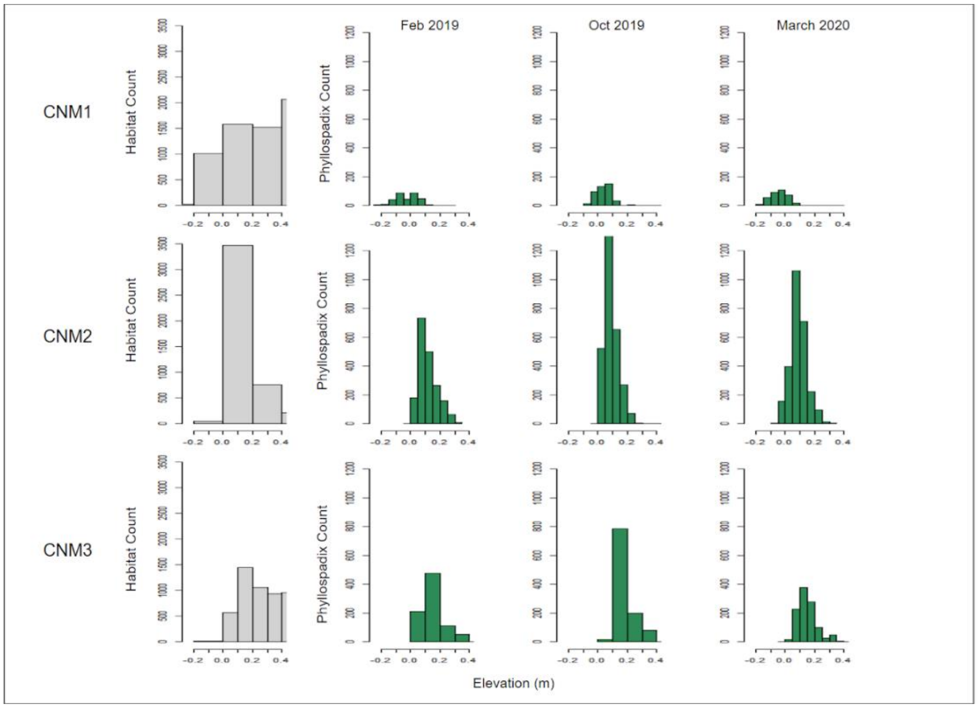

Figure 9: The amount of points within each elevation bin (grey) and the amount of points identified as *Phyllospadix* plotted against elevation (green) February 2019, October 2019 and March 2020. *Phyllospadix* does not display higher abundance as elevation drops, which can be accounted for by the few or complete lack of points in these elevation bins at the sites.

Table 2. Total percent cover of *Phyllospadix* (green) and habitat (gray) within each site for each time point. Habitat is defined as rock substrate within -0.3m to 0.2m elevation. The proportion of *Phyllospadix* to available habitat was calculated by dividing the *Phyllospadix* percent cover by the habitat percent cover and multiplying by 100. This was then averaged over the three time points for each site.

Time point	Total percent cover	CNM1	CNM2	CNM3
Feb 2019	Phyllospadix	3.4%	20%	9.1%
Feb 2019	*Habitat	32.4%	42.7%	31%
Oct 2019	Phyllospadix	4.4%	29.8%	11.5%
Oct 2019	*Habitat	30.5%	60.2%	30.4%
March 2020	Phyllospadix	3.7%	27.8%	11.5%
March 2020	*Habitat	35.1	53.6%	32.5%
Average proportion of *Phyllospadix* in available habitat		**11.7%**	**49.6%**	**34.2%**

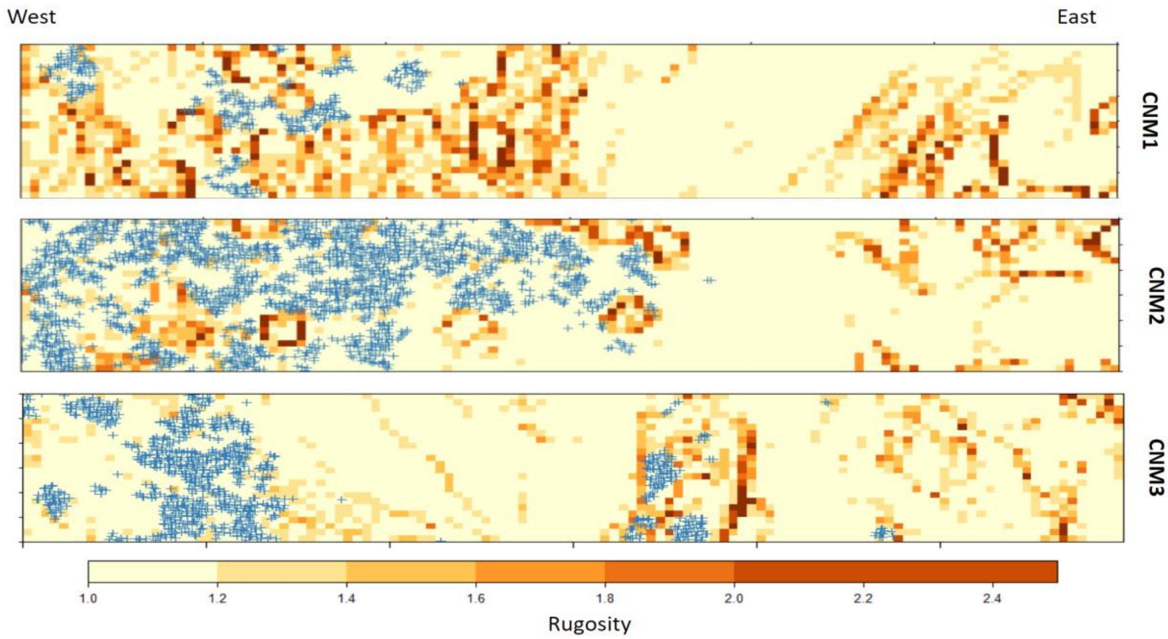

Figure 10: Structural complexity maps built from spatial data from February 2019 GPS measurements display an accurate representation of the topography of each site. Blue points (+) represent locations in the sites where *Phyllospadix* was identified. These maps provide visual evidence of the preference shown by *Phyllospadix* to inhabit areas of lower rugosity values.

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