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The role of colony morphology and substratum inclination on the distribution of *Eunicella verrucosa* on shallow reefs

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Abstract

Eunicella verrucosa plays an important role in shallow reefs, where they produce a complex 'sheet tree' morphology that supports a variety of benthic-dwelling organisms. *E. verrucosa* is considered 'vulnerable' by the IUCN Red List, which validates the importance of understanding the biotic and abiotic factors influencing the species morphology and survival. This study analyses how horizontal and vertical slope inclinations influence colony morphology. A population of 115 *E. verrucosa* colonies were observed at Plymouth's inner breakwater fort at 8–13.8m in depth. The influence of inclination on morphology was investigated by observing colony height, encrusting branch diameter and branch complexity for colonies on vertical and horizontal substratum. The influence of depth and substratum preference was also investigated as potential factors affecting colony morphology. Colonies on vertical surfaces were significantly taller and had wider encrusting branch diameters, primarily due to the speculated age of these colonies, as it was suggested that colonies on horizontal surfaces were more susceptible to abrasion and detachment from the substratum. The results suggest that steel substrate supports taller colonies as opposed to colonies attached to concrete despite the unstable nature of steel substrates, as it is more susceptible to flaking. However, further investigation is required to identify other biotic and abiotic factors, such as turf algae and hydrodynamics, that may be contributing to the variations seen in *E. verrucosa* morphology.

Keywords: *Eunicella verrucosa,* colony morphology, slope inclination, pink sea fan hydrodynamics, steel and concrete substrate, branch diameter, branch complexity.

Introduction

The pink sea fan *Eunicella verrucosa* is distributed along Britain and Ireland's south-to-west coasts, north-west Africa, and the western Mediterranean Sea (Hayward and Ryland, 1995). It is a temperate to cold water species with a depth range of 2 to 60m (Carpine and Grasshoff, 1975), representing a valuable species in sublittoral communities. *E. verrucosa* is an erect gorgonian coral that forms colonies by polyp iteration, where they branch profusely (Coz et al., 2012). A common feature of gorgonians is their habitat-forming three-dimensional structure, which allows for access to food and resources in the water column and the ability to alter their morphology (Sánchez et al., 2019). Branching increases surface area and the total number of polyps, thus allowing for increased nutrient intake (Sánchez et al., 2019) without the adhesion of the encrusted base spreading over the substratum (Jackson, 1979). These features are characteristic of 'ecosystem engineers', as they can modify, maintain, and create habitats (Jones et al., 1994). Despite *E. verrucosa* often being seen as separated from other colonies, individuals can grow in dense communities in some locations, creating a complex structure within a reef (Canessa et al., 2022). This structural complexity facilitates a range of sessile, mobile, and benthic-dwelling organisms with the provision of food, refuge, and suitable habitat (Stachowicz, 2001). Loss of habitat-forming species instigates change to associated coralligenous assemblages, reducing biodiversity (Piazzi et al., 2021). Thus, significant effort has been put into maintaining *E. verrucosa*, which is considered 'vulnerable' by the IUCN Red List (World Conservation Monitoring Centre, 1996). The UK Biodiversity Action Plan (BAP) lists them as a priority species, which was proposed due to the action needed for preventing biodiversity loss, as stated by the 1992 Convention on Biological Diversity (Pikesley et al., 2016).

Only in recent studies have the growth and morphology of *E. verrucosa* been closely observed. Generally, gorgonians are slow growing and take many years to recover from damage (Picton and Morrow, 2005). The age of colonies can be determined through growth ring analysis, where one ring indicates one year of growth (Hiscock, unpublished data). This growth can be highly variable, in the Mediterranean colonies were estimated to grow 0.6cm to 3.5cm year^{-1} (Munro and Munro, 2003), which is a representative estimate for other geographic locations, apart from British waters where growth was estimated to be slower, 1cm year^{-1} (Bunker, 1986). Sartoretto and Francour, (2012) formulated an equation that predicts the age of a colony based on its height. The equation suggested that the tallest colony they observed (42cm) would be at least 35 years old and colony heights of 10-20cm were estimated as 5-10 years old (Sartoretto and Francour, 2012). Growth rate decreases with colony age, which is relative to other gorgonians (Mitchell et al., 1993; Sartoretto and Francour, 2012). Thus, BAP's conservation action must be met; otherwise, the mortality of colonies with potentially 100 years of growth, (Hiscock, unpublished data) will 1require decades to recover and recolonise (Pikesley et al., 2016). *E. verrucosa* are vulnerable to mechanical damage and physical disturbance (Coz et al., 2012). Fishing pressure, such as scallop trawling, can have significant ecological effects on benthic assemblages and populations of *E. verrucosa* (Hall-Spencer and Moore, 2000). Hinz et al., (2011) found that scallop dredging did not majorly affect the size and abundance of *E. verrucosa*, this was likely because it has a more significant impact on flatter substrate as opposed to the complex topography that *E. verrucosa* favours. However, it does not protect populations from higher intensities of dredging that over more extended periods will lead to erosion of the substratum and the removal of associated assemblages (Hinz et al., 2011). No extensive reproductive data is available for *E. verrucosa*; however, the co-generic species *Eunicella singularis* are suspected to be lecithotrophic and have a mobile phase that lasts several hours to several days (Weinberg and Weinberg, 1979).

E. verrucosa requires a stable substratum for its basal holdfast to attach (Pikesley et al., 2016). This includes artificial substratum, bedrock and large boulders (Readman and Hiscock, 2017). The effect of substratum inclination on *E. verrucosa* morphology is yet to be researched. However, evidence suggests that water flow and circulation can significantly affect growth and survival (Peralta-Maraver et al., 2019; Edmunds, 1999). Inclination can potentially increase or decrease water flow depending on the angle of the substratum. On vertical slopes, water flows quickly over the surface due to gravity, which reduces the availability of oxygen and nutrients, potentially inhibiting the growth of organisms associated with the vertical substratum (Peralta- Maraver et al., 2019). However, Coz et al., (2012) speculated that vertical rocky walls that experience a higher current velocity would likely enhance the stability of colonies that must adapt to the harsher hydrodynamic forces. Compared to horizontal surfaces that are submitted to lower current velocities, likely due to increased frictional resistance (Cao et al., 2016). Understanding the influence of substratum and how varying inclinations may affect morphology is vital because colony branching is essentially a feeding adaption in gorgonians (Leversee, 1976). The morphological specialisation will greatly depend on current flow, velocity, and substratum characteristics (Leversee, 1976). Recognition that vertical substratum is favourable for colonial species is becoming more common in literature (Davies et al., 2013). With the implementation of more coastal defences, such as breakwaters understanding the colonisation of vertical slopes will allow us to put greater measures in place that protect these structures and the associated colonies (Firth et al*.,* 2016).

Edmunds, (1999) investigated the role of substratum inclination in the success of *Millepora alicornis.* The colonial fire coral is an influential reef builder with a calcareous skeleton that, like *E. verrucosa*, displays profuse ramifications and a "sheet tree" morphology (Hoeksema, et al., 2014). *M. alicornis* is distributed at depths of 1-40m (Lewis, 1989), where colonies on vertical surfaces were seen to have larger encrusting bases with longer perimeters and lower densities of branches (Edmunds, 1999). Colonies on horizontal surfaces were seen to have inhibited growth of the encrusting base due to algal turf and increased sedimentation (Edmunds, 1999). Turf algae can occupy space quickly and have often been considered one of the primary threats to colonial populations (Swierts and Vermeij 2016). Velimirov, (1976) investigated variations in *Eunicella cavolinii* morphology in relation to the intensity of water movement. Exposed colonies were found to have a larger fan surface and denser ramifications, allowing for increased resistance to water movement (Velimirov, 1976). However, with a larger fan surface, the chance of colonies tearing off the substratum increases (Velimirov, 1976). The optimal morphological adaptations in these exposed areas are long branches and a high abundance of polyps, which maximise food supply through the water column (Velimirov, 1976). Whereas in sheltered sites, it is advantageous to have narrower branches with higher structural complexity and fewer polyps (Velimirov, 1976). Water movement can cause sediment to accumulate, smothering immobile colonial species and can force mobile species to migrate (Foulquier et al., 2020). Wave exposure is one of the most dominant factors affecting the structure of benthic assemblages and colony settlement (Vaselli et al., 2008). Low-crested structures significantly dissipate wave energy and protect colonial assemblages (Powell and Allsop, 1985). A breakwater decreases water movement and sedimentation, facilitating higher recruitment and settlement rates among organisms (Vona et al., 2020). There can be negative consequences of submerged breakwaters on the inward side, as unnatural water flow can cause the accumulation of sediment, which negatively influences nourishment processes (Saengsupavanich et al., 2022). Moschella et al., (2005) suggested that breakwaters potentially alter the distribution and total abundance of epibiotic species, which controls algal growth. This indirectly affects colonial species competing with algae for space and resources, negatively influencing growth and survival. This study aimed to investigate the influence of substratum inclination on *Eunicella verrucosa* morphology, particularly the effects on colony height, encrusting branch diameter and branch complexity. Depth and temperature were investigated as potential variables affecting *E. verrucosa* morphology. Based on the observed literature the specific hypothesise were that: 1) Colonies on vertical surfaces are taller and have wider encrusting branch diameters. 2) At horizontal and vertical surfaces temperature variation is minimal. 3) Colonies at greater depths are taller and have wider encrusting branch diameter.

Methodology

Site description

The population of *Eunicella verrucosa* was observed at the sheltered site of Plymouth's inner breakwater (Fig.1) and was seen attached to artificial substratum consisting of steel and concrete. In 1865, the breakwater fort was built as a means of defence for Plymouth and its royal dockyards (Pye and Woodward, 1996). For many years, offshore and inshore dive training took place at the fort, where underwater cutting and welding took place as practice for divers. The underwater structure welders practiced on was used for the Certification Scheme for Welding Inspection Personnel (CSWIP). After commercial practice ceased, species accumulated on the CSWIP structure, creating an artificial habitat for *E. verrucosa*. In 1965, Colin Iwin started Project Glaucus, an experimental undersea habitat for human living (Heath, 1967). After the project failed, *E. verrucosa* colonised the habitat and is now seen thriving on the two-tonne 3.5m long cylinder which was left at the bottom of the breakwater fort.

Figure 1: Survey area (Plymouth Sound, Breakwater Fort, United Kingdom) and location of *Eunicella verrucosa* population (Map data provided by Google maps, 2023).

Biological data collection

SCUBA divers observed *E. verrucosa* (using air up to 60m) at Plymouth Breakwater fort (Fig.1). Divers surveyed colonies found on artificial structures around the fort. This consisted of the CSWIP, a steel structure with large beams providing both horizontal and vertical inclination for the growth of *E. verrucosa* at a ranged depth of 10.6 to 13.8m. Near the CSWIP, divers surveyed the lifting pontoon (steel substrate with a depth range of 8 to 9.4m), the Glaucus habitat (steel substrate with a depth range of 12.3 to 13.8m) and the fort wall (concrete substrate with a depth range of 8.3 to 11.6m). For each colony at the respective structure, divers measured the diameter of the encrusting branch, which is seen attached to the substrate and the inclination of the slope, which was observed as vertical or horizontal. Vertical inclination was classed as a 45° to 90° slope angle and horizontal as an inclination of 45° to 0°. Depth was measured using diver's gauges, which were calculated accordingly with fluctuating tides over the observation period. The Canon PowerShot G9 X Mark II was used to aid length and width measurements. For each colony, a photo was taken that captured the entirety of the organism's polyps. Photos of each colony contained a scale card held by the diver, which allowed for calculating colony length and width using the photo analysis software 'Tracker' (Brown et al., 2022). Colony branch complexity was determined subjectively based on the colonies' number of ramifications. A scale of 1 to 5 was used to indicate branch complexity (1 represents low complexity and 5 represents high complexity).

Temperature data

Temperature loggers were deployed at approximately 11m on a horizontal surface, a vertical surface, and a control site where *E. verrucosa* was absent. The temperature was recorded with a sampling interval of 30 minutes and a sampling resolution of 0.1°C. The loggers deployed at 11m took temperature readings for 48 days.

'Envlogger' was used to abstract the temperature data from the loggers after the course of the survey period.

Statistical analysis

The influence of inclination on colony morphology was analysed using RStudio (Posit team, 2022; Arnold, 2021; Fox and Weisberg, 2019; Pebesma and Bivand, 2005; Sievert, 2020; Wickham, 2016; Wickham, et al. 2019). Linear regression was used to investigate the relationship between colony height and encrusting branch diameter, depth and colony branch complexity. Multiple linear regression investigated the effect of slope inclination on the relationship between colony height and encrusting branch diameter, depth, and complexity. Linear regression models were used to examine the influence of colony branch complexity against colony length-to-width ratio and diameter. Multiple linear regression was used to test the significance of slope inclination in relation to colony branch complexity, colony length-to-width ratio and diameter. The temperature readings from the control site, vertical slope and horizontal slope were analysed using ANOVA. Bartlett's test and Levene's test were used to test for homogeneity of variances in the data set. The Welch two-sample t-test was used to test the significance of mean colony height associated with steel and concrete substrate, where ANOVA tested the effect of inclination on this relationship.

Results

There were 115 colonies of *Eunicella verrucosa* observed in the survey area (Plymouth inner breakwater) in the depth range of 8 to 13.8 m. Observed colonies were encrusted to artificial structures with concrete and steel-based substrate. The population ranged in height with the majority being small colonies (10-20 cm in height) representing 55% of the overall population, average colonies (20-30 cm in height) representing 36% and large colonies (>30 cm in height) representing 9% of the observed population. Sixty-one colonies were observed on vertical slopes and fifty-four on horizontal slopes. For each temperature logger (control site, vertical slope, and horizontal slope) there were 6912 temperature readings with a range of 9 to 11.4 °C. Between the three temperature loggers slope inclination had no significant effect on water temperature (ANOVA, F = 0.556, df = 2, P = 0.574). *E. verrucosa* colony height showed no significant difference with depth (linear regression model, t = 0.525, df = 113, P = 0.601) (see Figure 2) or inclination (multiple linear regression model, t = 1.310, df = 111 P = 0.193) (see Figure 2).

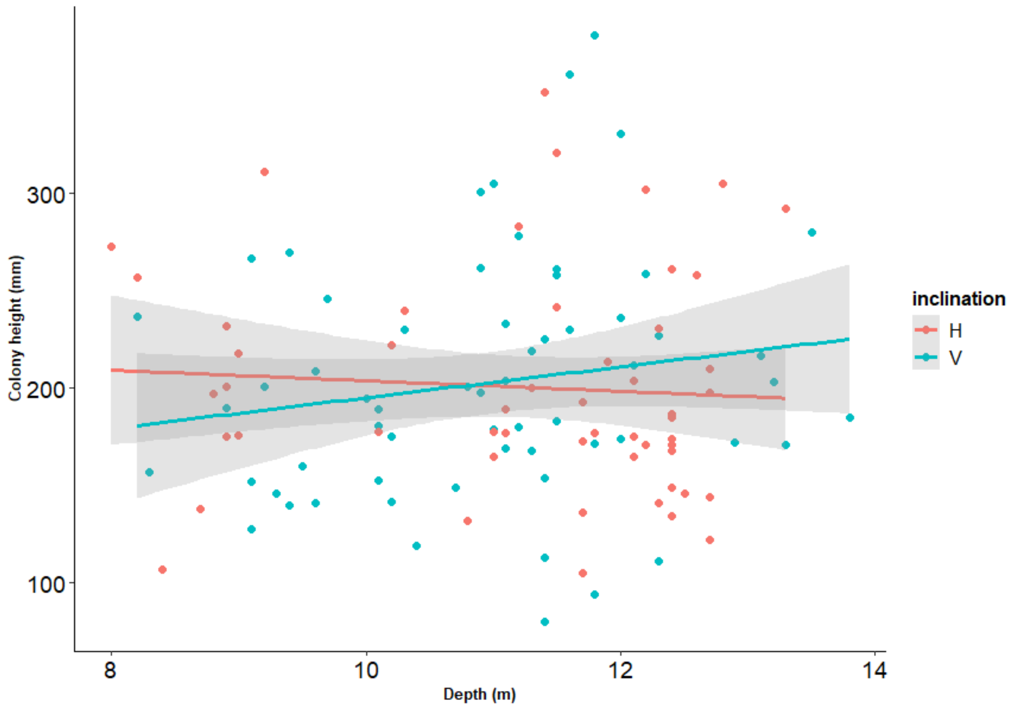

Figure 2: The relationship between depth and colony height of *Eunicella verrucosa*, based on the substratum inclination.

Encrusting branch diameter of *E. verrucosa* colonies ranged from 2 to 11 mm. There was a significant positive relationship between height and encrusting branch diameter (linear regression model, t = 2.946, df = 113, P<0.05) (see Figure 3). Slope inclination had no significant effect on the relationship between colony height and encrusting branch diameter (multiple linear regression, t = 1.351, df = 113, P = 0.179) (see Figure 3).

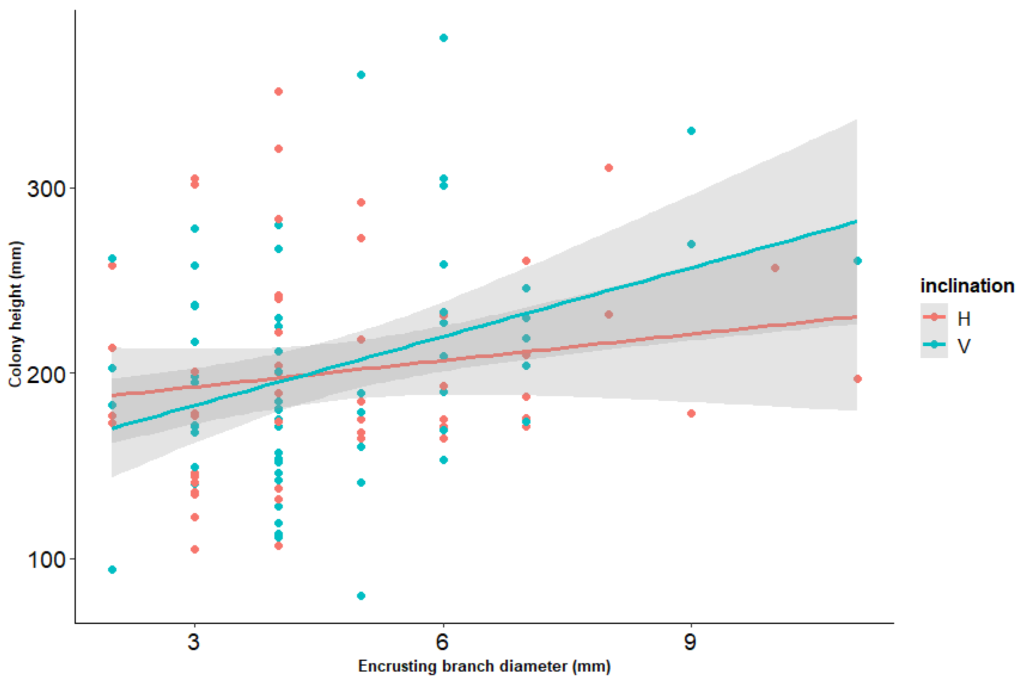

Figure 3: The relationship between colony height and encrusting branch diameter of Eunicella verrucosa, based on the substratum inclination.

Colonies observed on steel substrates were significantly taller than colonies observed on concrete substrates (Welch Two sample t-test, *t* = -2.1834, *df* = 37.637, *P*< 0.05) (see Figure 4). However, slope inclination had no significant effect on the relationship between colony height and substrate type (ANOVA, *F* = 1.708, *df* = 1, *P* = 0.1939).

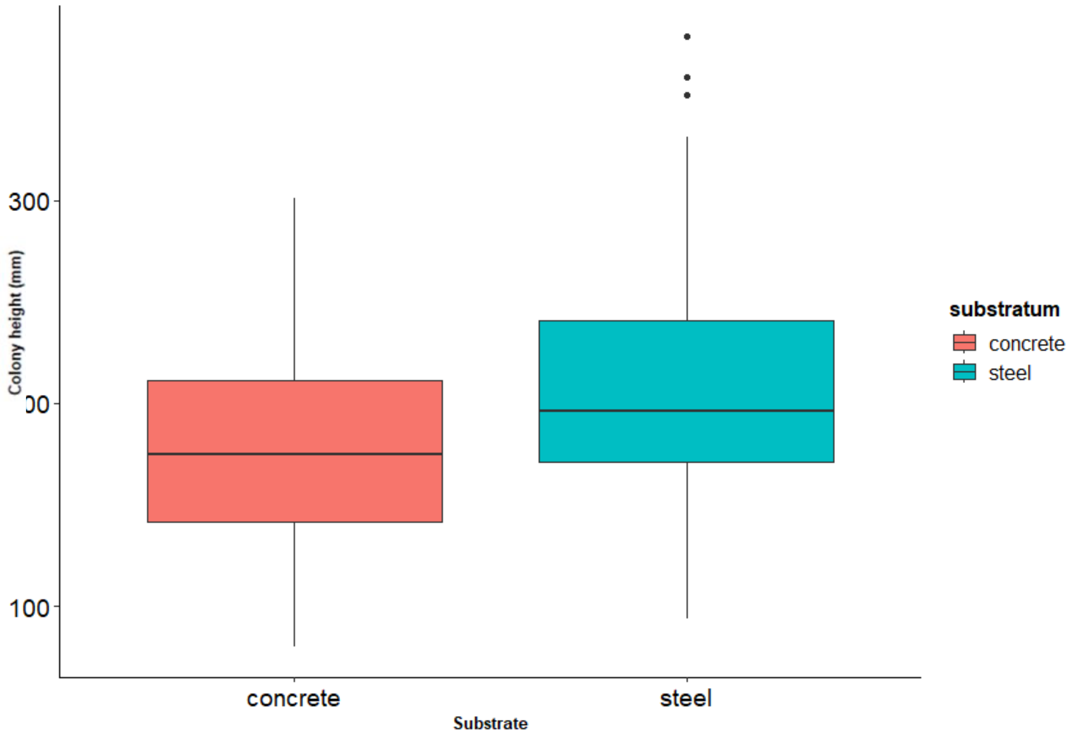

Figure 4: Variation in colony height of Eunicella verrucosa for concrete and steel substrates.

Wider, shorter colonies had a significantly larger branch complexity for both vertical and horizontal slope inclinations (linear regression model, *t* = -4.445, *df* = 111, *P*<0.05) (see Figure 5) While the slope inclination coefficients for this model did show a significant difference in the relationship between colony length to width ratio and colony branch complexity (multiple linear regression model, *t* = 0.154, *df* = 111, *P* = 0.878) (see Figure5).

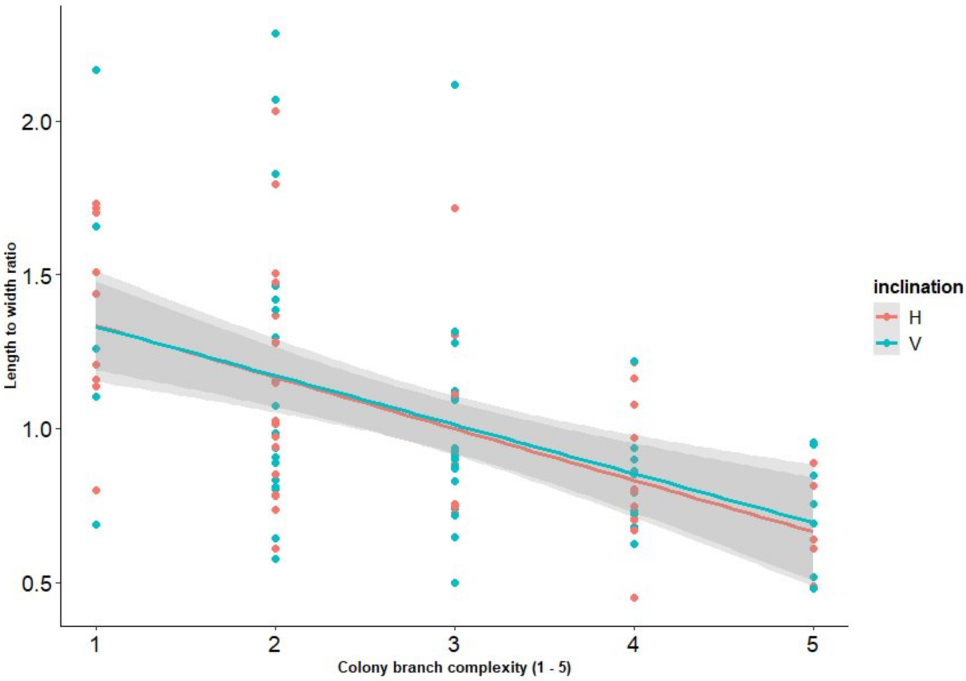

Figure 5: The relationship between colony length to width ratio and colony branch complexity of *Eunicella verrucosa*, based on the substratum inclination.

Colonies with a greater branch complexity had a significantly wider encrusting branch diameter (linear regression model, t = 8.716, df = 113, P<0.001) (see Figure 6) and a significantly taller colony height (linear regression model, t = 4.928, df = 113, P<0.001) (see Figure 6).

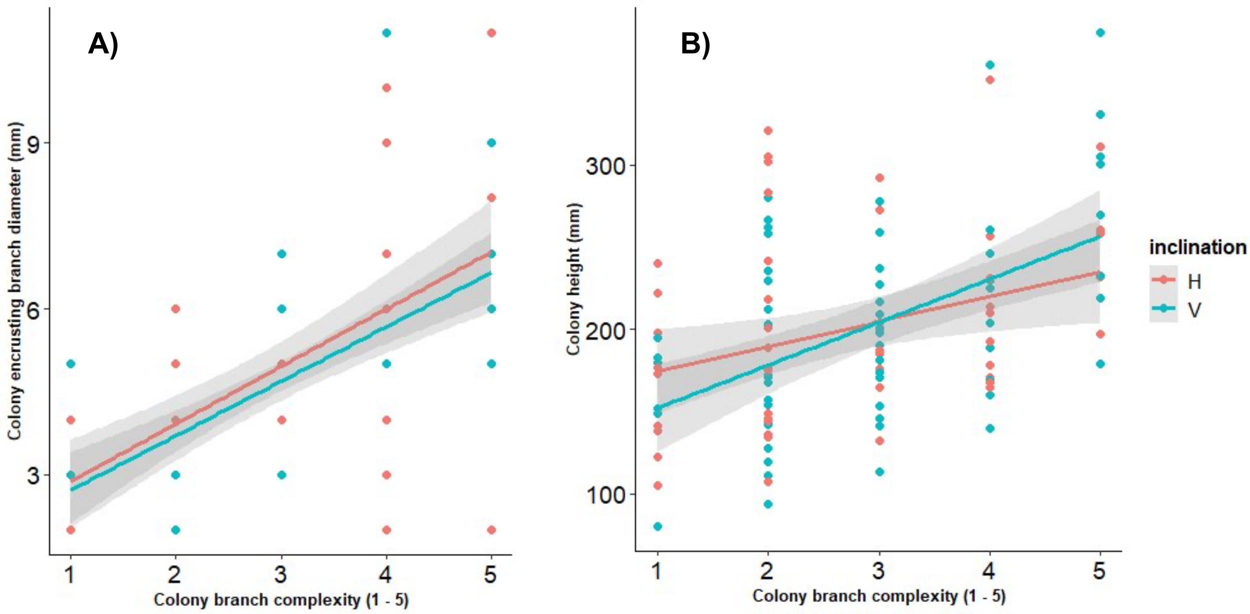

Figure 6: A) The relationship between colony encrusting branch diameter and colony branch complexity of *Eunicella verrucosa*, based on the substratum inclination. **B)** The relationship between colony height and colony branch complexity of *Eunicella verrucosa*, based on the substratum inclination.

Discussion

The outcomes of this research have provided insight into the influence of substratum inclination on *Eunicella verrucosa* morphology. The results suggest that the inclination of a slope does not significantly affect *E. verrucosa* morphology; however, through the interpretation of the figures provided, there are small morphological differences for colonies on vertical slopes showing larger colony heights, encrusting branch diameter and greater branch complexity. These results support current literature investigating the influence of slope inclination on the morphology of gorgonians and corals with a 'sheet tree' morphology (Velimirov, 1976; Edmunds, 1999; Coz et al., 2012). Encrusting branch diameter of colonies showed a significant positive relationship with colony height. The influence of slope inclination on this relationship revealed that colonies on vertical slopes had a greater encrusting branch diameter and height. These results support Edmunds, (1999) research on *Millepora alicornis* where he found that colonies on vertical surfaces had larger encrusting bases with longer perimeters. Algal turf accumulates sediment on horizontal surfaces, and the chance of sediment accumulating increases due to the horizontal profile (Birrell et al., 2005). This potentially explains the smaller colony height and diameter seen on horizontal surfaces, as sediments can inhibit coral settlement and growth (Birrell et al., 2005). Resistance to wave action on vertical slopes means that higher hydrodynamic forces will rarely affect colonies on vertical surfaces. Colonies on horizontal surfaces which are less protected are relatively short-lived, which suggests that colonies on vertical surfaces with a larger encrusting branch diameter is potentially due to greater age rather than faster growth.

The influence of depth on colony height showed no significant effect, which does not support findings from other literature but does support the hypothesis made. Cúrdia et al., (2012) found a significant difference in abundance of *E. verrucosa* between the depth ranges of 10-15m and 20-25m. This is likely because the lower beach profile limit is around 10m where wave action disturbs the seabed and from the turbulence created, it can increase the abrasion of colony tissue through suspended particles (Cúrdia et al., 2012). Turbulence also increases the risk of colonies detaching from the substratum (Cúrdia et al., 2012). Therefore, colonies at greater depths are at a lesser risk of detachment and abrasion due to decreased hydrodynamic pressure and colonies are likely older. Growth is linear with age; thus, height and encrusting branch diameter will increase over time (Sartoretto and Francour, 2012). The population of *E. verrucosa* in the observed area had a depth range of 8 to 13.8m. The linear regression model (Fig. 2) suggests a positive linear relationship for colonies on vertical slopes where taller colonies were found at greater depths. In contrast, horizontal surfaces showed a negative association with depth. A potential theory for this would be that inclination was the dominant factor affecting height, where colonies with wider encrusting branch diameters on vertical slopes are more resilient to detachment and therefore have developed longer parameters over time. The depth gradient was likely too small to attain significant height variations at depth; therefore, observing the influence of slope angle at a deeper site will provide insight into the potential morphological changes as depth increases.

Colonies observed on steel substrates were significantly taller than those on concrete. Fitzhardinge and Bailey-Brock (1989) found that the recruitment rate in juvenile corals, *Porites lobata* and *Pocillopora meandrina* was highest on steel substrate because more space was available and other fouling organisms showed a preference for concrete substrate. The results contradict the results of Creed and De Paula, (2007) who observed that despite the increased recruitment rate on steel substrate, *Tubastraea tagusensis* and *Tubastraea coccinea* colonies were smaller than colonies observed on concrete. They observed that steel was susceptible to flaking, making this substratum type unstable for colonies, which might explain why more space was available (Creed and De Paula, 2007). The colonies observed in this study do not support existing literature as colonies were taller on steel substrate than concrete substrate. Therefore, more analysis and investigation would be needed, to justify the substratum preference of *E. verrucosa* and how this influences colony morphology. Creed and De Paula, (2007) investigated colonisation rates on newly placed steel substrate, which do not account for long-term colonisation. To confidently determine whether the flaking of steel makes the surface unstable for *E. verrucosa*, you would need to determine whether flaking is occurring constantly over time or whether it only occurs for surface layers of steel.

Very few studies have investigated how slope angle influences temperature; however, it was expected that the slope angle would not significantly affect temperature. Generally, slope angle may affect the availability of light reaching the substratum, where vertical slopes receive less light due to shade, which will affect temperature to a small degree (Murdock and Dodds, 2007). Light will often limit benthic algae growth (Béchet et al., 2013), which in theory reduces algal turf, indirectly benefiting *E. verrucosa* growth and settlement (Edmunds, 1999). Based on limited literature and the slight variation in temperature across varying slope angles, it can be concluded that temperature has no significant effect. Investigating the influence of light availability on the photosynthesis of *E. verrucosa* could provide an understanding of whether growth is optimal on darker vertical slopes or lighter horizontal slopes.

The results indicated greater colony branch complexity was associated with wider, shorter colonies and wider encrusting branch diameters. Slope inclination did not appear to affect this relationship, which contradicts previous literature (Velimirov, 1976). Velimirov, (1976) observed that higher intensities of water movement influenced *Eunicella cavolinii* morphology, where colonies had a denser branch complexity. Therefore, it was expected that colonies on horizontal slopes would have a greater branch complexity as an adaptation to stronger water flow. However, Edmunds, (1999) concluded that other factors could influence branch complexity, such as chlorophyll content and biomass. As a result, it cannot be concluded that slope inclination effects branch complexity without exploring other influential factors, such as water flow.

Conclusion

Understanding the influence of slope inclination on colony morphology will allow us to understand *E. verrucosa's* specific adaptations that promote growth and survival. In addition, we must understand these factors when physical disturbance to these habitats occurs, such as trawling and the addition or removal of artificial structures. The result of these processes may cause the removal of this species from benthic communities and with *E. verrucosa* playing such an important role in biodiversity, the conservation of this species is vital. A general limitation of this study was the absence of hydrodynamic assessment and the influence this has on morphology. Many factors affect morphology, yet substratum inclination, which has an important influence on distribution, is currently understudied. Another critical factor to consider is the location of the *E. verrucosa* population at Plymouth's inner-breakwater fort. The breakwater receives minimal wave action, so we can only speculate on the influence of hydrodynamics on morphology. The minimal wave action may explain why the population has settled at shallower depths, as wave action typically causes colonies to detach from the substratum in the 0-10m depth zone (Cúrdia et al., 2012). However, with the protection of the breakwater, colonies are at a lesser risk of detachment and have a greater chance of survival. To better our understanding of the effect of slope inclination on colony morphology, observing colonies at an exposed site could provide insight into what degree water movement affects distribution and how this changes over varying slope angles. Turf algae could also be observed on vertical and horizontal surfaces to assess its influence on morphology. By measuring how this affects morphology, it could provide some understanding of the unexplained results of this study and better our knowledge of *E. verrucosa's* complex morphology.

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