MARCOS AGIANI TIEPPO JUNIOR

APPLIED STRUCTURE FROM MOTION PHOTOGRAMMETRY: HABITAT COMPLEXITY AND SPONGE DISTRIBUTION IN NATURAL ROCKY REEFS ADJACENT TO RIA FORMOSA (SOUTHERN PORTUGAL)

UNIVERSITY OF ALGARVE
Faculty of Sciences and Technology
2020

MARCOS AGIANI TIEPPO JUNIOR

APPLIED STRUCTURE FROM MOTION PHOTOGRAMMETRY: HABITAT COMPLEXITY AND SPONGE DISTRIBUTION IN NATURAL ROCKY REEFS ADJACENT TO RIA FORMOSA (SOUTHERN PORTUGAL)

Masters in Marine Biology

Thesis done under the supervision of:
Prof. Dr. Duarte Nuno Ramos Duarte
Prof. Dr. Eduardo Nuno Borges Pereira

UNIVERSITY OF ALGARVE
Faculty of Sciences and Technology
2020

APPLIED STRUCTURE FROM MOTION PHOTOGRAMMETRY: HABITAT COMPLEXITY AND SPONGE DISTRIBUTION IN NATURAL ROCKY REEFS ADJACENT TO RIA FORMOSA (SOUTHERN PORTUGAL)

Declaração de autoria de trabalho

Declaro ser o autor deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

I hereby declare to be the author of this work, which is original and unpublished. Authors and works consulted are properly cited in the text and included in the reference list.

(Marcos Agiani Tieppo Junior)

(Marcos Agiani Tieppo Junior)

Acknowledgements

I thank Professors Duarte Duarte and Eduardo Pereira for their support and guidance during this work.

I thank my parents, Marcos and Odete, for their whole support, not only during these last two years, but for my whole life.

A big thank you for my friends, especially the ones that pure chance brought to me when I first got here: Maria, Milla, Nathalie and Stéphanie. This would have been so boring without you...

Finally, I want to thank Alexandra Elbakyan for socialising science, and Stack Overflow for socialising codes. This, and many other works, would be impossible without you.

Resumo

O ambiente marinho, e as propriedades da água como fluido, expõem os organismos que nele habitam a uma força de arrasto muito maior do que o ambiente terrestre. Essa condição aumenta a necessidade dos organismos de procurarem por abrigos e refúgios. No caso dos organismos invertebrados sésseis, como as esponjas, que têm na fase planctônica larval o seu principal, ou único, modo de dispersão, a busca por um local ideal para o desenvolvimento é ainda mais importante, já que não podem se deslocar posteriormente. Portanto, o assentamento larval é um processo de vital importância para esses organismos, e leva em conta uma série de fatores, como luminosidade, presença de outros organismos e a topografia do fundo. Dessa forma, o estudo das estruturas que fornecem substrato para o assentamento larval, assim como de seus diferentes componentes, tanto bióticos como abióticos, é necessário para entender sua influência na distribuição dos organismos. Uma propriedade dos habitats, muito utilizada atualmente nesse tipo de estudo, é a complexidade do habitat.

Ecossistemas marinhos recifais em todo o mundo estão registrando perda de complexidade do habitat, uma característica ambiental que, de uma forma mais qualitativa, está relacionada com a variedade de elementos que constituem o habitat, como rochas, troncos de árvores ou algas. De uma forma mais quantitativa, pode ser descrita por variáveis que quantificam o arranjo espacial desses elementos, seus tamanhos, abundâncias, entre outras propriedades. Assim, a

complexidade do habitat é gerada tanto por elementos abióticos, como bióticos, e é uma característica ambiental essencial, não só para o assentamento larval, mas também para as relações ecológicas. A complexidade apresentou uma correlação positiva com a biodiversidade na maioria dos estudos já realizados. Apesar de os mecanismos por trás dessa relação não estarem totalmente claros, diferentes explicações foram propostas, como uma maior exploração de microhabitats, que geram mais nichos, uma maior produtividade gerada por uma maior área superficial, e uma maior riqueza de espécies devido à disponibilidade de refúgios de diferentes tamanhos.

Este trabalho, realizado no âmbito do projeto de investigação MaréFormosa, que decorre na Faculdade de Ciência e Tecnologia (FCT) da Universidade do Algarve, estuda a relação entre a complexidade do habitat, e a abundância e distribuição de esponjas em dois recifes rochosos no Sul de Portugal, ambos situados a aproximadamente 12 m de profundidade. Distribuição essa, que está fortemente relacionada com o assentamento das larvas das espécies encontradas, que são o principal mecanismo de dispersão para invertebrados bentônicos. A fim de analisar essa relação e testar a hipótese de uma correlação positiva, foram construidos modelos 3D, com escala, das áreas de estudo com a utilização de fotogrametria (Structure from Motion photogrammetry - SfM), uma técnica que utiliza um conjunto de fotografias com um grau mínimo de sobreposição para a construção dos modelos. No lugar das fotografias, foram utilizados frames individuais retirados de vídeos gravados com uma GoPro Hero 3 nos dois recifes escolhidos. Os vídeos foram feitos por um mergulhador, que percorreu uma longa extensão dos recifes ao longo de um transecto, mantendo uma distância de aproximadamente 1 m acima do fundo. Após a construção dos modelos, foram calculadas variáveis relacionadas com a complexidade do habitat. Valores de dimensão fractal (fractal dimension - FD) em três diferentes escalas (0.15 - 0.30, 0.30 - 0.60, 0.60 - 1.80 m), rugosidade e inclinação foram calculados para áreas de 2 x 2 m aleatoriamente amostradas a partir dos modelos gerados para os diferentes segmentos dos recifes, juntamente com a abundância de cada uma das espécies de esponja presentes em cada área.

A fim de analisar o potencial da SfM para a representação de estruturas complexas, como as das esponjas, também foram construidos dois modelos com escala de uma mesma esponja, utilizando dois conjuntos distintos de fotografias de alta resolução. Os dois modelos foram comparados com relação à area superficial e volume calculados, com o intuito de aferir a precisão da técnica para esse tipo de análise. Para a estimativa de precisão dos modelos dos recifes, foi construído um modelo com imagens de objetos de dimensões conhecidas, obtidas no mesmo ambiente dos recifes e com a mesma técnica, ou seja, sob as mesmas condições dos vídeos utilizados para os modelos dos recifes. Após fornecermos a escala para o modelo, as distâncias geradas pelo mesmo foram comparadas com os tamanhos reais dos objetos, fornecendo o valor do erro.

Os resultados mostraram uma afinidade da esponja *Phorbas* sp., uma das duas com maior abundância, por valores mais altos de FD no intervalo de 0.15 - 0.30 m, relacionado com a cobertura de algas, e de rugosidade e inclinação, indicando influência do terreno e do substrato na distribuição dessa espécie. A proximidade com a cobertura de algas pode ser um indicativo de um estímulo químico para o assentamento larval, produzido pelas algas, ou mesmo dos efeitos da cobertura algal na incidência de luz, produzindo zonas de sombra (preferíveis para larvas com fototaxia negativa), e no fluxo de água local, reduzindo o mesmo, o que também favoreceria o assentamento larval. Um comportamento de agregação também foi visto nessa espécie, com muitos adultos localizados próximos uns dos outros, o que indica a possibilidade de existência de um estímulo químico produzido pela própria espécie para o assentamento larval. *Spongia* sp., a outra esponja mais abundante, não apresentou o mesmo comportamento de agregação, e mostrou afinidade por valores mais altos de FD nos intervalos de 0.3 - 0.6 e 0.6 - 1.8 m, relacionados com estruturas maiores, como fendas. Alguns indivíduos dessa espécie realmente estavam localizados nas bordas de

fendas. No entanto, ambas as espécies apresentaram altas abundâncias em áreas expostas, sugerindo que os ambientes de baixa luminosidade não apenas fazem com que essas espécies não apresentem o típico comportamento das esponjas, de assentamento em áreas protegidas da luz, como também podem favorecê-las em detrimento das algas, que normalmente são suas competidoras por espaço. SfM gerou modelos 3D de alta resolução, com alta precisão (erros menores que 2%), detalhe suficiente para as menores escalas analisadas e uma grande área de cobertura para as maiores, provando ser uma técnica adequada para análise de complexidade e para mapeamento de habitats, inclusive para a nova aplicação, utilizada neste trabalho, de localização de organismos diretamente nos modelos. Também se mostrou adequada para a modelagem das estruturas de esponjas, representando bem os ósculos e a cobertura algal das esponjas, o que mostra o potencial para estimativas de área de cobertura e estudos de crescimento. Apesar de não ter havido uma clara correlação positiva entre a complexidade do habitat e a abundância de esponjas, houve indicações de uma influência das características do fundo na distribuição de esponjas, com diferenças entre as espécies.

Palavras chave: Fotogrametria; Esponjas; Complexidade do habitat; Assentamento larval

Abstract

Marine ecosystems all over the world are registering loss of habitat complexity, a key environmental feature for ecological relations, that presented a positive correlation with biodiversity in most previous studies. This work investigates the relationship between habitat complexity, and the abundance and distribution of sponges in two rocky reefs in Southern Portugal. To assess this relationship and test the hypothesis of a positive correlation, 3D models of the study areas were built using Structure from Motion photogrammetry (SfM), and habitat complexity related variables were calculated. Fractal dimension (FD) in three scales (0.15 - 0.30, 0.30 - 0.60, 0.60 - 1.80 m), rugosity and slope values were calculated for 2 x 2 m areas randomly sampled from models of different segments of the reefs, together with the abundance of each species of sponge present in each area. The results showed an affinity of *Phorbas* sp., one of the two most abundant sponges, for higher values of FD in the 0.15 - 0.30 m interval, related to algal cover, and of rugosity and slope, indicating an influence of the terrain on this species distribution. An aggregating behaviour was also noticed for this species. *Spongia* sp., the other abundant sponge, together with *Phorbas* sp., presented high abundances in exposed areas, suggesting that the low light environments not only make them avoid the typical sponge behaviour of settling in areas protected from light, but also might favour them in relation to algae. SfM generated high resolution models, with enough detail for the smaller scales and a wide area cover for the greater ones, proving to be an adequate technique for complexity analysis and, as a new application, for organisms localisation. Although there was not a clear positive correlation between habitat complexity and sponge abundance, there were indications of an influence of the terrain characteristics on the sponge distribution, with differences between species.

Keywords: Photogrammetry; Structure from Motion; Sponges; Habitat complexity; Larval settlement

Contents

List of Tables

List of Figures

List of Abbreviations

CCA	Canonical Correspondence Analysis
DEM	Digital Elevation Model
FD	Fractal Dimension
MD	Difference between means
N	Abundance of sponges
SfM	Surface from Motion photogrammetry

1

Introduction

1.1 Why to study sponges and ocean structures

The marine environment is occupied by water, which is a medium capable of dragging the organisms with a much greater force than the air in terrestrial environments. This brings the necessity of the organisms living in the marine environment to adapt to these conditions. Therefore, it can be said that these organisms are much dependent on the existence of structures that can provide refugia, not only from currents, but from predators. At the same time, it allows sessile invertebrates in their initial planktonic life stages (larvae) to move and settle where they find more fitting, even if it takes a relatively long time (Harrison and Wallace, 1990). In many cases, this is the organism's only mechanism of dispersal. Several advantages can come with this kind of life stage, such as wide distribution of offspring and gene flow (Platt, 1993). This process is of vital importance for the successful survival and development of the organism into the adult phase, besides influencing the distribution of the organisms and, consequently, the dynamics of populations (Cowen and Sponaugle, 2009).

There are different environmental cues that indicate settlement places for larvae, the chemical and biotic being the most studied ones, like the presence of bacterial biofilms (Hadfield and Paul, 2001; Hadfield, 2011; Lau *et al.*, 2005), host organisms (Swanson *et al.*, 2004; Williamson *et al.*, 2000), and conspecifics (Ettinger-Epstein *et al.*, 2008; Huggett *et al.*, 2006). However, coastal zones present structures, like rocky reefs, which reduce the flow due to bed friction (Cowen and Sponaugle, 2009), and favour larval settlement. Although important, the influence of these structures on the water flow and larval settlement are not well studied, with a few studies focusing only on the role of microtopography (Crisp and Ryland, 1960; Hills *et al.*, 1999; Whalan *et al.*, 2015), at scales close to the dimensions of the larvae.

Therefore, it can be said that larvae are much dependent on the existence of structures that can provide a substrate for settlement (Pineda and Caswell, 1997). This brings the importance of understanding how 3D structures forming marine habitats influence the diversity and distribution of species. A property of the habitats, directly related to these structures, that is currently used in a range of studies, is habitat complexity.

Among the sessile invertebrates that inhabit rocky benthic environments in temperate zones, there are the sponges (Bell and Barnes, 2000a). These organisms consume particulate organic matter, and dissolve these with the help of symbiotic microbes, while some of them have photosynthetic symbionts (Wulff, 2012). In turn, they can be predated by animals like nudibranchs and sea stars (Wulff, 2012), or even be victims of bulldozing by sea urchins (Maldonado and Uriz, 1998). Their distribution can be regulated by a series of factors, such as substrate type (Bell and Barnes, 2000b), sedimentation (Carballo, 2006), depth (Bell and Barnes, 2000c) and ecological interactions (Wulff, 2012). In rocky reef habitats, they have important ecological roles, like bentho-pelagic coupling and microhabitat provision for other organisms (Bell, 2008), but they can have many others, on different environments, such as bioerosion (Cruz-Barraza *et al.*, 2011; Nava and Carballo, 2008; Ward-Paige *et al.*, 2005), contribution to primary production (Wilkinson, 1987; Cheshire and Wilkinson, 1991), predation protection through association with other organisms (Clavico *et al.*, 2006; Marin and Belluga, 2005; Schejter and Spivak, 2005), settlement substrate (Bell, 2008) and biological disturbance through competition (Bell and Barnes, 2003; Diaz and Rützler, 2001; Rutzler and Ruetzler, 2003). Because of such an extensive variety of ecological roles, and their presence in rocky benthic habitats in all regions of the world, from tropical to polar, sponges should not be ignored in conservation actions nor during the design and monitoring of marine protected areas.

1.2 State of the art

1.2.1 Habitat complexity

The first study quantitatively analysing the effects of the complexity of an habitat on species diversity was published by MacArthur and MacArthur (1961). Since then, this has been a recurring theme in ecology, in both terrestrial and marine environments (with much more attention given to the marine), producing many studies which positively correlate habitat complexity with species richness and abundance. Although almost 60 years have passed, there is still discussion on the mechanisms that are behind this relationship.

A more qualitative view of marine habitat complexity is related to the variety of elements that constitute the habitat, like rocks, tree logs, kelps or seagrass. However, for a more in-depth analysis of complexity and its effects on biodiversity, a quantitative view, more focused on the structures themselves, is necessary. Tokeshi and Arakaki (2012) list five traits to be taken into account in habitat complexity assessments: scales of habitat complexity; diversity of complexity-generating elements; spatial arrangement of elements; sizes of elements; and abundance/density of elements. The majority of studies does not make analyses that comprehend all these traits, measuring variables that account for only one of them. Among those are fractal dimension, a very popular method for habitat complexity quantification used in recent studies (Fukunaga *et al.*, 2019; Leon *et al.*, 2015; Wildhaber *et al.*, 2003; Young *et al.*, 2017), which only emphasises the last trait, or substratum diversity (Öhman and Rajasuriya, 1998), which considers only the second one. It is important to consider more attributes of complexity, especially the scale of perception by the organisms of interest, which influence the effect of structural habitats (Kovalenko *et al.*, 2012).

Habitat complexity appears as one of the key environmental features that influences local biodiversity and ecological relations, especially in reef ecosystems (Graham and Nash, 2013; Lingo and Szedlmayer, 2006; Luckhurst and Luckhurst, 1978). Its effects were studied on organisms assemblages (Cranfield *et al.*, 2004; Hauser *et al.*, 2006), local biodiversity (Cranfield *et al.*, 2004; Darling *et al.*, 2017; Fabricius *et al.*, 2013; Komyakova *et al.*, 2013; Lingo and Szedlmayer, 2006), and predator-prey interactions (Grabowski *et al.*, 2008; Jana and Bairagi, 2014; Warfe and Barmuta, 2004). On the other hand, the effects on the general food web theory, trophic coupling, ecosystem stability, among others, are still largely unexplored (Kovalenko *et al.*, 2012). Its effects on the settlement of sessile invertebrates larvae, and on parameters that can influence it, like organic matter interception and microhabitat availability, are also largely unknown.

Although the real mechanisms behind the relationship between habitat complexity and increased richness and abundance are not entirely clear, many studies have detected it (Gilinsky, 1984; Harding and Mann, 2001; Kelaher and Carlos Castilla, 2005; Matias *et al.*, 2010; St. Pierre and Kovalenko, 2014), even showing its role in generating biodiversity (Price *et al.*, 2011). Most of these studies explore the diversity of fish species, with a lack of studies about the diversity of sessile invertebrates. Different explanations have been proposed for this relationship, including a greater exploration of microhabitats, which generates more niches (Gratwicke and Speight, 2005a; Willis *et al.*, 2005), a higher productivity caused by a greater surface area (Gratwicke and Speight, 2005a), and a higher species richness increased by the availability of refugia with different sizes (Luckhurst and Luckhurst, 1978). The last one can even determinate the dominance of a habitat by algae or coral, since key herbivores that predate on macroalgae use refugia to avoid predation, increasing herbivory and favouring coral dominance (Lee, 2006).

The terrain alone is not the only complexity creating agent. Sessile suspension feeders, which depend a lot on the structure of the habitat, since it influences the settlement of these organisms and of particulate food, cause an effect on other benthic organisms that depend on the habitats created by them (Burlakova *et al.*, 2012; Tokeshi and Arakaki, 2012). A variety of information on habitat complexity has been gathered recently, but there is still much to understand on the mechanics and implications of the structural complexity of habitats and its influences on ecological communities (Kovalenko *et al.*, 2012; Tokeshi and Arakaki, 2012).

When it comes to measuring the complexity of rocky habitats, studies have used from "chain and tape" techniques (Kostylev *et al.*, 2005) to wheels of different sizes to account for the scale (Wilding *et al.*, 2007). More modern methods to analyse the topographic complexity of reefs are, many times, cost-prohibitive and demand highly specialised personnel, like LIDAR (Brock *et al.*, 2004; Noernberg *et al.*, 2010) and acoustic multibeam observations (Andréfouët *et al.*, 2009; Lucieer, 2007), the first being also limited to shallow areas. Recently, Tokeshi and Arakaki (2012) developed a method based on the minimum-angles present on surface forms, capable of better characterising structures that generate complexity.

Regarding benthic organisms with complex 3D structures, like corals and sponges, there are still limitations on their description and quantification of their cover area on the substrate of reefs, since it is many times calculated as a 2D cover (Olinger *et al.*, 2019). To estimate growth and surface area of structurally complex sessile benthic organisms, like sponges, the methods are in general destructive, like the ones developed by Marsh (1970); Meyer and Schultz (1985); Stimson and Kinzie (1991). Even more recent methods still rely on the removal of the organisms, like radiocarbon dating (Fallon *et al.*, 2010).

As an alternative to these methods, for having a much lower cost, being nondestructive and producing accurate results, Structure-from-Motion photogrammetry (SfM) is now among the most used techniques to analyse the complexity of reef structures (Burns *et al.*, 2015b,a; Guo *et al.*, 2016; Leon *et al.*, 2015) and also to estimate sessile benthic organisms growth rates (Bennecke *et al.*, 2016; Bythell *et al.*, 2001; Ferrari *et al.*, 2017; Olinger *et al.*, 2019).

1.2.2 Photogrammetry

When digital photogrammetry first raised as a powerful tool for 3D modelling, using 2D photographs to reconstruct a 3D scene, it still relied on the necessity of stereoscopic photographs, which means that the scene should include previously specified targets with known 3D positions (Snavely *et al.*, 2008; Westoby *et al.*, 2012). SfM, on the other hand, does not have this necessity, since the geometry of the scene, camera positions and orientations are all solved automatically by a bundle adjustment procedure through the automatic identification of matching features in multiple images (Snavely *et al.*, 2008; Westoby *et al.*, 2012). Therefore, with SfM, simply estimating the camera's focal length as part of the bundle adjustment can produce good results (Snavely *et al.*, 2008).

With the relatively recent advances in computational processing power and the development of cloud computing, techniques that once demanded extremely expensive computers, that sometimes were not even available, now can be done even with personal laptops. SfM is one of these techniques, which uses a set of 2D photographs to create a 3D topographic reconstruction. Softwares like Agisoft® Metashape and Meshroom are able to create 3D textured mesh models from sets of pictures that present a minimum degree of superposition between each other. Some softwares also allow cloud computing, which is a very useful resource when working with a very large set of images, since all the heavy operations of the mesh creation are done in remote servers, allowing to simply download the final result and analyse it.

1.2.3 Ecological applications

The monitoring of marine ecosystems is getting more important each day, especially in a scenario where climate change and other forms of anthropogenic impacts are constant threats. A number of studies have described the loss of structural complexity that ecosystems around the world are suffering, and the impact it has on local fauna (Alvarez-Filip *et al.*, 2009; Fabricius *et al.*, 2013; Graham *et al.*, 2007; Gratwicke and Speight, 2005b; Pratchett *et al.*, 2008; Sano *et al.*, 1987; Wilson *et al.*, 2006). Therefore, it is important to apply robust methods to measure habitat complexity related variables, in order to quantify their influence in the condition of the ecosystem and provide data to a better analysis of the role and importance of the reef's services to the ecosystem. These kinds of analyses and the development of reliable ecological models are much more complete and precise when having a 3D representation of the habitat area. A 3D scaled model of a reef provides high-resolution data on physical properties and can be used to generate ecological models and monitor changes in the habitat (Burns *et al.*, 2015b; Raoult *et al.*, 2016).

The large quantities of data in high resolution, acquired in a low-cost manner and in a relatively short time, make SfM one of the most popular techniques nowadays for ecology studies (Agudo-Adriani *et al.*, 2016; Burns *et al.*, 2015b, 2019; Sánchez *et al.*, 2009), habitat mapping and characterisation (Abadie *et al.*, 2018; Anelli *et al.*, 2019; Gerdes *et al.*, 2019; Storlazzi *et al.*, 2016), and habitat monitoring (Marre *et al.*, 2019). It also allows to collect data using autonomous underwater vehicles (AUVs) or remotely operated vehicles (ROVs), which are much used in archaeology (Drap *et al.*, 2015; Nornes *et al.*, 2015; Yager *et al.*, 2019). Surface topography, obtained through SfM, is of high importance for understanding the influence of the terrain on larval settlement and species distribution, since it provides detailed and versatile information at different scales, which can be used in a wide range of different analyses.

1.3 Objectives and title justification

This research, done within the MaréFormosa project, of University of Algarve, had three objectives: to investigate the relationship between habitat complexity variables and the abundance and distribution of sponges two natural rocky reefs in Southern Portugal; to assess the adequacy of SfM for this type of study; and to assess the potential of SfM for the accurate characterisation of the 3D structures of marine sponges. The SfM models are also used to locate organisms (sponges), an uncommon use in previous studies. It is hypothesised that habitat complexity, regulated by local topography and the presence of organisms in the substrate, like algae and gorgonians, has a positive correlation with abundance of marine sponges. Marine sponges were chosen mainly because of their easy localisation in the models and vast presence in the reefs, while other organisms, especially the small and vagile ones, would require in situ surveys. Besides that, being sessile, their locations should, in theory, reflect preferences for certain substrate characteristics. Different variables such as fractal dimension, rugosity and slope, for representing habitat complexity were studied, as well as their significance in the identification of the spatial distribution of marine sponges. Although not done in this work for being out of scope, precise organisms identification and more analyses of habitat conditions, like local luminosity and currents, would enrich this type of study, bringing a more complete view of the local ecology.

2

Methods

2.1 Study area and field work

The first studied site was a rocky reef, Pedra da Cacela, located in the Cacela formation, approximately 1.5 miles from the coast of Cacela Velha village, in the Southern coast of Portugal (Figure 2.1), at a depth of 12 m. The second was another rocky reef, located 1.3 miles from the coast and called Pedra do Lacém (12 m deep), also in the Southern coast of Portugal (Figure 2.1). For practicality, they will be referred to as Cacela and Lacém reefs from this point onwards.

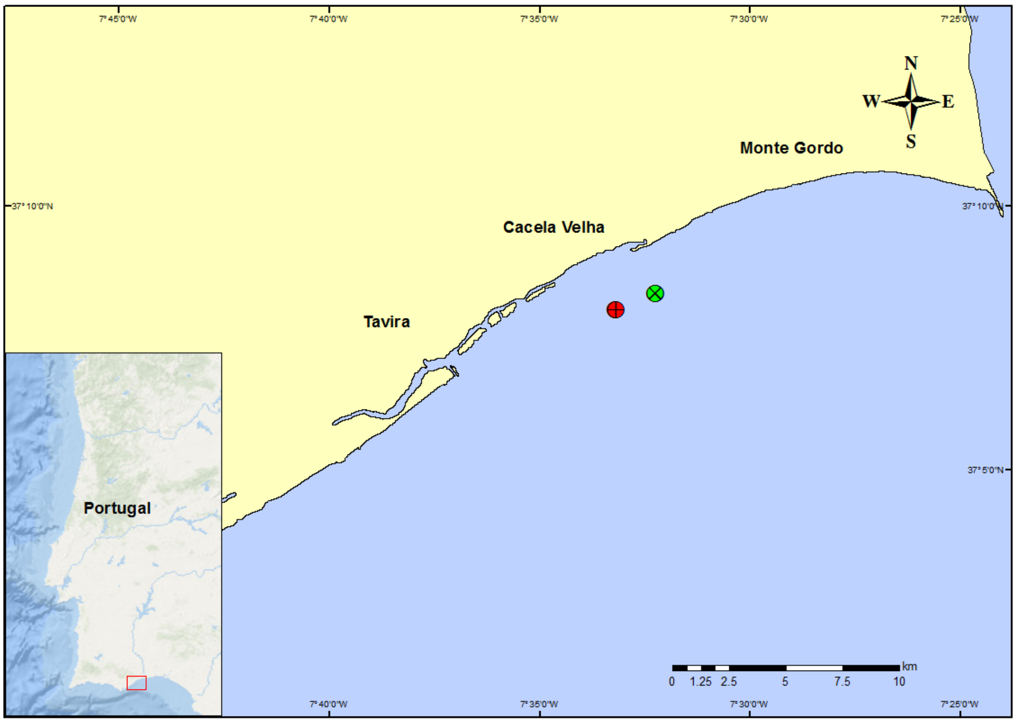


Figure 2.1: Map showing the area where Cacela (green "x" marker) (37°08.344′ N 07°32.261′ W) and Lacém (red "cross" marker) (37°08.040′ N 07°33.201′ W) rocky reefs are located in the Algarve region, Southern Portugal. Generated with ArcGIS® ArcMap.

After placing an object to serve as scale for the model, the SCUBA diver, using a GoPro Hero 3 with wide angle settings and equipped with artificial lights, started the video recording. The SCUBA diver swam over each reef, maintaining a distance of approximately 1 m from the bottom, and covering one transect of approximately 50 m in each one. Considering the horizontal field of view of the camera, of about 120°, the covered area was of approximately 170 m^2 in each reef. The zone covered was the one facing the coast, which is the one more protected from the currents and that shows a greater biodiversity. The camera was positioned horizontally, directly over the reef, with the minimum angle of inclination possible.

2.2 Models generation

Using the SfM technique, several 3D high resolution models of the two rocky reefs were built using sets of 2D frames obtained from the recorded videos. A post-processing was carried out by colour-correcting the images through the white balance for better quality and visualisation. The specific frames were selected using CyberLink PowerDirector®, always seeking to maintain a minimum superposition of 80% between images in the same transect, as suggested by the Agisoft Metashape ® (Metashape) user manual. Then the images were imported to Metashape, which was used for aligning the images and building the models. The lens type (focal length of 16.4 mm in full frame equivalent) and sensor size (6.17 mm x 4.55 mm) of the camera were informed to the software on the "Camera Calibration" tool for a more precise photo alignment.

The sequence of steps followed in Metashape's "Workflow" to generate the model were: Align Photos; Build Dense Cloud; Build Mesh; Build Texture; and Build DEM (Digital Elevation Model). All the default parameters were maintained. Before the last step, of building the DEM, markers were added to the objects placed on the scene to serve as scales, and the known sizes of the objects were informed, in order to allow the scaling of the whole model. Since the area covered was too large, making a single model was not possible, which led us to building several models of smaller segments of the reefs (Figure 2.2). In a subsequent stage, the sponges in the different segments were located throughout the frames, identified and marked on the models (Figure 2.2), so that their coordinates could be retrieved.

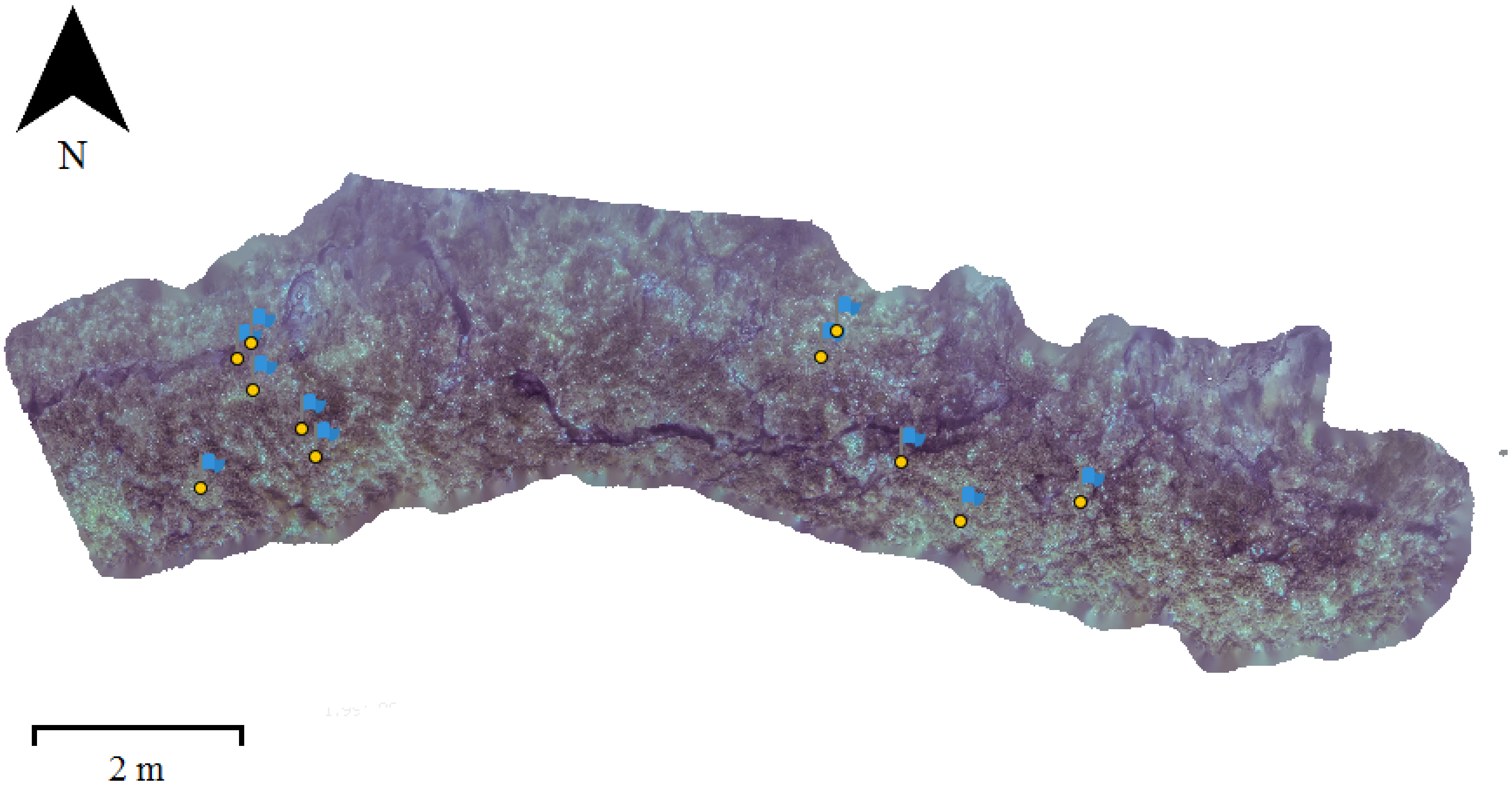


Figure 2.2: 3D model of a segment of Lacém reef. The yellow markers indicate the positions of the sponges located in the area. This model is available at https://skfb.ly/6VtYN. Generated with Agisoft® Metashape.

To assess the precision of SfM for modelling the structures of sponges, the differences between two models of the same sponge done with different sets of images were analysed. These sets of images were taken in sequence, with a Canon M3 and artificial lights, during the same dive and with the same camera settings, to maintain the same conditions between imaging sequences. Since it is a complex structure, the images were taken at a close distance, ensuring the maximum detail possible. In order to compare the effect of using artificial lighting, another set of images was taken only with natural light. The generated models done using natural or artificial lights were then compared.

The same technique used for modelling the reefs was used to generate the two models of the individual sponge, from the two sets of images taken in the field. These two models were used to assess the potential of SfM to study sponge structures. For this analysis, the surface area and volume of the sponge were also estimated using the software Autodesk ® Meshmixer. With the "Select" and "Analysis" tools, it was possible to select only the surface covered by the sponge (Figure 2.3) and then to calculate its area and volume. After carrying out this process with the two models of the same sponge, surface areas and volumes obtained were compared.

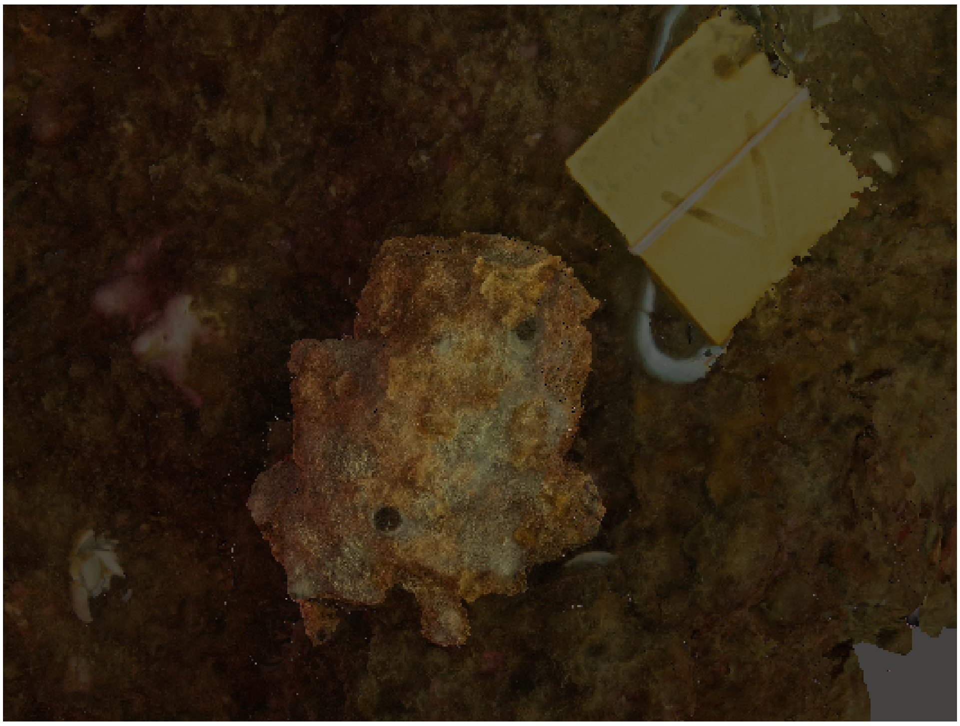


Figure 2.3: 3D model of an individual of *Spongia* sp. showing the part with sponge cover that was selected (highlighted), to calculate surface area and volume. The yellow square is the object with known size used as scale for the model. Generated with Autodesk® Meshmixer.

2.3 Complexity assessment

The DEM models (Figure 2.4), which were calculated after scaling the 3D models, show the bathymetry of the studied areas. After importing this to ArcGIS® ArcMap, the slope (Figure 2.5) was calculated using the Benthic Terrain Modeler tool. Slope is the first derivative of the bathymetric surface, and indicates the presence of cracks, crevices and other features. This variable was used to analyse the spatial arrangement of complexity-generating elements, through the measurement of the distances between these bathymetric features and the sponges. To obtain these distances, slopes with values higher than 60 were used, and the minimum distances between them and the sponges were calculated.

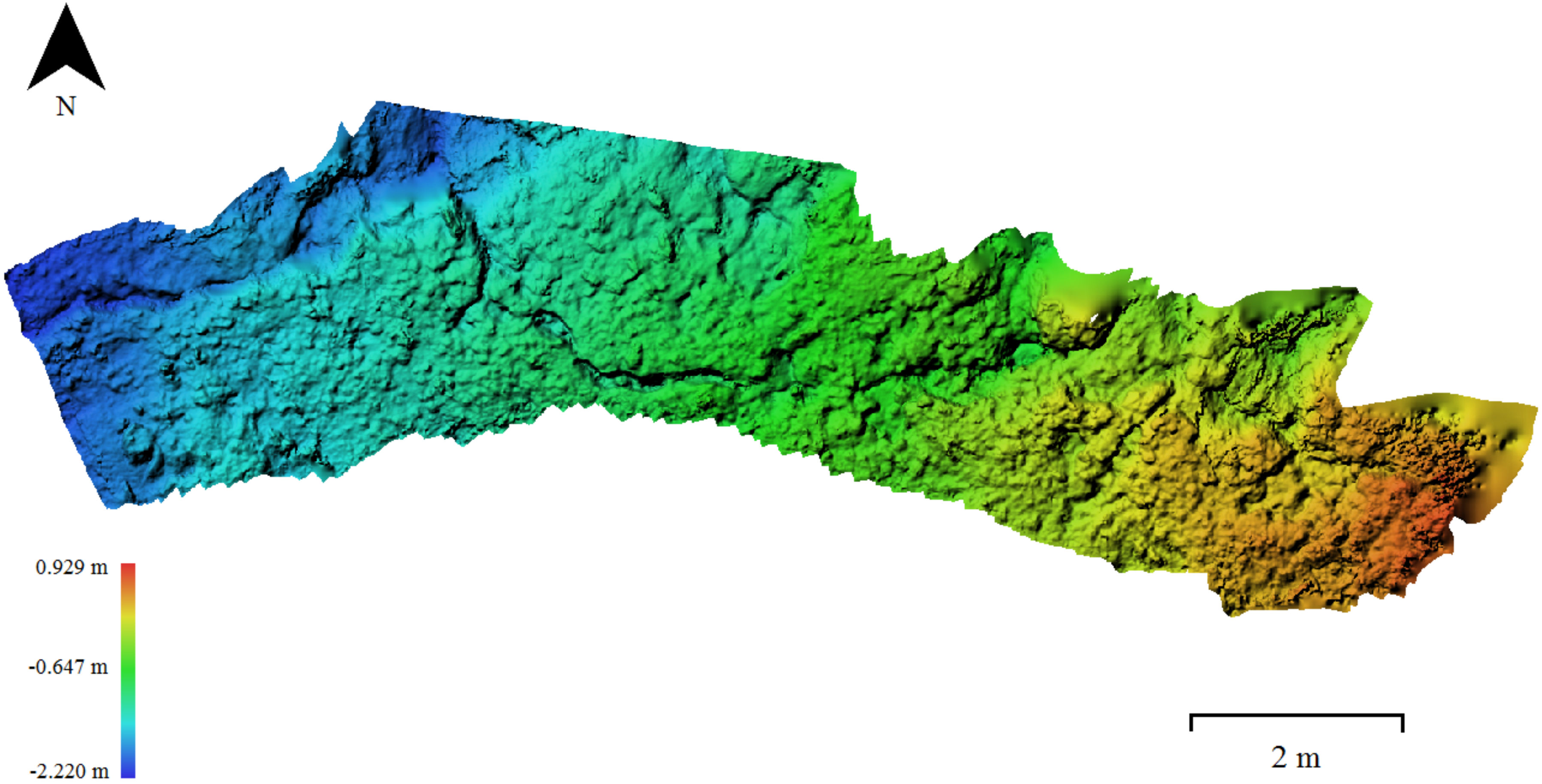


Figure 2.4: Digital elevation model (DEM) of a segment of Lacém reef. Generated with Agisoft® Metashape.

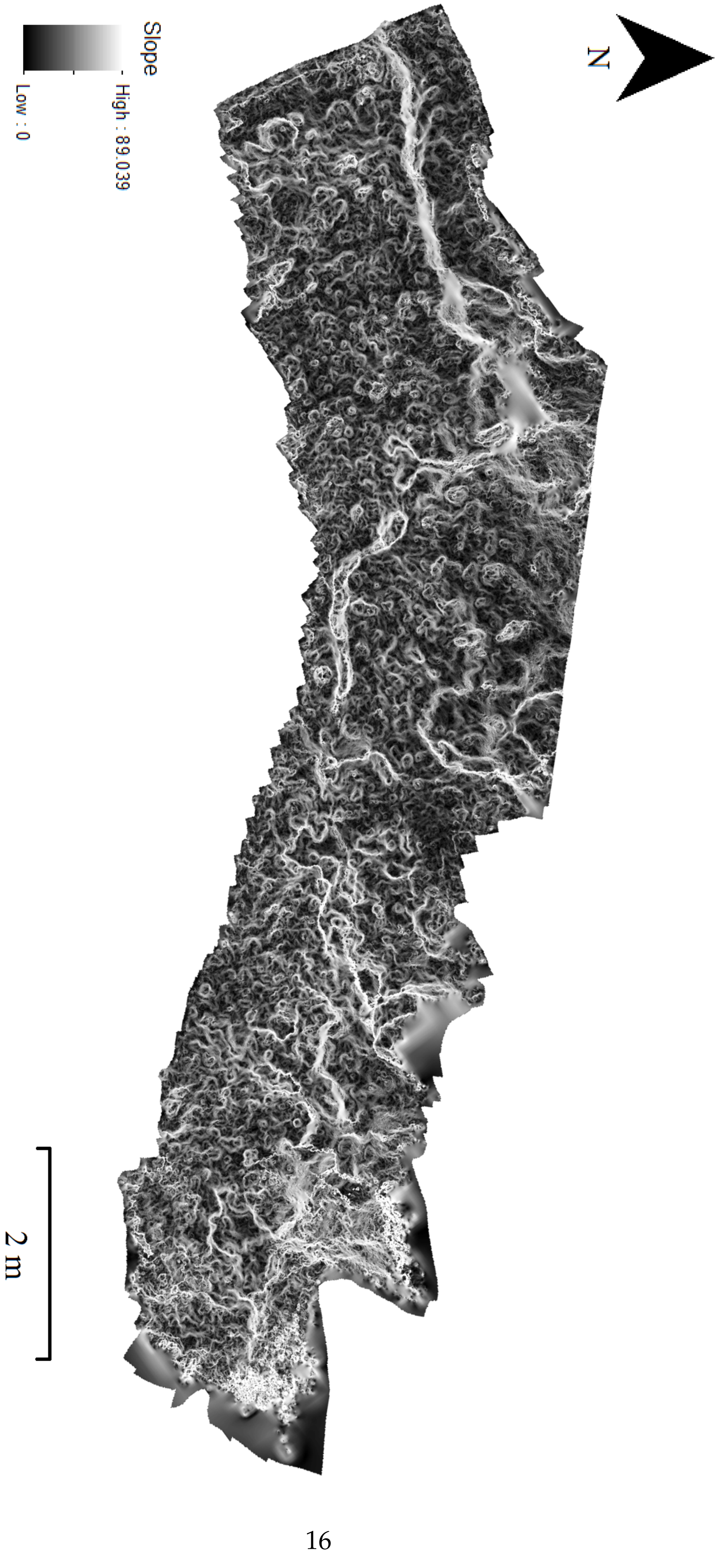


Figure 2.5: Map of the slope of a segment of Lacém reef. Generated with ArcGIS® ArcMap.

Subsequent analyses and calculations using these models were carried out in Robert McNeel's Rhinoceros 3D® (Rhino 3D). At this stage, two different metrics for habitat complexity were computed: rugosity and fractal dimension (FD). These metrics were calculated using the methods described in Young *et al.* (2017) and the Python scripts created by Grace C. Young (Young *et al.*, 2017). These calculations were done in random areas of 2 x 2 m that were "cut" from the meshes of the segments of the reefs (Figure 2.6). These areas were chosen randomly, and the only criterion used was to avoid areas dominated by sand, since this type of substrate usually does not contain any sponges and would cause a bias on the data.

Rugosity is usually calculated in situ by dividing the length a chain comprehends after being positioned over the terrain, by the total length of the chain. In this case it was calculated using the produced terrain digital models, for ten different parallel, equally distant, transects in each area (Figure 2.7), and then the average was calculated. The transects were obtained from the intersection between the mesh of the digital model and ten parallel vertical surfaces.

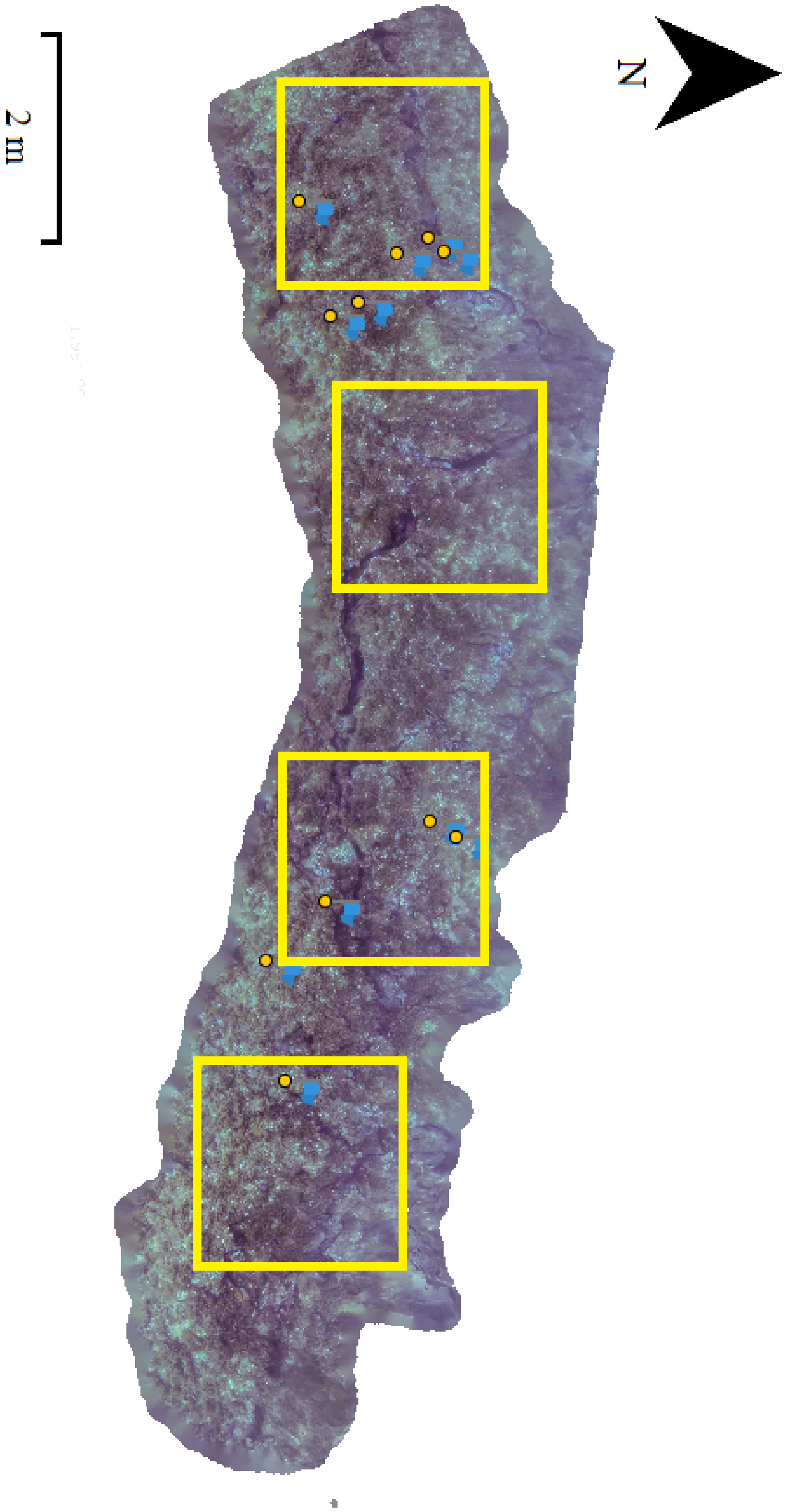


Figure 2.6: Selected 2 x 2 m areas of the mesh of a segment of Lacém reef. Generated with Rhino 3D®.

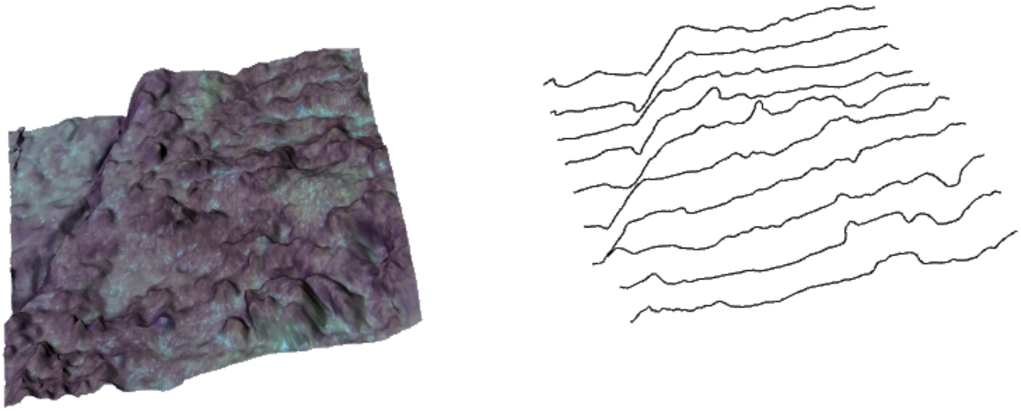


Figure 2.7: 2 x 2 m area of a segment of Lacém reef and the respective transects used for rugosity estimating. Generated with Rhino 3D®.

Fractal dimensions (Figure 2.8) were calculated for three intervals (1.8 - 0.6 m, 0.6 - 0.3 m, 0.3 - 0.15 m), selected based on the characteristic sizes of different structures that typically are regarded as influencing the settlement and development of sponges. The 1.8 - 0.6 m and the 0.6 - 0.3 m intervals include larger structures, like cracks, rifts and crevices. The 0.3 - 0.15 m interval covers smaller substrate structures, like algae and gorgonians, which also generate complexity.

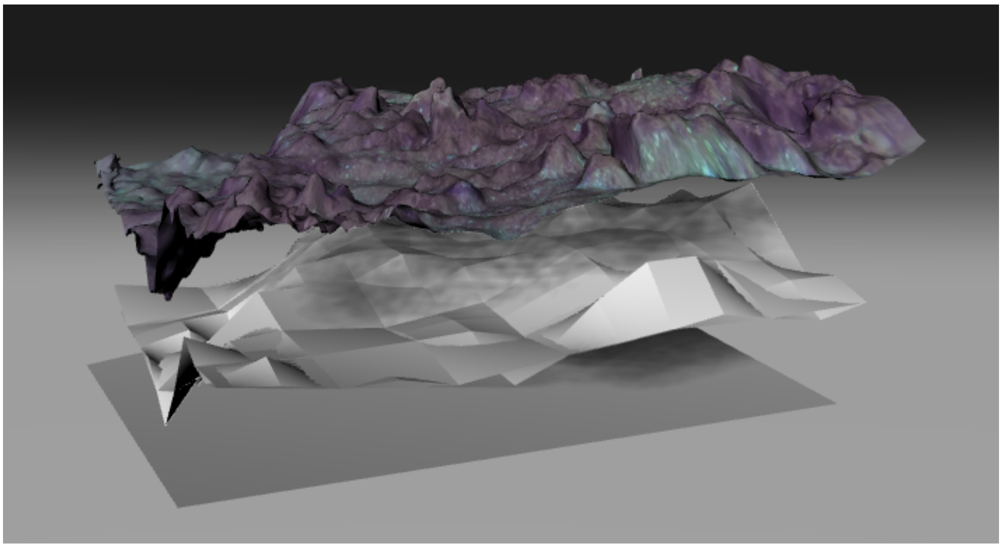


Figure 2.8: 2 x 2 m area of a segment of Lacém reef and the constructed surfaces used for fractal dimensions calculations. Generated with Rhino 3D®.

2.4 Accuracy assessment

An isolated footage was done with three objects, with known dimensions, positioned on top of the reef, to assess the accuracy of the model by comparing the calculated measures with the real ones. Care was taken so that the recording method was the same as the one used for obtaining the images of the reefs. This footage produced a model (Figure 2.9), generated using the same technique as the one used to build the digital models of the reefs, which was scaled using previously known measures. The relative error, which quantifies the accuracy, was estimated by dividing the absolute difference between the real and the model measures, by the real measure (Equation 2.1).

$$Accuracy = \frac{|ML - RL|}{RL}, \tag{2.1}$$

where *ML* is the length measured on the model and *RL* is the known length.

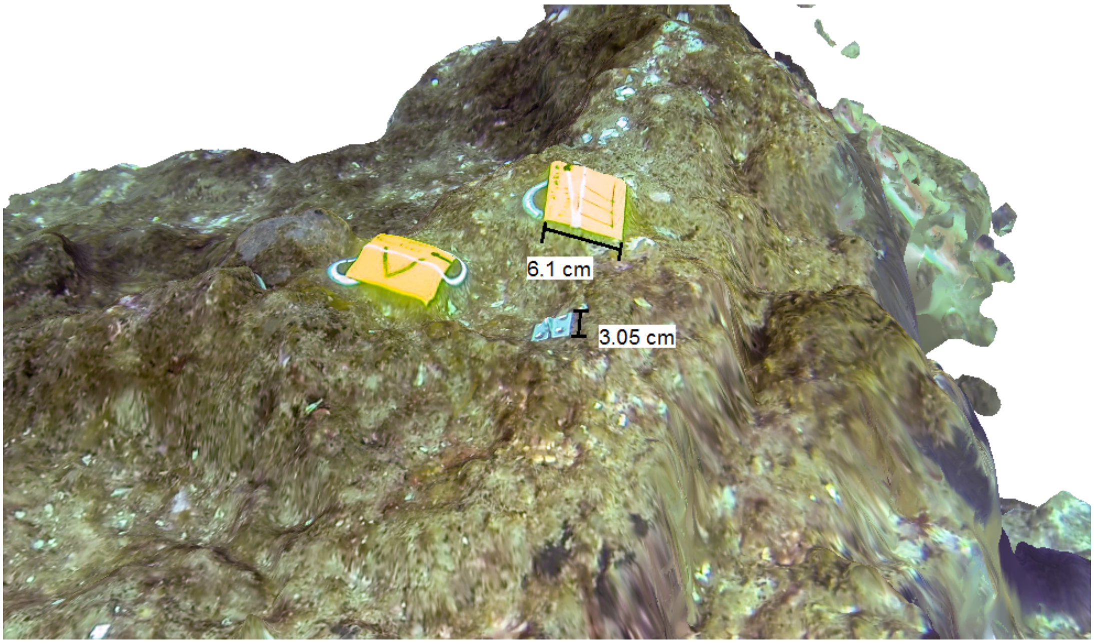


Figure 2.9: 3D model used for the accuracy assessment, showing the three objects with known dimensions used to test the distances calculated by the software. Two of the distances given by the model are shown as examples. Generated with Agisoft ® Metashape.

2.5 Sponge identification

To identify the main sponges found in the two rocky reefs studied, samples were collected using a scraper and tweezers. They were later transported in bags and analysed in laboratory, using a stereo microscope. Comparing the morphological structures visible in the stereo microscope, with the characteristics of different families and genera of Porifera commonly found in the Algarve region, described in Pires (2007), and using an identification key, the sponges were identified until genus level.

2.6 Statistical analysis

To assess the existence of correlation between the sponges abundance and the complexity variables (FD, rugosity and slope), a correlation analysis was used. In the context of this study, the most used correlation analysis is the Pearson correlation. However, since the dependent variables (sponges abundance) did not present a normal distribution (verified by visual analysis of histograms and Shapiro–Wilk tests, not presented here), and the variables did not show a linear relationship between each other (plots in the "Exploratory analysis" section in the "Results" chapter), this analysis was not used. Data transformation techniques, like square root and logarithmic, did not work either. For that reason, Spearman ranked correlation was used, considering the number of sponges as ranks and also transforming the habitat complexity variables values in ranks. Spearman correlation's only assumption is that the variables present a monotonic relationship between each other, which can be observed in scatter plots presented in the "Exploratory analysis" section in the "Results chapter".

To analyse the influence of habitat complexity on the presence of sponges, a logistic regression was applied. For that, the values of abundance of sponges were transformed into Boolean variables (0 or 1), indicating the presence (1) or absence (0) of sponges. Therefore, the quantity of sponges in each area was ignored, being considered only their presence.

The relationships between the diversity and abundance of sponges, and the different metrics related to habitat complexity, were assessed through scatter plots, which allowed an exploratory analysis of the data. This analysis was done through plots of the total abundance of sponges (N) and abundances of the two most common species (*Spongia* sp. and *Phorbas* sp.) against the complexity variables (FD, rugosity and slope). The characteristics that pointed to these two species are described in the "Exploratory analysis" section of the "Results" chapter.

In order to assess the influence of the different metrics used to quantify habitat complexity, on the abundance and diversity of sponges in the modelled areas, a canonical correspondence analysis (CCA) was conducted using the software Past4, a technique developed to evaluate the effects of environmental variables on community composition (Ter Braak, 1986). This analysis was done with the data of both reefs together, and then with each reef separately, to check if there were differences in the behaviour observed. Before running the CCA, the variables were tested for multicolinearity. To assess the probability of the found relationships to be caused by chance, Monte Carlo permutation tests (Efron and Tibshirani, 1985) with 10000 permutations were performed.

Frequency distributions of the distances between the different species of sponges, and the areas with high slope values were represented in histograms, aiming to analyse if there was a preference of the sponges for proximity or distance from these features. To calculate those distances, an inferior limit of 60 for the slope value was used to define what would be considered as "high slope". Therefore, the minimum distance obtained was the distance between the positions of the sponge and of the nearest high slope feature, the latter being the one of the point closest to the sponge.

A t-test was done to check if the different species showed a significant difference regarding the distances to the structures with higher slope values, in both reefs separately. Before doing that, normality and homogeneity of variance were tested. The same test was applied to check the null hypothesis of absence of difference between means of different variables from different reefs. The variables analysed were total number of sponges (N), the abundances of the species found, and the habitat complexity variables (FD, rugosity and slope).

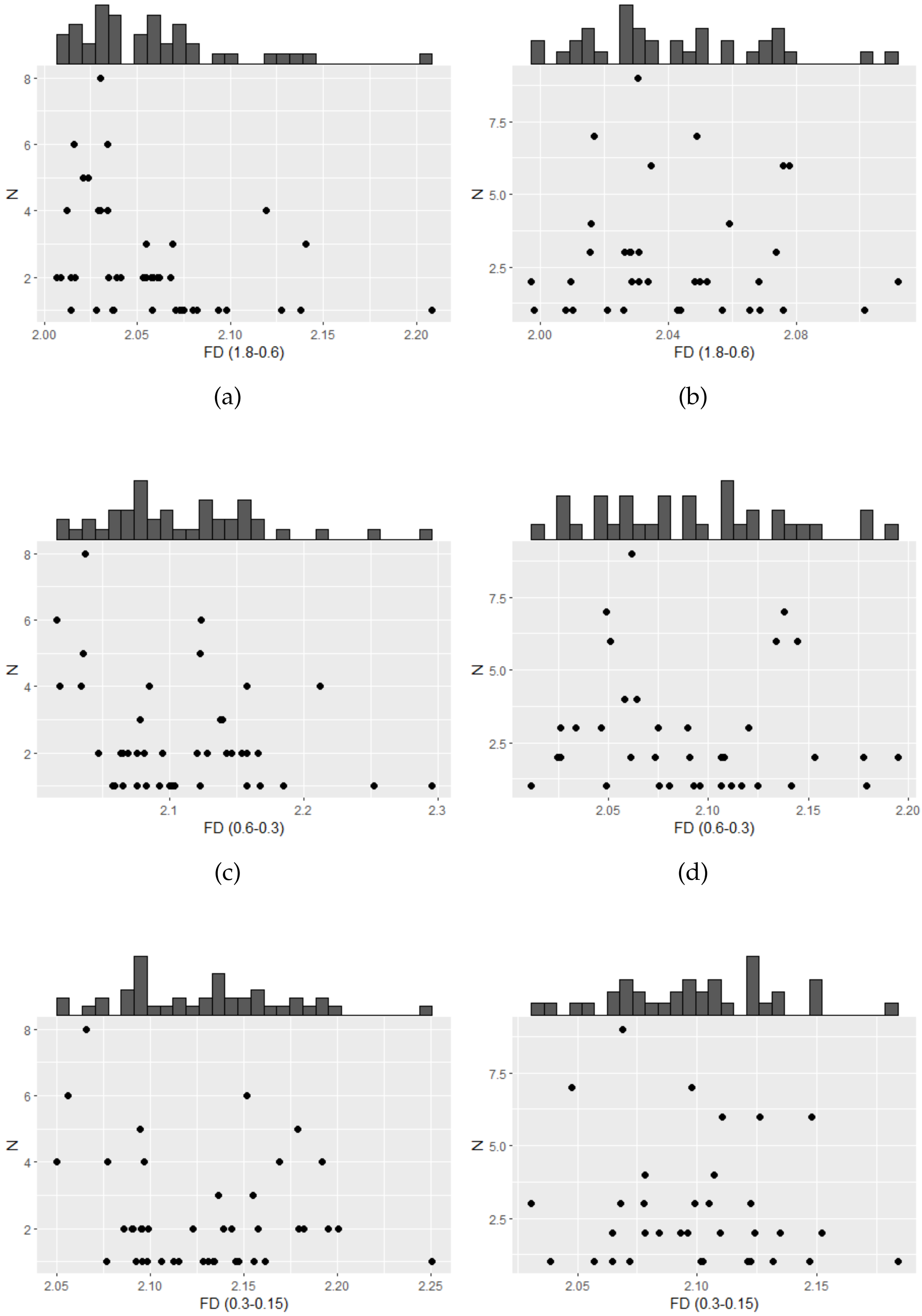
3

Results

3.1 Exploratory analysis

Only two sponges had a significant presence in the reef areas, which led to the decision to identify and analyse them individually. The morphological characteristics and the identification key allowed to identify them as belonging to *Spongia* and *Phorbas* genera. Based on the description of species commonly found in the Algarve region done by Pires (2007), their probable species were *Spongia officinalis* and *Phorbas fictitius*. The first was characterised by a grey colour, some large oscules and a reticulated skeleton with primary and secondary fibres, and without filaments. The second presented a reddish colour, with a surface covered by small halos and oscules, and fibres that grew like a plume. However, here they will only be refereed to by their genera (*Spongia* sp. and *Phorbas* sp.), since identification until species level would require the analysis of spicules, which was not the aim of the study.

The following scatter plots present the raw data obtained from 62 different areas in Cacela and 48 in Lacém, and show the relationships between the biotic variables (abundances of *Spongia* sp., *Phorbas* sp. and of all species together) and the habitat complexity variables. The areas which were used to generate these results were sampled from the reefs' segments presented in Appendix A, while the values of the variables used are presented in the tables in Appendix B. The strongest correlation is between total abundance of sponges and the fractal dimension in the 1.8 - 0.6 m interval (Figure 3.1a), which is reflected in the Spearman correlation analysis (Table 3.1).

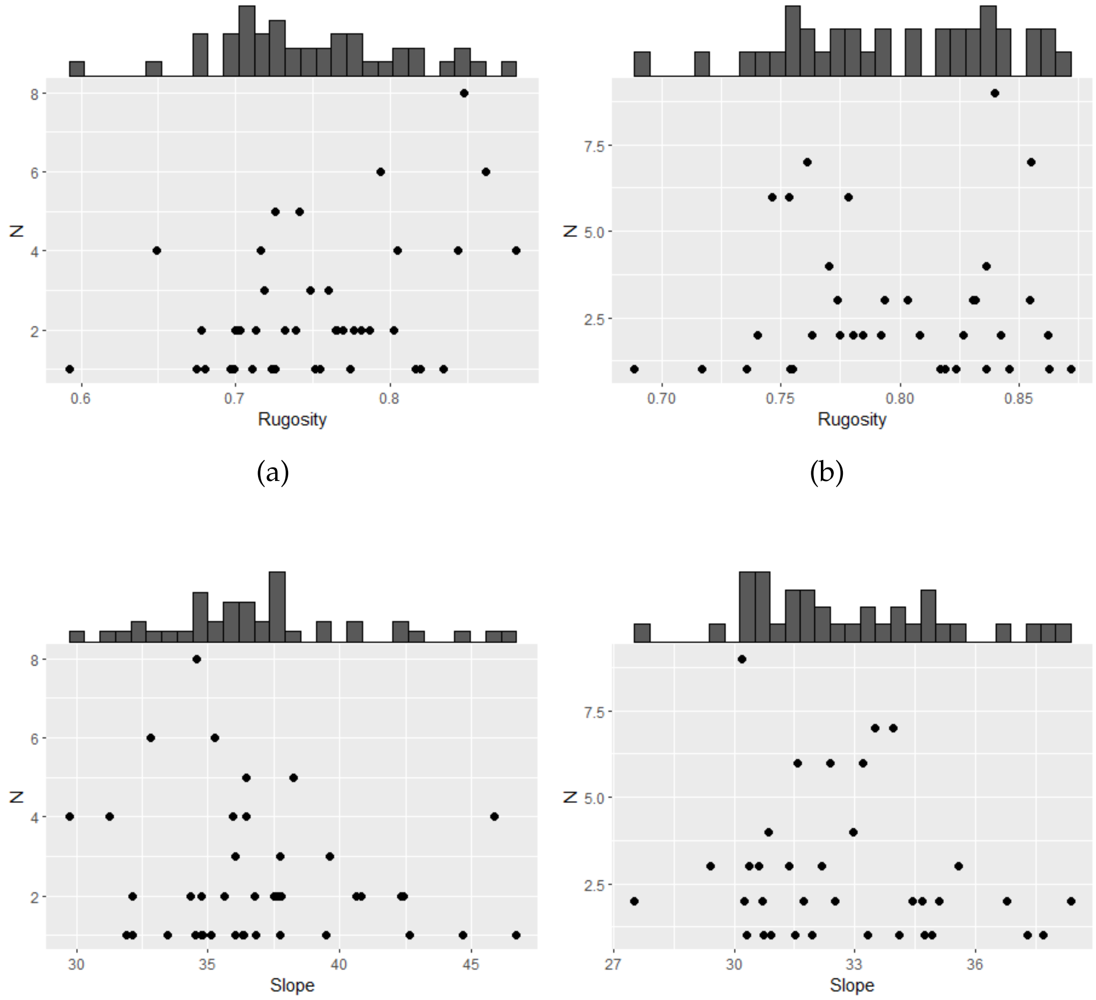


(a) (b)

(c) (d)

(e) (f)

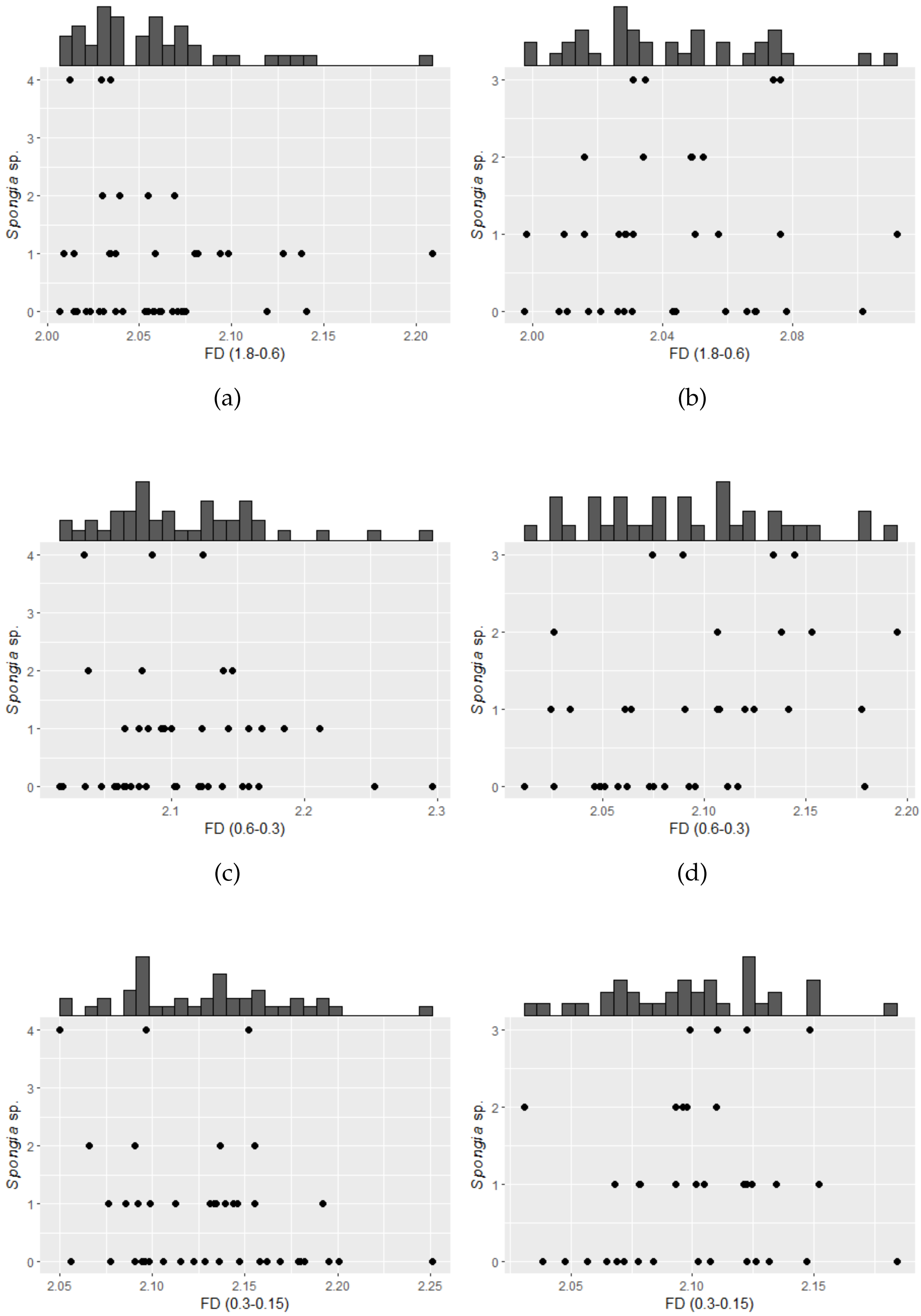
Figure 3.1: Scatter plots of the total abundance of sponges (N) as a function of the fractal dimensions of the three scales analysed, 1.8 - 0.6 m (a, b), 0.6 - 0.3 m (c, d) and 0.3 - 0.15 (e, f), in both Cacela (a, c, e) and Lacém (b, d, f) reefs. Generated with R®.



(a) (b)

(c) (d)

Figure 3.2: Scatter plots of the total abundance of sponges (N) as a function of the rugosity (a, b) and the slope (c, d), in both Cacela (a, c) and Lacém (b, d) reefs. Generated with R®.

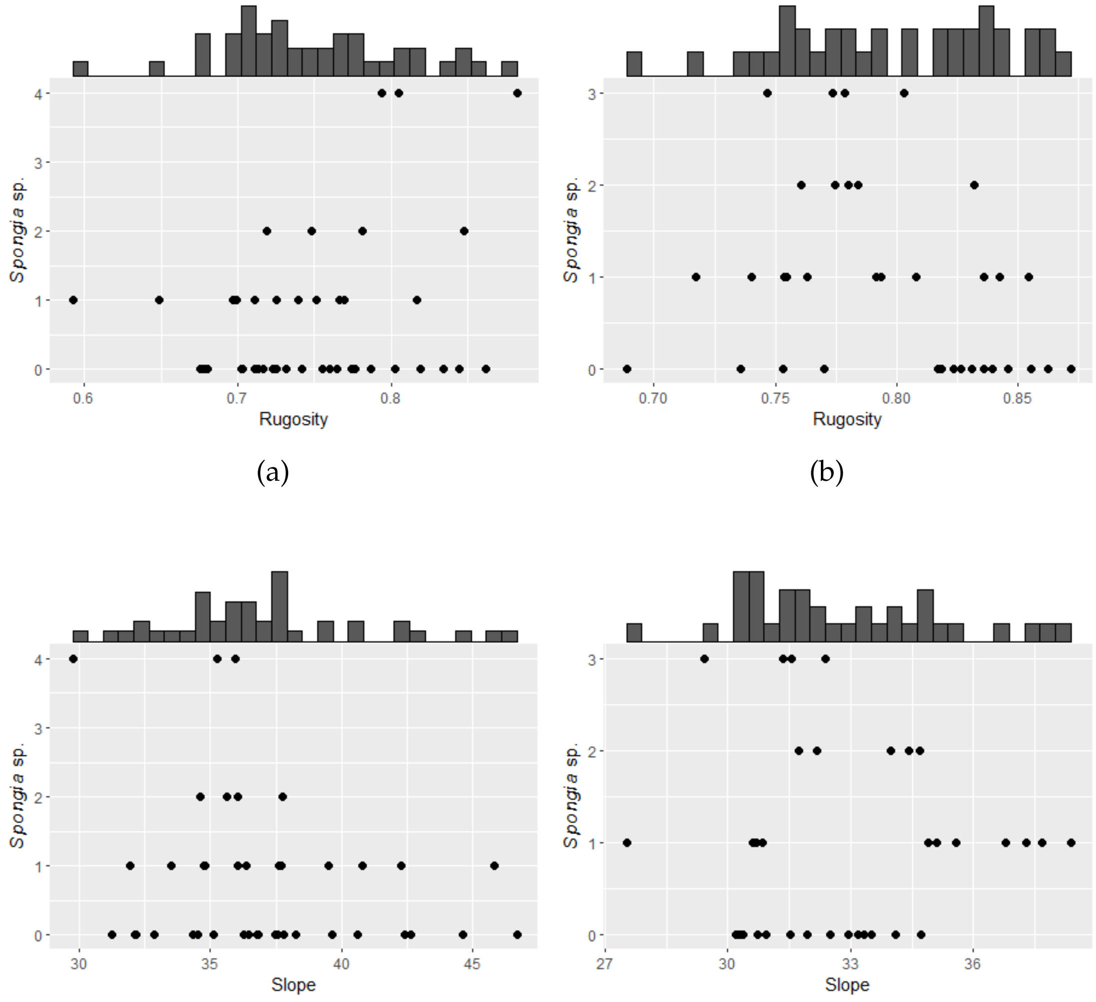


(a) (b)

(c) (d)

(e) (f)

Figure 3.3: Scatter plots of the abundance of *Spongia* sp. as a function of the fractal dimensions of the three scales analysed, 1.8 - 0.6 m (a, b), 0.6 - 0.3 m (c, d) and 0.3 - 0.15 (e, f), in both Cacela (a, c, e) and Lacém (b, d, f) reefs. Generated with R®.



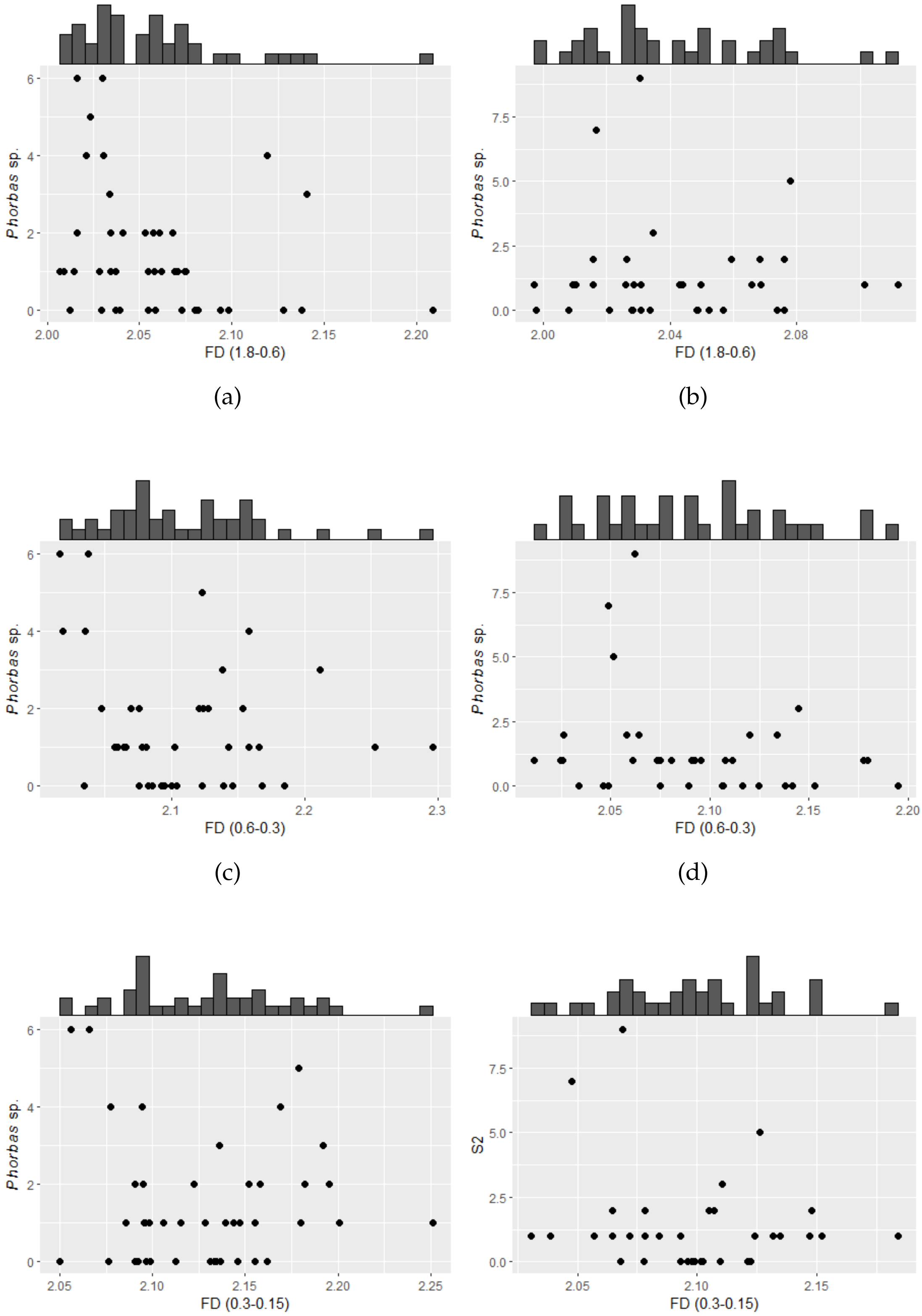
(a)

(b)

(c)

(d)

Figure 3.4: Scatter plots of the abundance of *Spongia* sp. as a function of the rugosity (a, b) and the slope (c, d), in both Cacela (a, c) and Lacém (b, d) reefs. Generated with R®.

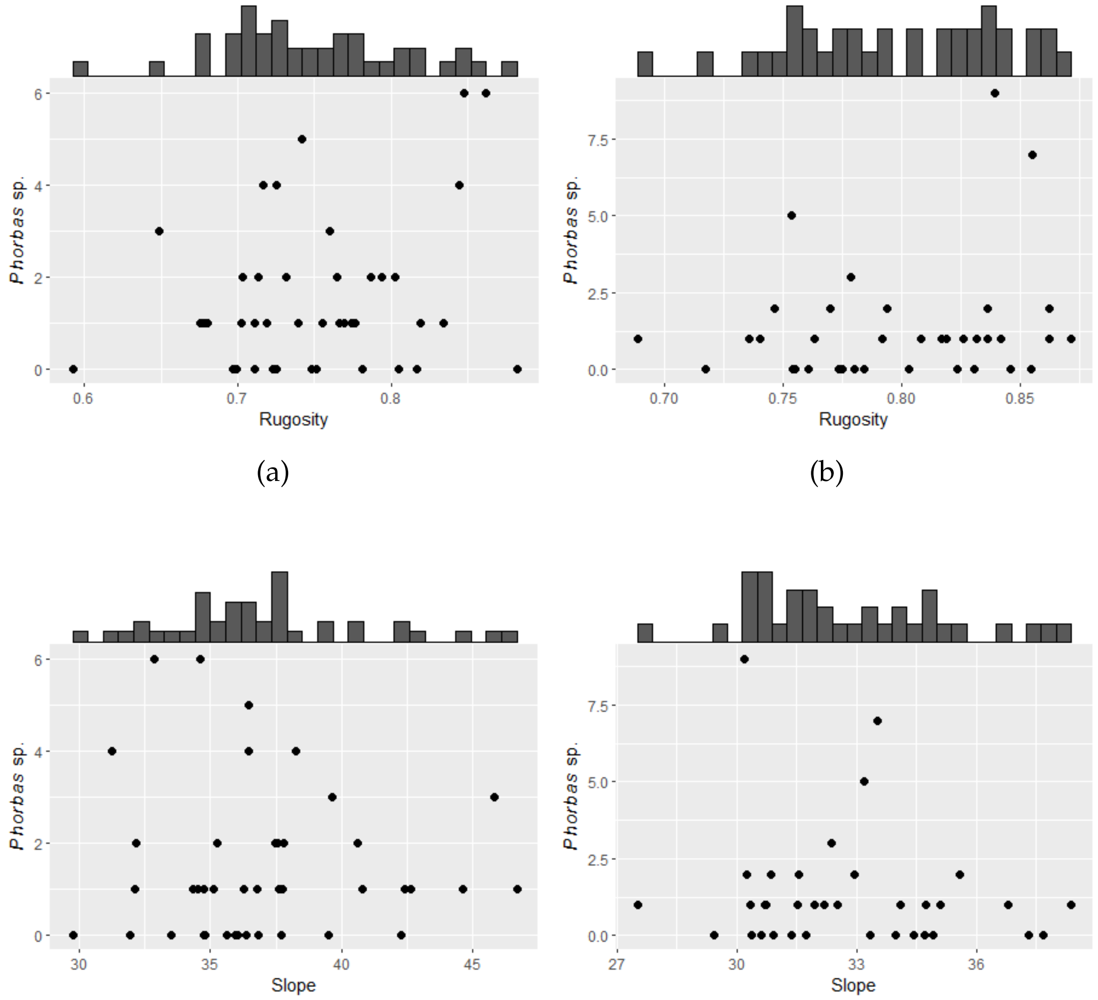


(a) (b)

(c) (d)

(e) (f)

Figure 3.5: Scatter plots of the abundance of *Phorbas* sp. as a function of the fractal dimensions of the three scales analysed, 1.8 - 0.6 m (a, b), 0.6 - 0.3 m (c, d) and 0.3 - 0.15 (e, f), in both Cacela (a, c, e) and Lacém (b, d, f) reefs. Generated with R®.



(a) (b)

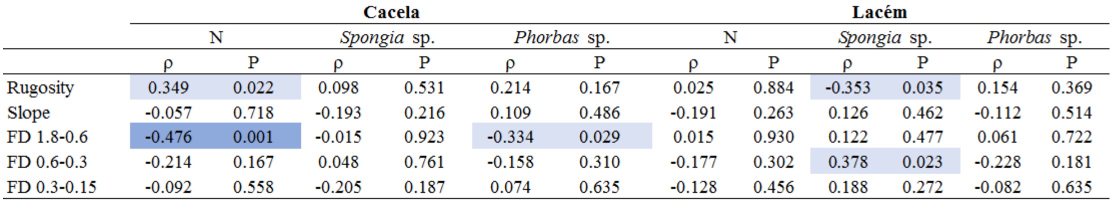
(c) (d)

Figure 3.6: Scatter plots of the abundance of *Phorbas* sp. as a function of the rugosity (a, b) and the slope (c, d), in both Cacela (a, c) and Lacém (b, d) reefs. Generated with R®.

3.2 Correlation analyses

The Spearman correlation analysis found a significant (P = 0.001) moderate negative correlation (-0.476) between the total abundance of sponges (N) and the fractal dimension in the 1.8 - 0.6 m interval (FD 1.8-0.6) in the Cacela reef (Table 3.1). Weaker correlations ($\rho < 0.4$) were also found and are highlighted on table 3.1.

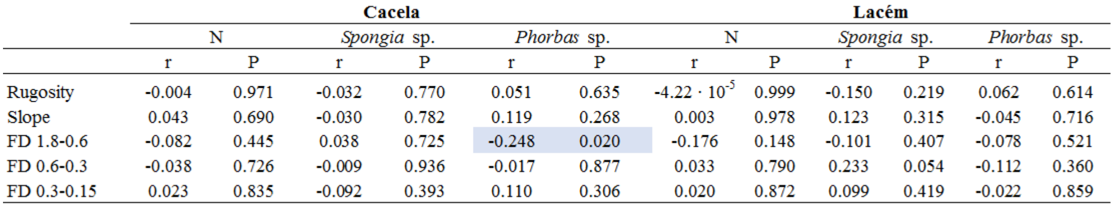
Table 3.1: Results of the Spearman correlation analysis for both Cacela and Lacém reefs, with the correlation coefficients (ρ) and the P-values (P). The highlighted values are the significant correlations, for a significance level of 0.05. The only moderate correlation ($\rho > 0.4$) is highlighted in a darker blue.



	Cacela						**Lacém**					
	N		*Spongia* sp.		*Phorbas* sp.		N		*Spongia* sp.		*Phorbas* sp.	
	ρ	P	ρ	P	ρ	P	ρ	P	ρ	P	ρ	P
Rugosity	0.349	0.022	0.098	0.531	0.214	0.167	0.025	0.884	-0.353	0.035	0.154	0.369
Slope	-0.057	0.718	-0.193	0.216	0.109	0.486	-0.191	0.263	0.126	0.462	-0.112	0.514
FD 1.8-0.6	-0.476	0.001	-0.015	0.923	-0.334	0.029	0.015	0.930	0.122	0.477	0.061	0.722
FD 0.6-0.3	-0.214	0.167	0.048	0.761	-0.158	0.310	-0.177	0.302	0.378	0.023	-0.228	0.181
FD 0.3-0.15	-0.092	0.558	-0.205	0.187	0.074	0.635	-0.128	0.456	0.188	0.272	-0.082	0.635

The logistic regression analysis found only one significant result (P = 0.020), for a significance level of 0.05, with a weak regression coefficient (r = -0.248), between the presence of *Phorbas* sp. and the fractal dimension in the 1.8 - 0.6 m interval (FD 1.8-0.6) in the Cacela reef (Table 3.2).

Table 3.2: Results of the logistic regression analysis for both Cacela and Lacém reefs, with the regression coefficients (r) and the P-values (P). The highlighted value is the significant correlation, for a significance level of 0.05.



	Cacela						**Lacém**					
	N		*Spongia* sp.		*Phorbas* sp.		N		*Spongia* sp.		*Phorbas* sp.	
	r	P	r	P	r	P	r	P	r	P	r	P
Rugosity	-0.004	0.971	-0.032	0.770	0.051	0.635	$-4.22 \cdot 10^{-5}$	0.999	-0.150	0.219	0.062	0.614
Slope	0.043	0.690	-0.030	0.782	0.119	0.268	0.003	0.978	0.123	0.315	-0.045	0.716
FD 1.8-0.6	-0.082	0.445	0.038	0.725	-0.248	0.020	-0.176	0.148	-0.101	0.407	-0.078	0.521
FD 0.6-0.3	-0.038	0.726	-0.009	0.936	-0.017	0.877	0.033	0.790	0.233	0.054	-0.112	0.360
FD 0.3-0.15	0.023	0.835	-0.092	0.393	0.110	0.306	0.020	0.872	0.099	0.419	-0.022	0.859

3.3 Correspondence analysis

The CCA of Cacela and Lacém reefs together (Figure 3.7) showed that *Phorbas* sp. has more affinity for areas with higher slope and rugosity values, and higher values of fractal dimension on the 0.3 - 0.15 m interval. On the other hand, *Spongia* sp. has more affinity for areas with higher fractal dimensions on the 1.8 - 0.6 and 0.6 - 0.3 m intervals. The total number of sponges present did not show a visually significant difference between conditions.

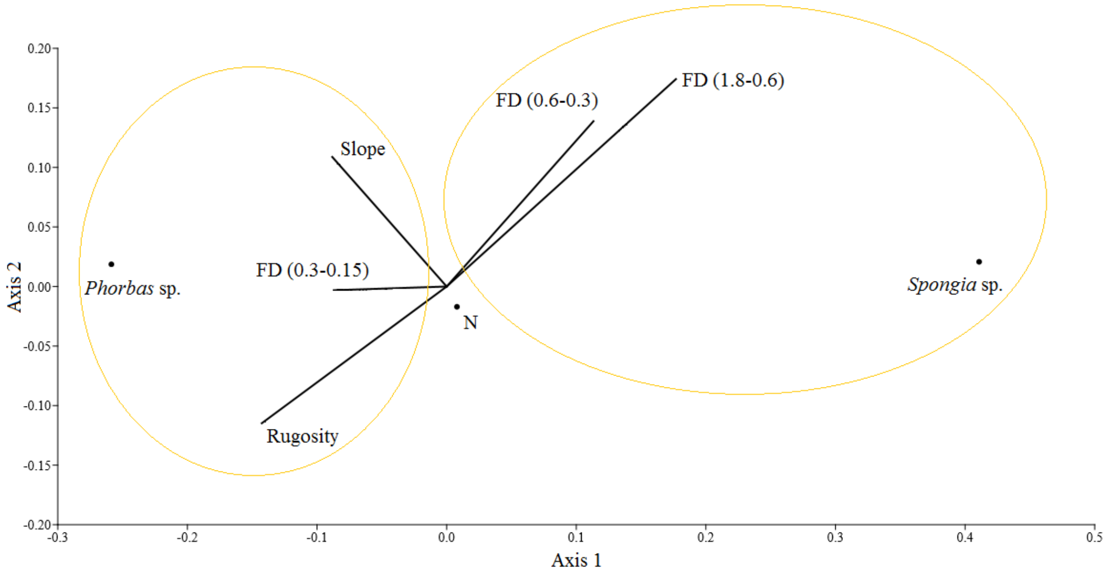


Figure 3.7: CCA for Cacela and Lacém reefs showing the total number of sponges found in each area (N), the two main species found *Spongia* sp. and *Phorbas* sp. and their relationship with the five different environmental variables, rugosity, slope and fractal dimensions in the 1.8 - 0.6 m (FD 1.8-0.6), 0.6 - 0.3 m (FD 0.6-0.3) and 0.3 - 0.15 m (FD 0.3-0.15) intervals. The highlighted areas in yellow show the elements with greater affinity. Axis 1 accounts for 99.33% of the variance, with a P-value of 0.054 obtained from a Monte-Carlo permutation test (10000 permutations). Generated with Past4®.

The CCA of Cacela reef (Figure 3.8) showed that *Phorbas* sp. has more affinity for areas with higher slope and rugosity values, and higher values of fractal dimension on the 0.3 - 0.15 m interval, accompanying the result of both reefs together. On the other hand, *Spongia* sp. has more affinity for areas with higher fractal dimensions on the 1.8 - 0.6 interval. The total number of sponges present, again, did not show a visually significant difference between conditions.

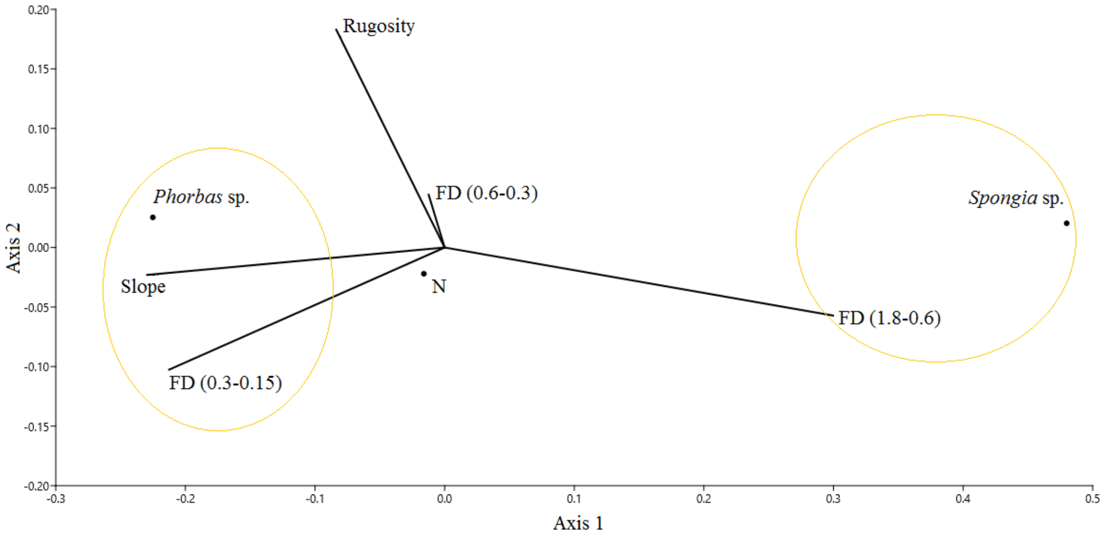


Figure 3.8: CCA for Cacela reef showing the total number of sponges found in each area (N), the two main species found (*Spongia* sp. and *Phorbas* sp.) and their relationship with the five different environmental variables, rugosity, slope and fractal dimensions in the 1.8 - 0.6 m (FD 1.8-0.6), 0.6 - 0.3 m (FD 0.6-0.3) and 0.3 - 0.15 m (FD 0.3-0.15) intervals. The highlighted areas in yellow show the elements with greater affinity. Axis 1 accounts for 99.05% of the variance, with a P-value of 0.278 obtained from a Monte-Carlo permutation test (10000 permutations). Generated with Past4®.

The CCA of Lacém reef (Figure 3.9) showed that *Phorbas* sp. has more affinity only for areas with higher rugosity values, while *Spongia* sp. has more affinity for areas with higher fractal dimensions on the 1.8 - 0.6 and 0.6 - 0.3 m intervals, and higher slope values. The total number of sponges present, again, did not show a visually significant difference between conditions.

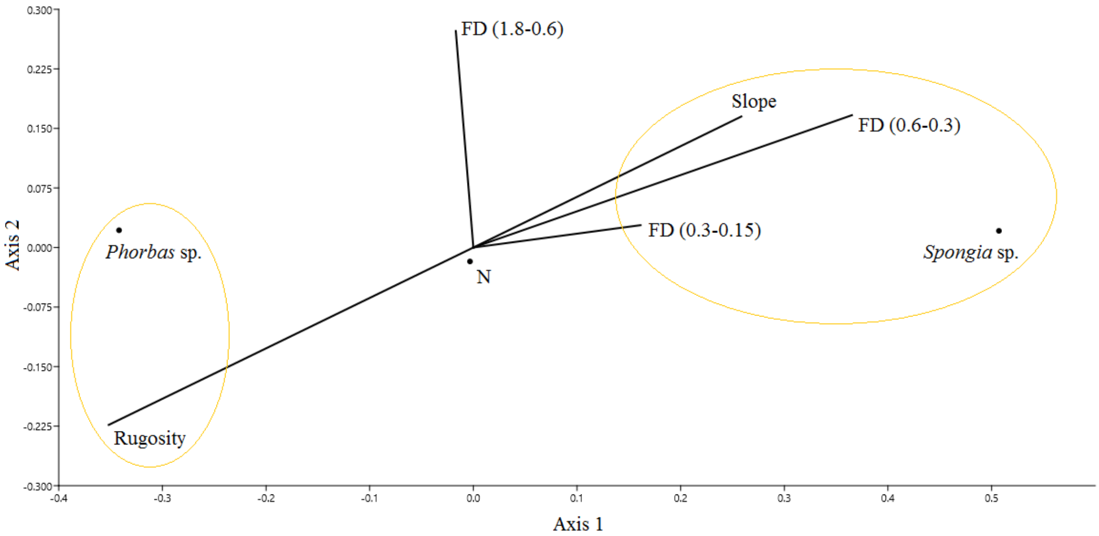
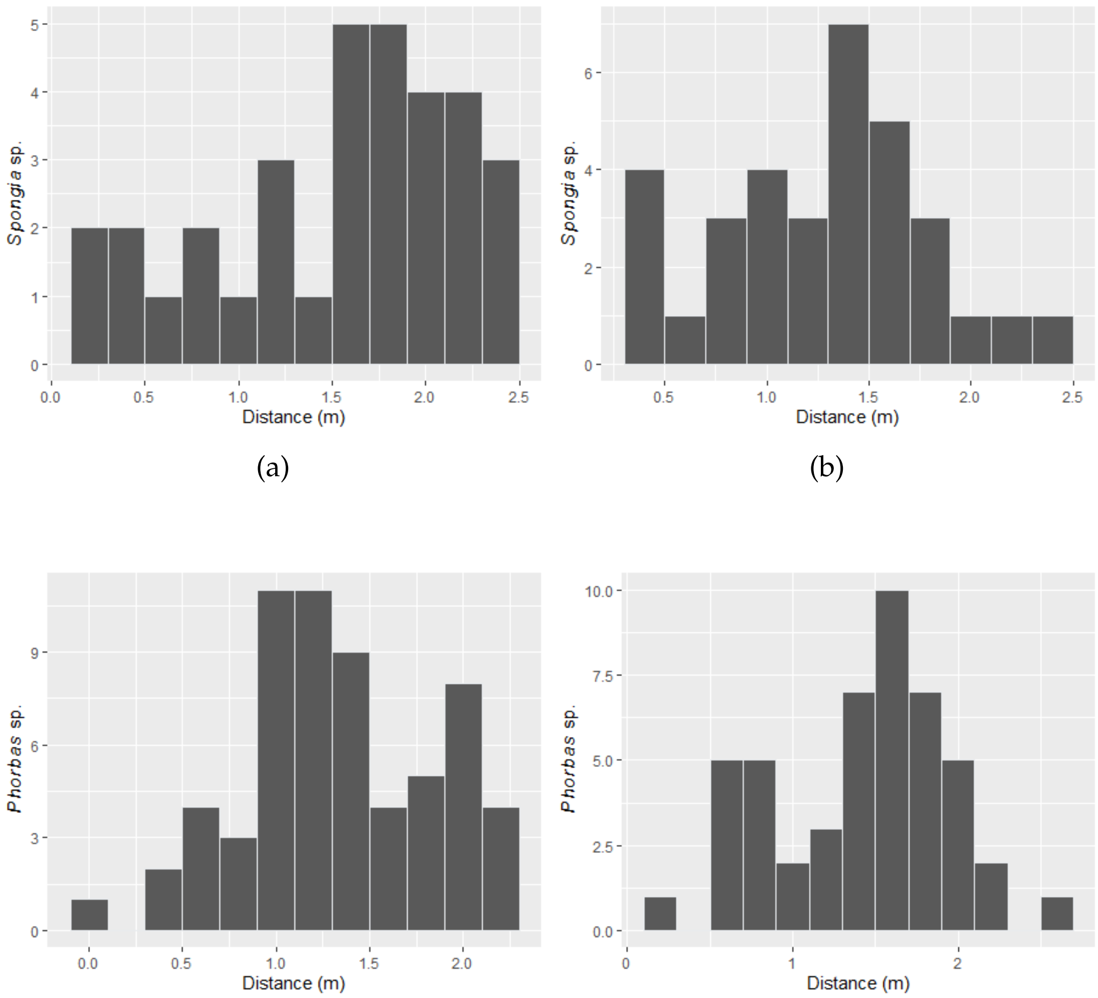


Figure 3.9: CCA for Lacém reef showing the total number of sponges found in each area (N), the two main species found (*Spongia* sp. and *Phorbas* sp.) and their relationship with the five different environmental variables, rugosity, slope and fractal dimensions in the 1.8 - 0.6 m (FD 1.8-0.6), 0.6 - 0.3 m (FD 0.6-0.3) and 0.3 - 0.15 m (FD 0.3-0.15) intervals. The highlighted areas in yellow show the elements with greater affinity. Axis 1 accounts for 99.52% of the variance, with a P-value of 0.157 obtained from a Monte-Carlo permutation test (10000 permutations). Generated with Past4®.

3.4 Comparison between means

Histograms of the distances between the sponges analysed (*Spongia* sp. and *Phorbas* sp.), and the features with high slope values for Cacela and Lacém reefs (Figure 3.10), show distributions through large ranges, without clear preferences for specific distances.



(a) (b)

(c) (d)

Figure 3.10: Histograms of the distances between the sponges analysed (*Spongia* sp. and *Phorbas* sp.) and the features with high slope values for Cacela (a, c) and Lacém (b, d) reefs. Generated with R®.

The t test comparing *Spongia* sp. and *Phorbas* sp. in relation to their mean distances from high slope features in the areas analysed (Table 3.3), showed that the null hypothesis of absence of difference between means cannot be rejected. This result was obtained for both Cacela (P = 0.113) and Lacém (P = 0.186) reefs. Shapiro-Wilk and F tests confirmed the normality and homogeneity of variances, respectively, of the analysed samples for a significance level of 0.01.

Table 3.3: Results of the t tests comparing *Spongia* sp. and *Phorbas* sp. in relation to their mean distances from high slope features in the areas analysed, for Cacela and Lacém reefs. The differences between the means (MD) are also presented.

	***Spongia* sp.**		***Phorbas* sp.**		**MD**		**P**
	Mean	CI (95%)	Mean	CI (95%)	Value	CI (95%)	
Cacela	1.525	1.296 - 1.755	1.333	1.205 - 1.462	0.192	-0.047 - 0.431	0.113
Lacém	1.274	1.090 - 1.459	1.431	1.281 - 1.580	0.156	-0.077 - 0.389	0.186

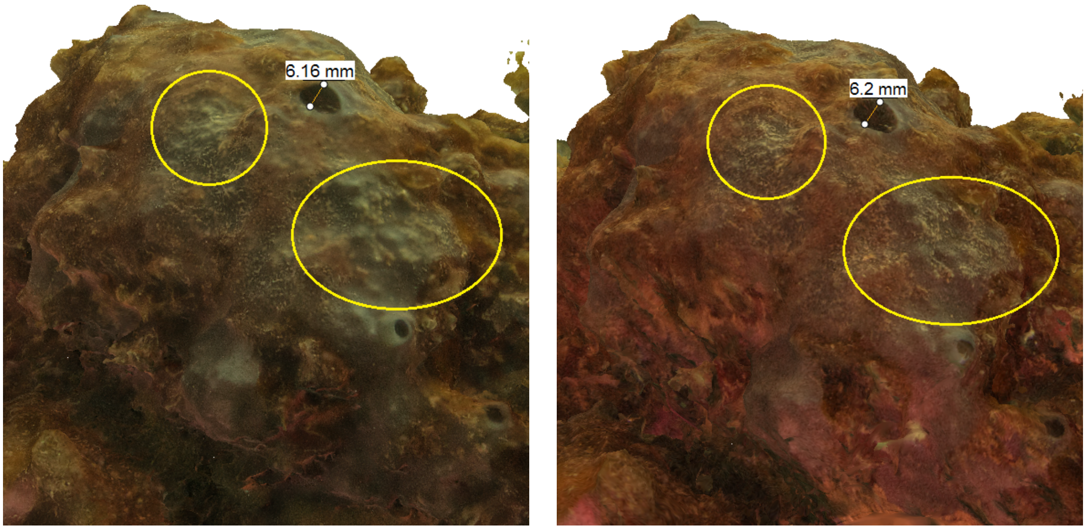
Comparing the abundance of sponges (N) between Cacela and Lacém reefs, the Mann-Whitney test, used because of lack of normality of the samples means, indicated that there was no significant difference between them (P = 0.529). The abundance by species also did not show significant differences (P = 0.601 for *Phorbas* sp. and P = 0.683 for *Spongia* sp.). On the other hand, t tests comparing values of rugosity, slope and fractal dimensions in the three different scales, from Cacela and Lacém reefs, showed significant differences between these reefs, with all P-values lower than 0.05. All these results are presented in table 3.4.

Table 3.4: Results of the t tests for comparison of the means of abundances of sponges (three top rows) and complexity variables (five bottom rows) between Cacela and Lacém reefs. The differences between the means (MD) are also presented. The highlighted values are the significant correlations, for a significance level of 0.05. The values highlighted by a darker blue are the very significant results.

	Cacela		**Lacém**		**MD**		**P**
	Mean	CI (95%)	Mean	CI (95%)	Value	CI (95%)	
N	2.40	1.88 - 2.91	2.75	2.04 - 3.46	0.36	-0.47 - 1.17	0.529
Spongia sp.	2.14	1.63 - 2.64	1.65	1.27 - 2.03	0.49	-0.13 - 1.06	0.683
Phorbas sp.	2.14	1.63 - 2.64	2.09	1.18 - 3.00	0.05	-0.86 - 1.09	0.601
Rugosity	0.749	0.736 - 0.761	0.798	0.784 - 0.812	0.049	0.030 - 0.068	$8.502 \cdot 10^{-7}$
Slope	36.802	35.806 - 37.799	32.757	32.002 - 33.511	4.046	2.746 - 5.345	$6.341 \cdot 10^{-9}$
FD 1.8-0.6	2.061	2.053 - 2.070	2.047	2.040 - 2.055	0.014	0.002 - 0.025	0.046
FD 0.6-0.3	2.112	2.099 - 2.126	2.090	2.080 - 2.100	0.022	0.004 - 0.040	0.016
FD 0.3-0.15	2.127	2.117 - 2.137	2.099	2.090 - 2.107	0.028	0.015 - 0.042	$5.016 \cdot 10^{-5}$

3.5 Sponge structure analysis

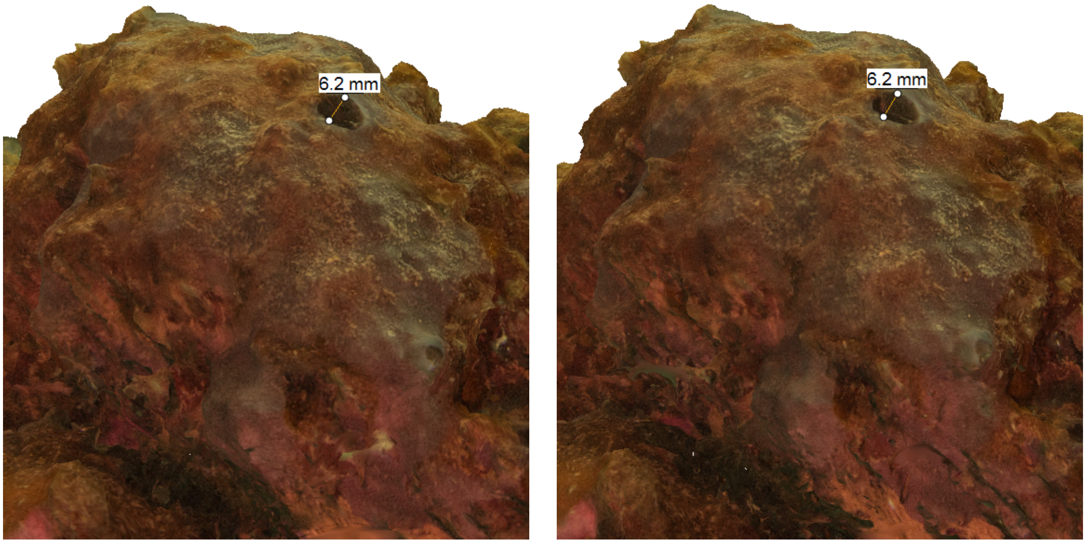
The differences between models generated from photographs taken with and without the use of artificial lights, can be seen clearly on the degree of detail of each model (Figure 3.11). The photographs taken with artificial lights generated a model (can be accessed on https://skfb.ly/6UXv7) capable of representing smaller structures, giving much more detail and definition to the model, as it is seen in the highlighted areas of the images. There was also a recover of the red colour by the artificial lights.



(a) (b)

Figure 3.11: 3D models of the selected sponge (*Spongia* sp.) generated without (a) and with (b) the use of artificial lights. The highlighted areas are the ones which better illustrate the difference in the degree of detail. Generated with Agisoft® Metashape.

Visually, the differences between the models generated from different sets of photographs (Figure 3.12) were relatively small. The definition and the degree of detail were approximately the same, with excellent capability of representing small structures. The values of surface area and volume calculated for both models (Table 3.5) were also close to each other, with a difference of 1.44 cm^2 (0.96%) for the surface area, and 12.17 cm^3 (8.98%) for the volume.



(a) (b)

Figure 3.12: 3D models of the selected sponge (*Spongia* sp.) generated from the first (a) and from the second (b) sets of photographs, both with the use of artificial lights. Generated with Agisoft® Metashape.

Table 3.5: Values of surface area (SA) and volume (V) for the two models generated from different sets of photographs.

Model	SA (cm^2)	V (cm^3)
1	148.57 ± 1.22	129.48 ± 3.84
2	150.01 ± 1.22	141.65 ± 4.08

Small differences were also found in point-to-point distances calculated to assess the accuracy of the reefs' models (Table 3.6), which showed majorly small errors (lower than 2%).

Table 3.6: Values of model (ML) and real (RL) measured lengths for the objects put on the reef to assess the accuracy of the model, together with the errors obtained by comparing these two lengths.

RL (cm)	ML (cm)	Error (%)
6.00	6.09	1.50
6.00	6.12	2.00
6.00	6.12	2.00
6.00	6.1	1.67
3.00	3.05	1.67
2.80	2.7	3.57

4

Discussion

4.1 Complexity and sponge abundance

Differently from the initial hypothesis of this study, there was little to no correlation between habitat complexity variables and the abundance of sponges in the two rocky reef areas analysed, suggesting that habitat complexity, in the analysed scales, is not a significant driver for their distribution. This is seen in the scatter plots (Figures 3.1 - 3.6), which lack a clear relationship between variables, and in the Spearman correlation analysis (Table 3.1). The sparse distribution of sponges, with high variability of abundance depending on the reef segment analysed, as can be seen on the images in Appendix A, was already an indication of this lack of relationship in the scales analysed. Since the larval stage is largely responsible for distribution patterns of sessile invertebrates (Cowen and Sponaugle, 2009; Whalan *et al.*, 2012), like sponges, and those patterns are influenced by a range of factors, like light (Ettinger-Epstein *et al.*, 2008), biofilm components (Hadfield, 2011) and other chemical cues (Pawlik, 1992), these results are an indication that these previously studied factors are dominant on the settlement of sponge larvae in the studied reefs and, consequently, on the distribution patterns of the organisms.

Another factor that should be taken into consideration, like alerted by Tokeshi and Arakaki (2012), are the scales of the analysis of habitat complexity. Whalan *et al.* (2015) showed that surface microtopography affects larval settlement, providing holes with the same size as the larvae. Maldonado and Uriz (1998) showed that microrefuges enhance survival rate on post-larval phases. Differently from their results, topographic features on the scales analysed here show a weak correlation with sponge abundance, which may indicate also a weak effect on larval settlement of the sponge species in the analysed reefs.

There was a difference between the distribution pattern of *Spongia* sp. and *Phorbas* sp. that was clearly visible in the field and also in the models (Appendix A). *Spongia* sp. tends to be found as bigger organisms, but far apart from each other, while *Phorbas* sp. tends to distribute as smaller, but aggregated organisms. This behaviour indicates that *Phorbas* sp. possibly has, differently from *Spongia* sp., an influence of conspecifics, larvae and/or adults, on the larval settlement, like was found in other studies (Burke, 1986; Dreanno *et al.*, 2006; Ettinger-Epstein *et al.*, 2008; Huggett *et al.*, 2006). Since many aggregations were composed of sponges of different sizes, it is possible that there is a settlement response to the presence of adults, although this hypothesis should be tested in future studies. Another possibility for the aggregating behaviour of *Phorbas* sp. is asexual propagation of the adults (Hadfield and Paul, 2001).

The aggregating behaviour of *Phorbas* sp., possibly influenced by conspecific cues, increased the abundance of this species in many areas. This effect seems to be much more significant for the spatial distribution of the species, at least in relation to local abundance, than habitat complexity features, which may have contributed to the lack of correlation between these last two. However, *Spongia* sp. also showed weak or no correlation with complexity variables, indicating that even without the effect of aggregation due to conspecific cues, the complexity variables analysed might have little influence on sponge distribution in the studied areas.

Another possible factor influencing the distribution of sponges in the analysed reefs is the presence of biofilms. Formed mainly by different species of bacteria, these structures are possibly related to the settlement of marine invertebrate larvae since ancient times, given that sponges have many genes related to sense organs (Jacobs *et al.*, 2007). The reduction of sensory anterior structures, present in sponge larvae, to attachment surfaces after settlement (Hadfield, 2011), is a strong indication that they are used only during larval stage for a unique purpose. Further studies analysing the presence of biofilms on the studied reefs are necessary to address this hypothesis.

The logistic regression (Table 3.2), which included the areas without sponges, differently from the other analyses, showed no significant relationships between the presence of sponges and habitat complexity, with the exception of a weak negative regression coefficient between *Phorbas* sp. and FD between 1.8 and 0.6 m. This confirms the lack of correlation between the studied variables, extending it to the presence or not of sponges, and bringing the strong possibility of influence of other factors and of simple chance.

4.2 Comparison between complexity variables effects on sponge abundance

Although the correlation and exploratory analyses indicated an absence of significant relationship between habitat complexity variables and the distribution of sponges, CCA was able to show some patterns, confirming field observations and what is seen in the models. The affinity of *Phorbas* sp. for higher values of FD on the 0.3 - 0.15 m interval suggests a relationship with foliose algae and gorgonians, which are the main generators of complexity at this scale. This is corroborated by field observations and by the models, which show *Phorbas* sp. usually surrounded by or located near them. Normally, algae and sponges are spatial competitors, and the first are favoured by high light environments, where sponges are often restricted to shaded areas (Irving and Connell, 2002; Konar and Iken, 2005). However, this does not seem to be the case here, where they seem positively correlated. This might be due to a chemical cue produced by the algae, which enhance larval settlement. This was already observed in foliose macroalgae and coral larvae (Birrell *et al.*, 2008), but on sponge larval settlement, only the influence of crustose (Whalan *et al.*, 2012) and erect coralline algae (Palumbi, 1985) were observed. Symbiotic relationships between sponges and algae were already observed before (Ávila *et al.*, 2007; Carballo and Ávila, 2004), which influence their spatial distribution. Another possibility is the effect of the foliose algae on light, producing shaded zones, that are preferable for some species of sponge larvae with negative phototaxis (Maldonado and Uriz, 1998), or on water flow, attenuating it and reducing its velocity (Ackerman and Okubo, 1993; Gambi *et al.*, 1990; Jackson, 1997), which could facilitate the settlement of sponge larvae.

The possibility of algae affecting water flow and larval settlement is corroborated by the affinity of *Phorbas* sp. for higher values of rugosity and slope (Figure 3.7), which indicates a possible influence of the topography in the larval settlement of this species. It is known that the substrate affects the water flow and the formation of the benthic boundary layer (BBL) (Abelson and Denny, 1997; Metaxas, 2001), which is of great importance for the settlement of larvae that, even when motile, have low speeds (Chia *et al.*, 1984), lower than the water flow near the substrate (Butman, 1987). For these reasons, the transport of the sponge larvae to the substrate must be due to passive motion (Abelson and Denny, 1997), and affected by the rugosity and mean slope of the terrain.

The influence of water flow on the settlement of invertebrates larvae is a recurrent theme in studies about biofouling (Koehl, 2007), but the effects of small-scale topography vary a lot between species. There are studies showing an increase in larval settlement caused by surface roughness (Czarnoleski *et al.*, 2004; Lee *et al.*, 2004; Skinner and Coutinho, 2005), while others show a decrease (Berntsson *et al.*, 2000, 2004; Osman and Whitlatch, 1995). This illustrates the difficulty in drawing conclusions from the results obtained here, and shows that more studies on the hydrodynamics of water flows near the bottom are necessary to understand the effects of topography in different scales on larval settlement.

Smith *et al.* (2014) showed that the relative importance of basal substrate complexity, which can be related to the topography of the reef itself (abiotic), in organisms settling, seems to decrease together with the availability of bare space, while the complexity related to biotic elements becomes more important. This could explain the lack of correlation between sponge abundance distribution and the variables analysed, since the bare space available in the studied reefs is way bellow the threshold of 30 to 50% established by the cited study, that would produce significant effects. It also could explain the apparent greater importance of the relationship between algae and *Phorbas* sp., when compared to the abiotic complexity variables in other scales.

Differently from *Phorbas* sp., *Spongia* sp. was more present in areas with higher values of FD on the 1.8 - 0.6 m and 0.6 - 0.3 m intervals (Figure 3.7), which agrees with field observations and the models, that show this species sometimes located near crevices and, many times, on their edges. This might be related to the usual negative phototaxis behaviour of sponge larvae (Gaino *et al.*, 2007), which would seek zones more protected from light. However, this larval behaviour does not reflect on all the adults, since the majority of individuals from this species were located in open areas, exposed to light. This suggests that larvae might have a preference for microrefuges, that offer protection during post-settlement stage, but do not offer protection in the adult phase, like Maldonado and Young (1996) suggest. Another local factor that may explain the presence of both sponge species in areas exposed to light, is the fact that both rocky reefs are low light environments. Although the small depths, there is, regularly, a high concentration of sediments in the water, which refracts and absorbs light. The low light intensity that reaches the bottom, might limit the abundance of algae, which allows the sponges to occupy the more exposed areas, especially since high light is a detrimental factor for sponges (Roberts *et al.*, 2006).

The CCAs of both reefs together (Figure 3.7) and of Cacela reef alone (Figure 3.8) showed similar results, but the analysis of Lacém reef (Figure 3.9) diverged from them. Greater slope and FD (0.3-0.15), which were more related to *Phorbas* sp., shifted to *Spongia* sp. in Lacém reef. This might be related to the reduced algal and gorgonian cover, caused by dredge fishing, that is known to happen in this location. This can affect the analysis, since it influences on the FD on smaller scales. The fact that only the analysis that gathered the data from both reefs (Figure 3.7) presented a result close to being significant (P = 0.054), for a confidence level of 0.05, probably happened due to the increase in the number of samples, which lowered the P-value.

4.3 Comparison between reefs and between sponge species

The comparison between family individuals in relation to the distances to high slope features (Table 3.3) showed that, besides some individuals of *Spongia* sp. being located near crevices or in their edges, there was no significant difference between them. Looking at the differences between means (MD), it can be seen that they are small compared to the mean values (approximately 13% for Cacela and 12% for Lacém), which confirms a small difference between species. The fact that *Spongia* sp. presents greater distances in Cacela, but smaller ones in Lacém, is another evidence of the lack of a major preference, of one of the species, for proximity to high slope features, in comparison to the other. The long range of distances from those high slope features, that each species shows (Figure 3.10), indicates that there is not a preference for a specific, shorter, range of distances, and that those high slope features do not affect the distribution of sponges in the studied reefs. This is another evidence that, besides the fact that many sponge larvae present a negative phototaxis behaviour, it did not show a visible effect on the distribution of the analysed sponges, like a cryptic behaviour. These results go against the ones obtained by Preciado and Maldonado (2005), which found a strong correlation between substratum inclination (slope) and distribution of sponge abundance, and also against the ones obtained by Cárdenas *et al.* (2012), which found not only a positive correlation with inclination, but also a negative one with algae abundance (although some species also showed a preference for high light habitats dominated by algae). This might be due, again, to the low light conditions found at Cacela and Lacém reefs, which decreases the need of the sponges to settle at shaded places, with higher inclinations. Further studies on the local water flows are necessary to understand if there is a relationship between the average distances of sponges to high slope features, and protection from strong water flows.

The t-tests comparing the means of sponge abundance and complexity variables between the two reefs (Table 3.4) showed significant differences between them, in relation to habitat complexity. However, looking at MD, it can be seen that they are small in relation to the means of the variables, with approximate values of 6% for rugosity, 10% for slope and 1% for the FD. Therefore, although the differences were statistically significant for all complexity variables, the real effect caused by a reef change was small, showing that both reefs have similar habitat complexities for the analysed scales.

Comparing MD values of the abundances of sponges with those of FD at all scales (Table 3.4), which are variables in the same order of magnitude, it can be seen that although MDs are much larger for the abundances, they were not significant. This happened because, as it is seen in the confidence intervals of the means, the data for FD were much more precise, with much smaller confidence intervals when compared to the abundance data. Because of this variability in the abundance data, the probability of not rejecting the null hypothesis when it is false increases, making it difficult to say if there is a real difference in the abundance of sponges between the two reefs.

4.4 Sponge structure analysis

SfM proved to be an adequate method for the modelling of sponge structures. The definition was really good, with the oscula and the algal cover being also well modelled (Figure 3.12). The degree of detail, together with the reproducibility showed by the technique, which produced very similar models with two different sets of photographs, highlight the potential of SfM for sponge growth studies, like the one done by Olinger *et al.* (2019).

What must be observed carefully in this kind of studies is the capacity of the observer to identify, in the models, the limits of the sponge body. Especially when the species, like the one modelled here, has a neutral colour and is covered by algae. Even with this difficulty, the difference of surface area between models was relatively small (Table 3.5), of less than 1%, showing the precision of the technique and its potential for sponge growth analysis. The difference in volumes (Table 3.5), on the other hand, was of almost 10%, showing that this variable is more affected by small differences between models and by human error. Considering the low growth rates of sponges, the volume analysis would cause an unacceptably large error when estimating growth rates, since the error would probably be larger than the difference in body size caused by growth.

These differences were caused mainly by the difficulty of the observer in identifying the limits of the sponge body in the models. However, if the species has a colour that highlights from the substrate around, this error should be much smaller. Even then, surface area seems to be a better alternative to estimate growth rates, since volume appears to be much more sensitive to small changes in the selected area.

Another evidence that the differences in surface area and volume between the two models, come from the difficulty of the observer in identifying the limits of the sponge body, is the accuracy assessment of the technique used to generate the reefs' models. The error analysis gave a relative error of approximately 2%, for a model generated from GoPro video frames. This indicates that the error in distances determination of a model built with much higher resolution photographs is much lower than 2%, attesting the high accuracy of the model.

5

Conclusions

This work aimed to investigate the relationships between habitat complexity related variables, and the distribution of sponges in two rocky reefs adjacent to Ria Formosa, in Southern Portugal. Based on the correlation, CCA and means comparison analyses, it can be concluded that there was little to no significant positive correlation between habitat complexity and the abundance of sponges (only one significant positive correlation of 0.378 found on the logistic regression), which was the initial hypothesis of this study. However, there were evidences, uncovered mainly by the CCA, of effects of the substrate, especially algal cover, on the sponge distribution, possibly related to effects on the larval settlement. The results indicate that the local algae population may influence the settlement of *Phorbas* sp. larvae through a chemical cue or direct influence on water flow.

Besides that, there was visual evidence in the 3D models, of the aggregating behaviour of this species, indicating the presence of conspecific cues on larval settlement. On the other hand, *Spongia* sp. showed no aggregating tendency, and no preference for a specific kind of substrate topography, being located both near crevices and in open areas. The presence of both species in open areas indicates that the regular low light conditions of both reefs, verified through a large number of dives done in different seasons of the year, may favour the sponges in relation to algae.

SfM proved to be an adequate method for modelling rocky reefs, even under low visibility conditions. The results produced using only a GoPro show that a low-cost equipment is enough for this kind of study, showing the potential of the method even for citizen science (Raoult *et al.*, 2016). The distance of 1 m maintained from the bottom during image acquisition, allowed to cover a large area, while keeping enough detail for the representation of smaller structures, like algae and gorgonians, and also for the localisation and identification of the sponges directly in the models, which was an uncommon application of the method. The high accuracy of the models, evidenced by the small errors found (less than 2%) when comparing model measured lengths with known ones, confirms the potential of the method used, for analysing habitat complexity metrics related to the topography of the terrain and organisms cover.

While the data acquisition method did not allow an analysis on a larger scale (whole reef scale), considering the distribution of certain complexity generating elements, like rocks or the orientation of reef segments, it produced a large quantity of data on smaller scales (from tens of centimetres to a few metres). The low P-values obtained in the majority of the statistical analyses were probably not due to small samples (70 areas for Lacém and 89 for Cacela, if we count the ones without sponges), but to the large variability on sponges abundance data between areas with similar habitat complexity values. In future studies, this can be avoided by sampling larger areas than 2 x 2 m squares, or quantifying abundance on a different way. Based on the sparse distribution of sponges, which had a high concentration in one segment of the reef and no individuals in the next (addressed in the discussion of the thesis), entire segments of several metres should be modelled, ensuring a smaller variation of abundance data and the analysis of complexity on larger scales. However, this approach should still ensure enough detail of the bottom, to allow an accurate identification of the individual sponges. The scales analysed reflect mainly on the effects of structures that are in the middle of the size spectrum, between small (centimetres) and large features (tens of metres). Further research is needed on the extremes of this spectrum, analysing the effects of microtopography and of entire segments of reefs. Other factors, that were outside the scope of this work, but that are important to be analysed in future studies, are the geomorphology of the reefs and local hydrodynamics and luminosity, since they can affect the distribution of sponges and other benthic species, especially the larval settlement.

The work demonstrated that habitat complexity on greater scales (0.3 - 1.8 m) has a small effect on the distribution of sponges in the studied reefs, which points towards a greater influence of other types of cues for larval settlement, like the chemical ones, or influence of complexity on other scales, like microtopography. Further studies are necessary to address these hypotheses. Besides that, this study showed the distribution of *Phorbas* sp., characterised by proximity to algal cover and aggregating behaviour, and its possible relation to conspecific cues and algae influence during larval settlement, indicated by the relationship between complexity on the 0.15 - 0.3 m scale and the species distribution. On the other hand, *Spongia* sp. was usually found as isolated individuals, and without relationship with algal cover. This kind of study is important for better understanding the factors that affect distribution of species, and to guide conservation actions, like the development of artificial reefs.

Bibliography

Abadie, A., Boissery, P., and Viala, C. (2018). Georeferenced underwater photogrammetry to map marine habitats and submerged artificial structures. *Photogrammetric Record*, 33(164):448–469.

Abelson, A. and Denny, M. (1997). Settlement of marine organisms in flow. *Annual Review of Ecology and Systematics*, 28:317–139.

Ackerman, J. D. and Okubo, A. (1993). Reduced Mixing in a Marine Macrophyte Canopy. *Functional Ecology*, 7(3):305.

Agudo-Adriani, E. A., Cappelletto, J., Cavada-Blanco, F., and Croquer, A. (2016). Colony geometry and structural complexity of the endangered species *Acropora cervicornis* partly explains the structure of their associated fish assemblage. *PeerJ*, 2016(4).

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Co^té, I. M., and Watkinson, A. R. (2009). Flattening of caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, 276(1669):3019–3025.

Andréfouët, S., Cabioch, G., Flamand, B., and Pelletier, B. (2009). A reappraisal of the diversity of geomorphological and genetic processes of New Caledonian coral reefs: A synthesis from optical remote sensing, coring and acoustic multibeam observations. *Coral Reefs*, 28(3):691–707.

Anelli, M., Julitta, T., Fallati, L., Galli, P., Rossini, M., and Colombo, R. (2019). Towards new applications of underwater photogrammetry for investigating coral reef morphology and habitat complexity in the Myeik Archipelago, Myanmar. *Geocarto International*, 34(5):459–472.

Ávila, E., Carballo, J. L., and Cruz-barraza, J. A. (2007). Symbiotic relationships between sponges and other organisms from the Sea of Cortes (Mexican Pacific coast): same problems , same solutions. *Porifera Research: Biodiversity, Innovation and Sustainability*, pages 147–156.

Bell, J. J. (2008). The functional roles of marine sponges. *Estuarine, Coastal and Shelf Science*, 79(3):341–353.

Bell, J. J. and Barnes, D. K. (2000a). A sponge diversity centre within a marine 'island'. In *Hydrobiologia*, volume 440, pages 55–64.

Bell, J. J. and Barnes, D. K. (2000b). The distribution and prevalence of sponges in relation to environmental gradients within a temperate sea lough: Inclined cliff surfaces. *Diversity and Distributions*, 6(6):305–323.

Bell, J. J. and Barnes, D. K. (2000c). The influences of bathymetry and flow regime upon the morphology of sublittoral sponge communities. *Journal of the Marine Biological Association of the United Kingdom*, 80(4):707–718.

Bell, J. J. and Barnes, D. K. (2003). The importance of competitor identity, morphology and ranking methodology to outcomes in interference competition between sponges. *Marine Biology*, 143(3):415–426.

Bennecke, S., Kwasnitschka, T., Metaxas, A., and Dullo, W. C. (2016). In situ growth rates of deep-water octocorals determined from 3D photogrammetric reconstructions. *Coral Reefs*, 35(4):1227–1239.

Berntsson, K. M., Jonsson, P. R., Larsson, A. I., and Holdt, S. (2004). Rejection of unsuitable substrata as a potential driver of aggregated settlement in the barnacle *Balanus improvisus*. *Marine Ecology Progress Series*, 275:199–210.

Berntsson, K. M., Jonsson, P. R., Lejhall, M., and Gatenholm, P. (2000). Analysis of behavioural rejection of micro-textured surfaces and implications for recruitment by the barnacle *Balanus improvisus*. *Journal of Experimental Marine Biology and Ecology*, 251(1):59–83.

Birrell, C. L., McCook, L. J., Willis, B. L., and Harrington, L. (2008). Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*. *Marine Ecology Progress Series*, 362:129–137.

Brock, J. C., Wright, C. W., Clayton, T. D., and Nayegandhi, A. (2004). LIDAR optical rugosity of coral reefs in Biscayne National Park, Florida. *Coral Reefs*, 23(1):48–59.

Burke, R. D. (1986). Pheromones and the gregarious settlement of marine invertebrate larvae. *Bulletin of marine science*, 39(2):323–331.

Burlakova, L. E., Karatayev, A. Y., and Karatayev, V. A. (2012). Invasive mussels induce community changes by increasing habitat complexity. *Hydrobiologia*, 685(1):121–134.

Burns, J. H., Delparte, D., Gates, R. D., and Takabayashi, M. (2015a). Utilizing underwater three-dimensional modeling to enhance ecological and biological studies of coral reefs. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 40(5W5):61–66.

Burns, J. H., Fukunaga, A., Pascoe, K. H., Runyan, A., Craig, B. K., Talbot, J., Pugh, A., and Kosaki, R. K. (2019). 3D habitat complexity of coral reefs in the Northwestern Hawaiian islands is driven by coral assemblage structure. In *ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences*, volume 42, pages 61–67.

Burns, J. H. R., Delparte, D., Gates, R. D., and Takabayashi, M. (2015b). Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ*, 2015(7):e1077.

Butman, C. (1987). Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. *Oceanogr. Mar. Biol*, 25:113–165.

Bythell, J., Pan, P., and Lee, J. (2001). Three-dimensional morphometric measurements of reef corals using underwater photogrammetry techniques. *Coral Reefs*, 20(3):193–199.

Carballo, J. L. (2006). Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Ecoscience*, 13(1):119–130.

Carballo, J. L. and Ávila, E. (2004). Population dynamics of a mutualistic interaction between the sponge *Haliclona caerulea* and the red alga *Jania adherens*. *Marine Ecology Progress Series*, 279:93–104.

Cárdenas, C. A., Davy, S. K., and Bell, J. J. (2012). Correlations between algal abundance, environmental variables and sponge distribution patterns on southern hemisphere temperate rocky reefs. *Aquatic Biology*, 16(3):229–239.

Cheshire, A. C. and Wilkinson, C. R. (1991). Modelling the photosynthetic production by sponges on Davies Reef, Great Barrier Reef. *Marine Biology*, 109(1):13–18.

Chia, F. S., Buckland-Nicks, J., and Young, C. M. (1984). Locomotion of marine invertebrate larvae: a review. *Canadian Journal of Zoology*, 62(7):1205–1222.

Clavico, E. E., Muricy, G., Da Gama, B. A., Batista, D., Ventura, C. R., and Pereira, R. C. (2006). Ecological roles of natural products from the marine sponge *Geodia corticostylifera*. *Marine Biology*, 148(3):479–488.

Cowen, R. K. and Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Annual Review of Marine Science*, 1:443–466.

Cranfield, H. J., Rowden, A. A., Smith, D. J., Gordon, D. P., and Michael, K. P. (2004). Macrofaunal assemblages of benthic habitat of different complexity and the proposition of a model of biogenic reef habitat regeneration in Foveaux Strait, New Zealand. *Journal of Sea Research*, 52(2):109–125.

Crisp, D. and Ryland, J. (1960). Influence of filming and of surface texture on the settlement of marine organisms. *Nature*, 185(4706):119–119.

Cruz-Barraza, J. A., Carballo, J. L., Bautista-Guerrero, E., and Nava, H. (2011). New species of excavating sponges (Porifera: Demospongiae) on coral reefs from the Mexican Pacific Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 91(5):999–1013.

Czarnoleski, M., Michalczyk, Ł., and Pajdak-Stós, A. (2004). Substrate preference in settling zebra mussels *Dreissena polymorpha*. *Archiv fur Hydrobiologie*, 159(2):263–270.

Darling, E. S., Graham, N. A., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., and Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, 36(2):561–575.

Diaz, M. C. and Rützler, K. (2001). Sponges: An essential component of Caribbean coral reefs. *Bulletin of Marine Science*, 69(2):535–546.

Drap, P., Seinturier, J., Hijazi, B., Merad, D., Boi, J. M., Chemisky, B., Seguin, E., and Long, L. (2015). The ROV 3D project: Deep-sea underwater survey using photogrammetry: Applications for underwater archaeology. *Journal on Computing and Cultural Heritage*, 8(4).

Dreanno, C., Kirby, R. R., and Clare, A. S. (2006). Locating the barnacle settlement pheromone: Spatial and ontogenetic expression of the settlement-inducing protein complex of *Balanus amphitrite*. *Proceedings of the Royal Society B: Biological Sciences*, 273(1602):2721–2728.

Efron, B. and Tibshirani, R. (1985). The bootstrap method for assessing statistical accuracy. *Behaviormetrika*, 12(17):1–35.

Ettinger-Epstein, P., Whalan, S., Battershill, C. N., and De Nys, R. (2008). A hierarchy of settlement cues influences larval behaviour in a coral reef sponge. *Marine Ecology Progress Series*, 365:103–113.

Fabricius, K. E., De'ath, G., Noonan, S., and Uthicke, S. (2013). Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proceedings of the Royal Society B: Biological Sciences*, 281(1775).

Fallon, S. J., James, K., Norman, R., Kelly, M., and Ellwood, M. J. (2010). A simple radiocarbon dating method for determining the age and growth rate of deep-sea sponges. *Nuclear Instruments and Methods in Physics Research, Section B: Beam Interactions with Materials and Atoms*, 268(7-8):1241–1243.

Ferrari, R., Figueira, W. F., Pratchett, M. S., Boube, T., Adam, A., Kobelkowsky-Vidrio, T., Doo, S. S., Atwood, T. B., and Byrne, M. (2017). 3D photogrammetry quantifies growth and external erosion of individual coral colonies and skeletons. *Scientific Reports*, 7(1):16737.

Fukunaga, A., Burns, J. H., Craig, B. K., and Kosaki, R. K. (2019). Integrating three-dimensional benthic habitat characterization techniques into ecological monitoring of coral reefs. *Journal of Marine Science and Engineering*, 7(2):27.

Gaino, E., Baldacconi, R., and Corriero, G. (2007). Post-larval development of the commercial sponge *Spongia officinalis* L. (Porifera, Demospongiae). *Tissue and Cell*, 39(5):325–334.

Gambi, M., Nowell, A., and Jumars, P. (1990). Flume observations on flow dynamics in *Zostera marina* (eelgrass) beds. *Marine Ecology Progress Series*, 61:159–169.

Gerdes, K., Arbizu, P. M., Schwarz-Schampera, U., Schwentner, M., and Kihara, T. C. (2019). Detailed mapping of hydrothermal vent fauna: A 3D reconstruction approach based on video imagery. *Frontiers in Marine Science*, 6(MAR).

Gilinsky, E. (1984). The role of fish predation and spatial heterogeneity in determining benthic community structure. *Ecology*, 65(2):455–468.

Grabowski, J. H., Hughes, A. R., and Kimbro, D. L. (2008). Habitat complexity influences cascading effects of multiple predators. *Ecology*, 89(12):3413–3422.

Graham, N. A. and Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, 32(2):315–326.

Graham, N. A., Wilson, S. K., Jennings, S., Polunin, N. V., Robinson, J., Bijoux, J. P., and Daw, T. M. (2007). Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation biology*, 21(5):1291–1300.

Gratwicke, B. and Speight, M. (2005a). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of fish biology*, 66(3):650–667.

Gratwicke, B. and Speight, M. R. (2005b). Effects of habitat complexity on caribbean marine fish assemblages. *Marine Ecology Progress Series*, 292:301–310.

Guo, T., Capra, A., Troyer, M., Gruen, A., Brooks, A. J., Hench, J. L., Schmitt, R. J., Holbrook, S. J., and Dubbini, M. (2016). Accuracy assessment of underwater photogrammetric three dimensional modelling for coral reefs. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences - ISPRS Archives*, 41:821–828.

Hadfield, M. G. (2011). Biofilms and marine invertebrate larvae: What bacteria produce that larvae use to choose settlement sites. *Annual Review of Marine Science*, 3:453–470.

Hadfield, M. G. and Paul, V. J. (2001). Natural chemical cues for settlement and metamorphosis of marine invertebrate larvae. *Marine chemical ecology*, 13:431–461.

Harding, J. M. and Mann, R. (2001). Oyster reefs as fish habitat: opportunistic use of restored reefs by transient fishes. *Journal of Shellfish Research*, 20(3):951.

Harrison, P. L. and Wallace, C. (1990). Reproduction, dispersal and recruitment of scleractinian corals. *Ecosystems of the world*, 25:133–207.

Hauser, A., Attrill, M. J., and Cotton, P. A. (2006). Effects of habitat complexity on the diversity and abundance of macrofauna colonising artificial kelp holdfasts. *Marine Ecology Progress Series*, 325:93–100.

Hills, J., Thomason, J., and Muhl, J. (1999). Settlement of barnacle larvae is governed by euclidean and not fractal surface characteristics. *Functional Ecology*, 13(6):868–875.

Huggett, M. J., Williamson, J. E., De Nys, R., Kjelleberg, S., and Steinberg, P. D. (2006). Larval settlement of the common Australian sea urchin *Heliocidaris erythrogramma* in response to bacteria from the surface of coralline algae. *Oecologia*, 149(4):604–619.

Irving, A. D. and Connell, S. D. (2002). Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: Algal versus invertebrate dominated assemblages. *Marine Ecology Progress Series*, 245:83–91.

Jackson, G. A. (1997). Currents in the high drag environment of a coastal kelp stand off California. *Continental Shelf Research*, 17(15):1913–1928.

Jacobs, D. K., Nakanishi, N., Yuan, D., Camara, A., Nichols, S. A., and Hartenstein, V. (2007). Evolution of sensory structures in basal metazoa. *Integrative and Comparative Biology*, 47(5):712–723.

Jana, D. and Bairagi, N. (2014). Habitat complexity, dispersal and metapopulations: Macroscopic study of a predator-prey system. *Ecological Complexity*, 17(1):131–139.

Kelaher, B. P. and Carlos Castilla, J. (2005). Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale coastal upwelling on the coast of Northern Chile. *Estuarine, Coastal and Shelf Science*, 63(1-2):155–165.

Koehl, M. R. (2007). Mini review: Hydrodynamics of larval settlement into fouling communities. *Biofouling*, 23(5):357–368.

Komyakova, V., Munday, P. L., and Jones, G. P. (2013). Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE*, 8(12).

Konar, B. and Iken, K. (2005). Competitive dominance among sessile marine organisms in a high Arctic boulder community. *Polar Biology*, 29(1):61–64.

Kostylev, V. E., Erlandsson, J., Mak, Y. M., and Williams, G. A. (2005). The relative importance of habitat complexity and surface area in assessing biodiversity: Fractal application on rocky shores. *Ecological Complexity*, 2(3):272–286.

Kovalenko, K. E., Thomaz, S. M., and Warfe, D. M. (2012). Habitat complexity: Approaches and future directions. *Hydrobiologia*, 685(1):1–17.

Lau, S. C., Thiyagarajan, V., Cheung, S. C., and Qian, P.-Y. (2005). Roles of bacterial community composition in biofilms as a mediator for larval settlement of three marine invertebrates. *Aquatic microbial ecology*, 38(1):41–51.

Lee, J. T., Widdows, J., Jones, M. B., and Coleman, R. A. (2004). Settlement of megalopae and early juveniles of the velvet swimming crab *Necora puber* (Decapoda: Portunidae) in flow conditions. *Marine Ecology Progress Series*, 272:191–202.

Lee, S. C. (2006). Habitat complexity and consumer-mediated positive feedbacks on a caribbean coral reef. *Oikos*, 112(2):442–447.

Leon, J. X., Roelfsema, C. M., Saunders, M. I., and Phinn, S. R. (2015). Measuring coral reef terrain roughness using 'Structure-from-Motion' close-range photogrammetry. *Geomorphology*, 242:21–28.

Lingo, M. E. and Szedlmayer, S. T. (2006). The influence of habitat complexity on reef fish communities in the northeastern Gulf of Mexico. *Environmental Biology of Fishes*, 76(1):71–80.

Lucieer, V. (2007). Morphometric characterisation of rocky reef using multibeam acoustic bathymetric data. In *International Geoscience and Remote Sensing Symposium (IGARSS)*, pages 905–909. IEEE.

Luckhurst, B. E. and Luckhurst, K. (1978). Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology*, 49(4):317–323.

MacArthur, R. H. and MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42(3):594–598.

Maldonado, M. and Uriz, M. J. (1998). Microrefuge exploitation by subtidal encrusting sponges: Patterns of settlement and post-settlement survival. *Marine Ecology Progress Series*, 174:141–150.

Maldonado, M. and Young, C. M. (1996). Effects of physical factors on larval behavior, settlement and recruitment of four tropical demosponges. *Marine Ecology Progress Series*, 138(1-3):169–180.

Marin, A. and Belluga, M. D. L. (2005). Sponge coating decreases predation on the bivalve *Arca noae*. *Journal of Molluscan Studies*, 71(1):1–6.

Marre, G., Holon, F., Luque, S., Boissery, P., and Deter, J. (2019). Monitoring marine habitats with photogrammetry: A cost-effective, accurate, precise and high-resolution reconstruction method. *Frontiers in Marine Science*, 6(May).

Marsh, J. A. (1970). Primary Productivity of Reef-Building Calcareous Red Algae. *Ecology*, 51(2):255–263.

Matias, M. G., Underwood, A. J., Hochuli, D. F., and Coleman, R. A. (2010). Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates. *Ecology*, 91(7):1908–1915.

Metaxas, A. (2001). Behaviour in flow: Perspectives on the distribution and dispersion of meroplanktonic larvae in the water column. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(1):86–98.

Meyer, J. L. and Schultz, E. T. (1985). Tissue condition and growth rate of corals associated with schooling fish. *Limnology and Oceanography*, 30(1):157–166.

Nava, H. and Carballo, J. L. (2008). Chemical and mechanical bioerosion of boring sponges from Mexican Pacific coral reefs. *Journal of Experimental Biology*, 211(17):2827–2831.

Noernberg, M. A., Fournier, J., Dubois, S., and Populus, J. (2010). Using airborne laser altimetry to estimate *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs volume in tidal flat environments. *Estuarine, Coastal and Shelf Science*, 90(2):93–102.

Nornes, S. M., Ludvigsen, M., Ødegrd, Ø., and Sørensen, A. J. (2015). Underwater photogrammetric mapping of an intact standing steel wreck with ROV. *IFAC-PapersOnLine*, 28(2):206–211.

Öhman, M. C. and Rajasuriya, A. (1998). Relationships between habitat structure and fish communities on coral. *Environmental biology of fishes*, 53(1):19–31.

Olinger, L. K., Scott, A. R., McMurray, S. E., and Pawlik, J. R. (2019). Growth estimates of Caribbean reef sponges on a shipwreck using 3D photogrammetry. *Scientific reports*, 9(1):18398.

Osman, R. W. and Whitlatch, R. B. (1995). The influence of resident adults on recruitment: a comparison to settlement. *Journal of Experimental Marine Biology and Ecology*, 190(2):169–198.

Palumbi, S. R. (1985). Spatial Variation in an Alga-Sponge Commensalism and the Evolution of Ecological Interactions. *The American Naturalist*, 126(2):267–274.

Pawlik, J. R. (1992). Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and marine biology: an annual review. Vol. 30*, pages 273–335.

Pineda, J. and Caswell, H. (1997). Dependence of settlement rate on suitable substrate area. *Marine Biology*, 129(3):541–548.

Pires, F. R. (2007). Padrões de distribuição e taxonomia para os porifera da região central do algarve. Master's thesis, University of Algarve.

Platt, T. (1993). Concepts in biological oceanography: An interdisciplinary primer (P. A. Jumars). *Limnology and Oceanography*, 38(8):1842–1843.

Pratchett, M. S., Munday, P., Wilson, S. K., Graham, N., Cinner, J. E., Bellwood, D. R., Jones, G. P., Polunin, N., and McClanahan, T. (2008). Effects of climate-induced coral bleaching on coral-reef fishes. *Ecological and economic consequences. Oceanography and Marine Biology: Annual Review*, 46:251–296.

Preciado, I. and Maldonado, M. (2005). Reassessing the spatial relationship between sponges and macroalgae in sublittoral rocky bottoms: A descriptive approach. *Helgoland Marine Research*, 59(2):141–150.

Price, S. A., Holzman, R., Near, T. J., and Wainwright, P. C. (2011). Coral reefs promote the evolution of morphological diversity and ecological novelty in labrid fishes. *Ecology Letters*, 14(5):462–469.

Raoult, V., David, P. A., Dupont, S. F., Mathewson, C. P., O'Neill, S. J., Powell, N. N., and Williamson, J. E. (2016). GoPros^{TM} as an underwater photogrammetry tool for citizen science. *PeerJ*, 2016(4):e1960.

Roberts, D. E., Davis, A. R., and Cummins, S. P. (2006). Experimental manipulation of shade, silt, nutrients and salinity on the temperate reef sponge *Cymbastela concentrica*. *Marine Ecology Progress Series*, 307:143–154.

Rutzler, K. and Ruetzler, K. (2003). Sponges on coral reefs: a community shaped by competitive cooperation. *Boll Mus Ist Biol Univ Genova*, 68:85–148.

Sánchez, F., Serrano, A., and Ballesteros, M. G. (2009). Photogrammetric quantitative study of habitat and benthic communities of deep Cantabrian Sea hard grounds. *Continental Shelf Research*, 29(8):1174–1188.

Sano, M., Shimizu, M., and Nose, Y. (1987). Long-term effects of destruction of hermatypic corals by *Acanthaster planci* infestation on reef fish communities at Iriomote Island, Japan. *Mar Ecol Prog Ser*, 37:191–199.

Schejter, L. and Spivak, E. (2005). Morphometry, sexual maturity, fecundity and epibiosis of the South American spider crab *Libidoclaea granaria* (Brachyura: Majoidea). *Journal of the Marine Biological Association of the United Kingdom*, 85(4):857–863.

Skinner, L. F. and Coutinho, R. (2005). Effect of microhabitat distribution and substrate roughness on barnacle *Tetraclita stalactifera* (Lamarck, 1818) settlement. *Brazilian Archives of Biology and Technology*, 48(1):109–113.

Smith, R. S., Johnston, E. L., and Clark, G. F. (2014). The role of habitat complexity in community development is mediated by resource availability. *PLoS ONE*, 9(7).

Snavely, N., Seitz, S. M., and Szeliski, R. (2008). Modeling the world from Internet photo collections. *International Journal of Computer Vision*, 80(2):189–210.

St. Pierre, J. I. and Kovalenko, K. E. (2014). Effect of habitat complexity attributes on species richness. *Ecosphere*, 5(2):1–10.

Stimson, J. and Kinzie, R. A. (1991). The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *Journal of Experimental Marine Biology and Ecology*, 153(1):63–74.

Storlazzi, C. D., Dartnell, P., Hatcher, G. A., and Gibbs, A. E. (2016). End of the chain? Rugosity and fine-scale bathymetry from existing underwater digital imagery using structure-from-motion (SfM) technology. *Coral Reefs*, 35(3):889–894.

Swanson, R. L., Williamson, J. E., De Nys, R., Kumar, N., Bucknall, M. P., and Steinberg, P. D. (2004). Induction of settlement of larvae of the sea urchin *Holopneustes purpurascens* by histamine from a host alga. *The Biological Bulletin*, 206(3):161–172.

Ter Braak, C. J. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67(5):1167–1179.

Tokeshi, M. and Arakaki, S. (2012). Habitat complexity in aquatic systems: Fractals and beyond. *Hydrobiologia*, 685(1):27–47.

Ward-Paige, C. A., Risk, M. J., Sherwood, O. A., and Jaap, W. C. (2005). Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. *Marine Pollution Bulletin*, 51(5-7):570–579.

Warfe, D. M. and Barmuta, L. A. (2004). Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia*, 141(1):171–178.

Westoby, M. J., Brasington, J., Glasser, N. F., Hambrey, M. J., and Reynolds, J. M. (2012). 'Structure-from-Motion' photogrammetry: A low-cost, effective tool for geoscience applications. *Geomorphology*, 179:300–314.

Whalan, S., Abdul Wahab, M. A., Sprungala, S., Poole, A. J., and De Nys, R. (2015). Larval settlement: The role of surface topography for sessile coral reef invertebrates. *PLoS ONE*, 10(2).

Whalan, S., Webster, N. S., and Negri, A. P. (2012). Crustose coralline algae and a cnidarian neuropeptide trigger larval settlement in two coral reef sponges. *PLoS ONE*.

Wildhaber, M. L., Lamberson, P. J., and Galat, D. L. (2003). A Comparison of Measures of Riverbed Form for Evaluating Distributions of Benthic Fishes. *North American Journal of Fisheries Management*, 23(2):543–557.

Wilding, T. A., Rose, C. A., and Downie, M. J. (2007). A novel approach to measuring subtidal habitat complexity. *Journal of Experimental Marine Biology and Ecology*, 353(2):279–286.

Wilkinson, C. R. (1987). Interocean differences in size and nutrition of Coral Reef sponge populations. *Science*, 236(4809):1654–1657.

Williamson, J. E., De Nys, R., Kumar, N., Carson, D. G., and Steinberg, P. D. (2000). Induction of metamorphosis in the sea urchin *Holopneustes purpurascens* by a metabolite complex from the algal host delisea pulchra. *The Biological Bulletin*, 198(3):332–345.

Willis, S., Winemiller, K., and Lopez-Fernandez, H. (2005). Habitat structural complexity and morphological diversity of fish assemblages in a neotropical floodplain river. *Oecologia*, 142(2):284–295.

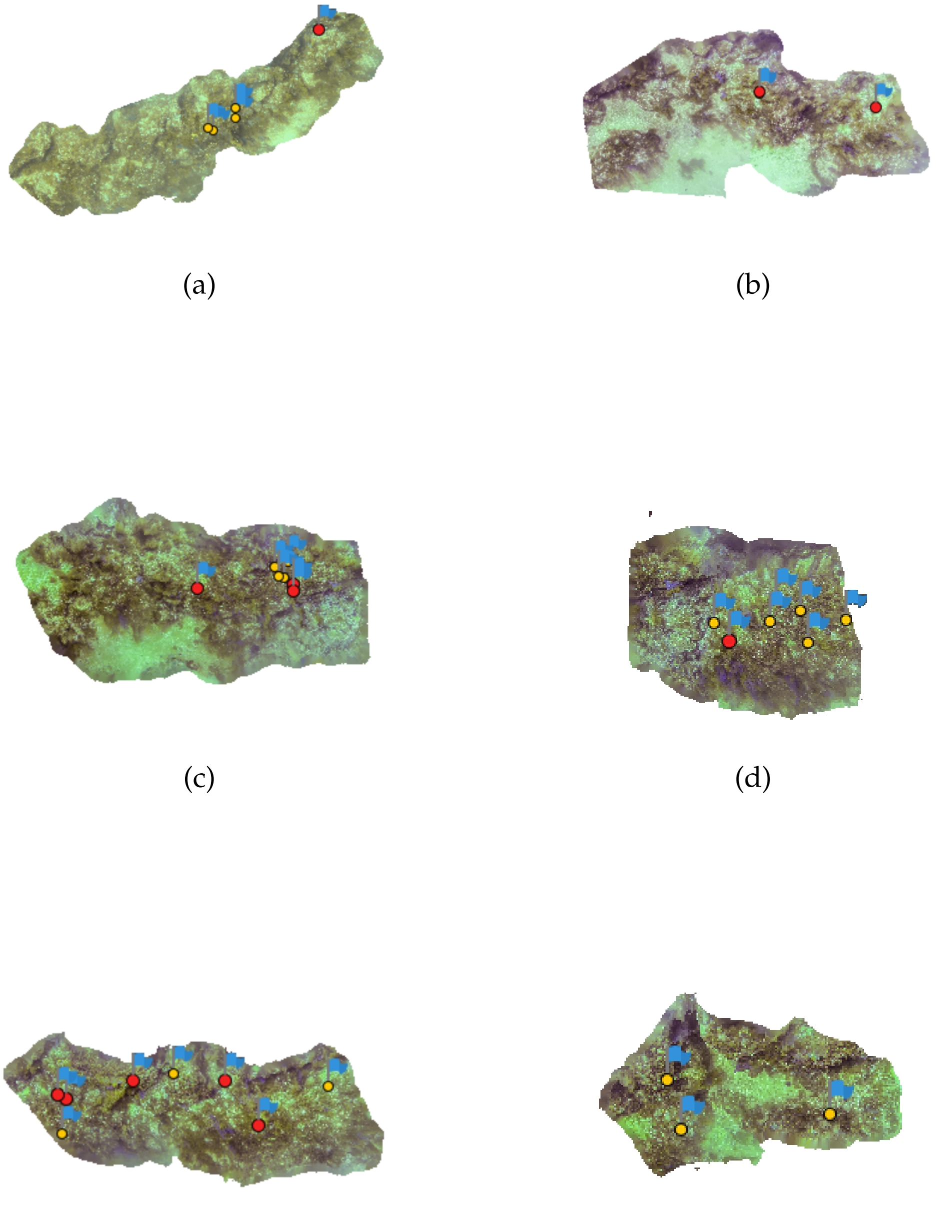
Wilson, S. K., Graham, N. A., Pratchett, M. S., Jones, G. P., and Polunin, N. V. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology*, 12(11):2220–2234.

Wulff, J. (2012). Ecological Interactions and the Distribution, Abundance, and Diversity of Sponges. In *Advances in Marine Biology*, volume 61, pages 273–344. Elsevier.

Yager, K., Clark, C., Gambin, T., and Wood, Z. J. (2019). Underwater Photogrammetry Reconstruction: GPU Texture Generation from Videos Captured via AUV. In *Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics)*, volume 11844 LNCS, pages 127–138.

Young, G. C., Dey, S., Rogers, A. D., and Exton, D. (2017). Cost and time-effective method for multiscale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D models. *PLoS ONE*, 12(4).

Appendix A - Models

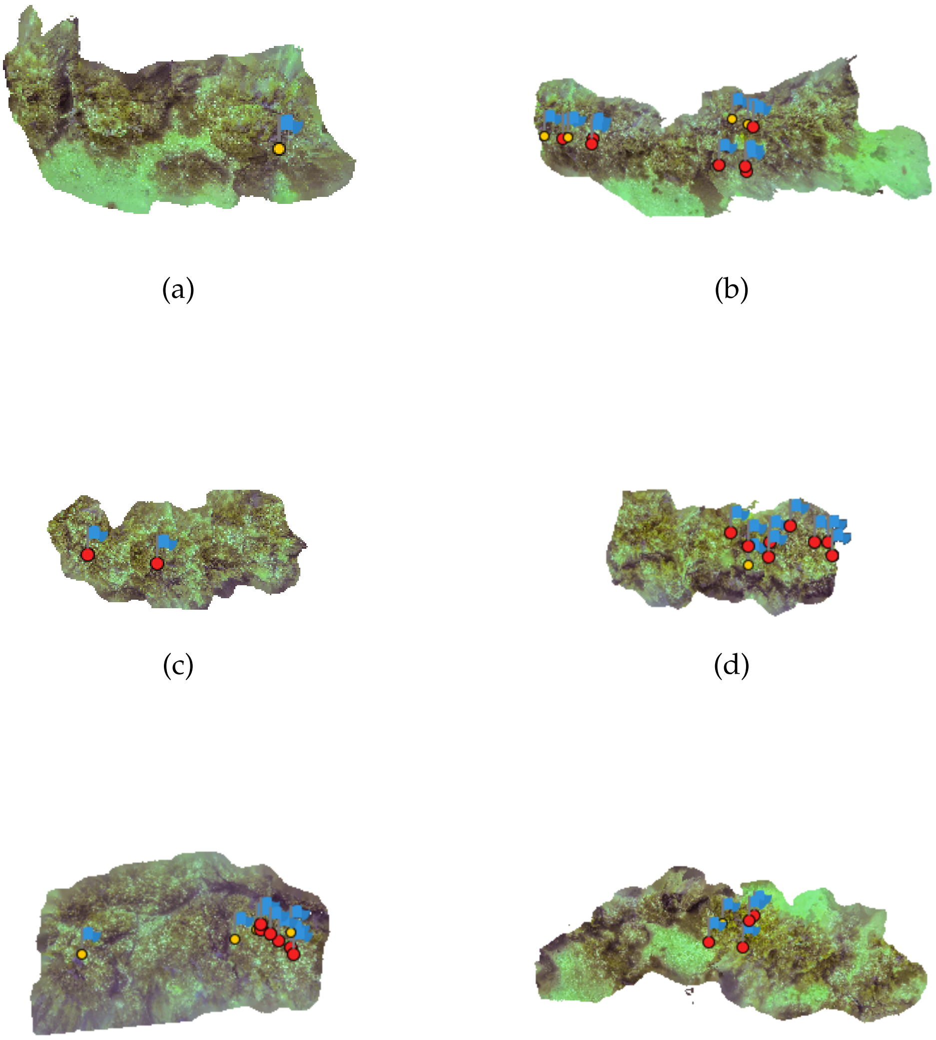


(a) (b)

(c) (d)

(e) (f)

Figure 5.1: Images of the 3D models of different areas of Pedra da Cacela reef. The red markers show the positions of *Phorbas* sp., and the yellow markers the positions of *Spongia* sp.. Generated with Agisoft® Metashape.

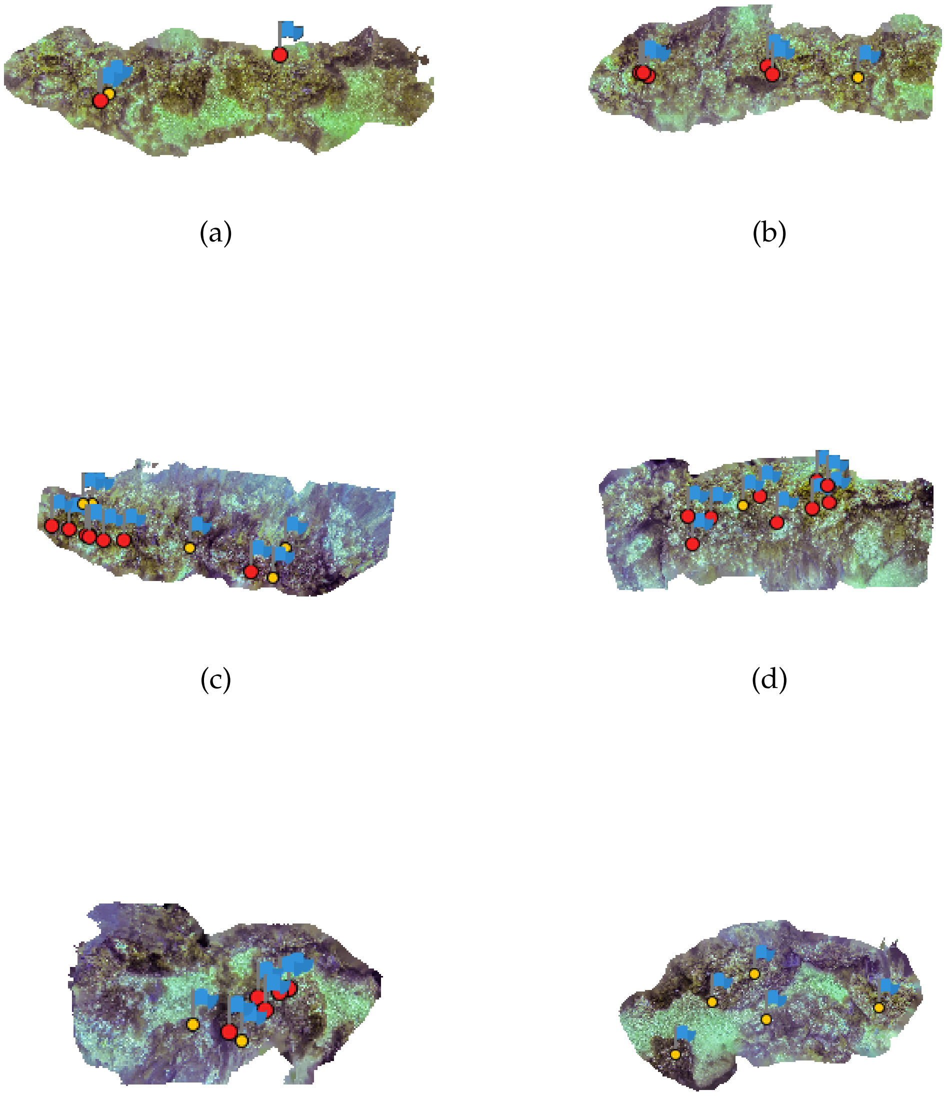


(a) (b)

(c) (d)

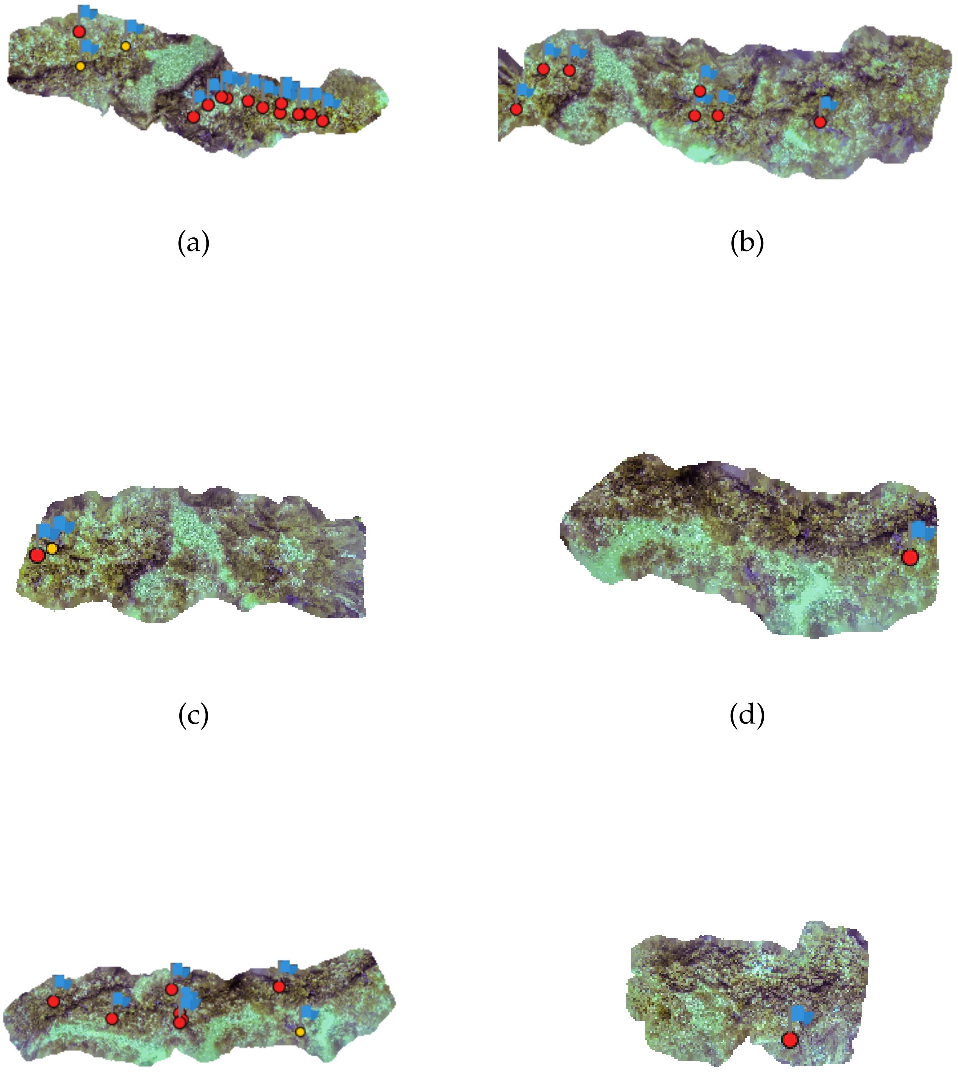
(e) (f)

Figure 5.2: Images of the 3D models of different areas of Pedra da Cacela reef. The red markers show the positions of *Phorbas* sp., and the yellow markers the positions of *Spongia* sp.. Generated with Agisoft® Metashape.



(a) (b) (c) (d) (e) (f)

Figure 5.3: Images of the 3D models of different areas of Pedra da Cacela reef. The red markers show the positions of *Phorbas* sp., and the yellow markers the positions of *Spongia* sp.. Generated with Agisoft® Metashape.



(a)

(b)

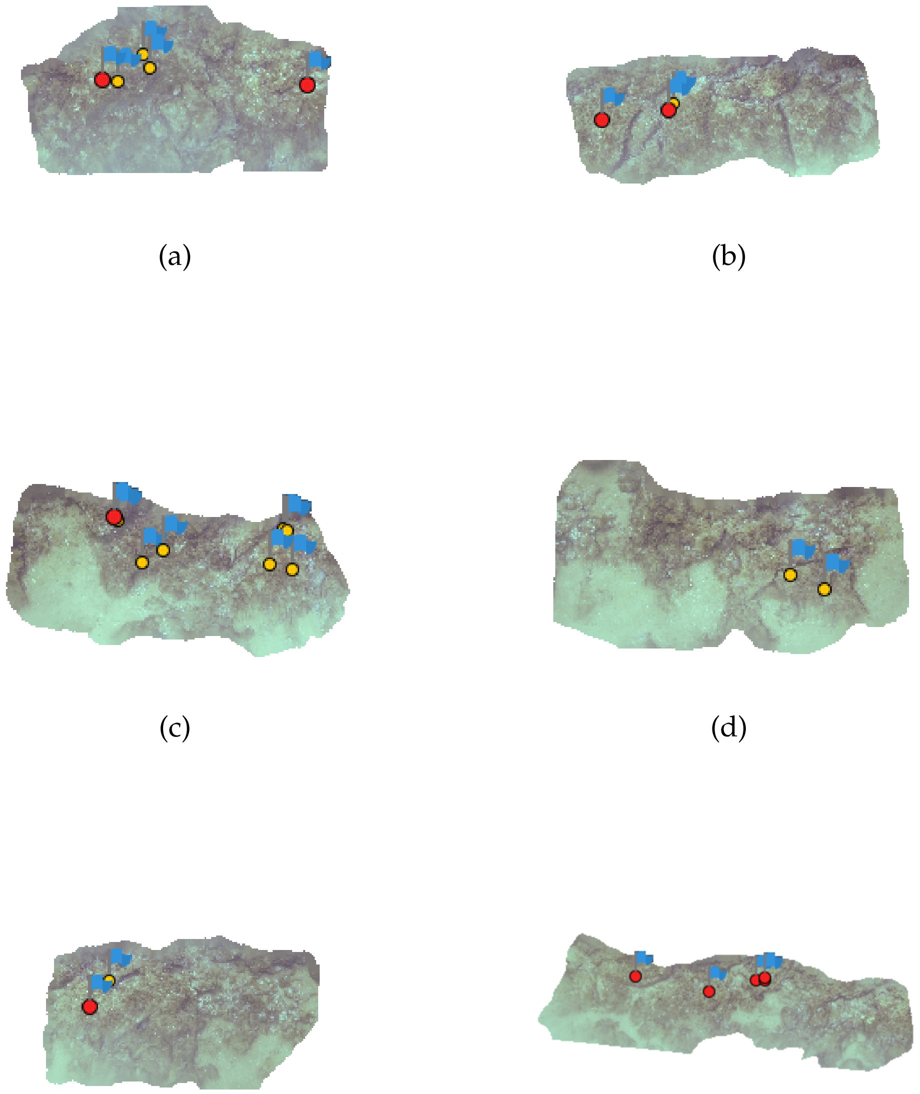
(c)

(d)

(e)

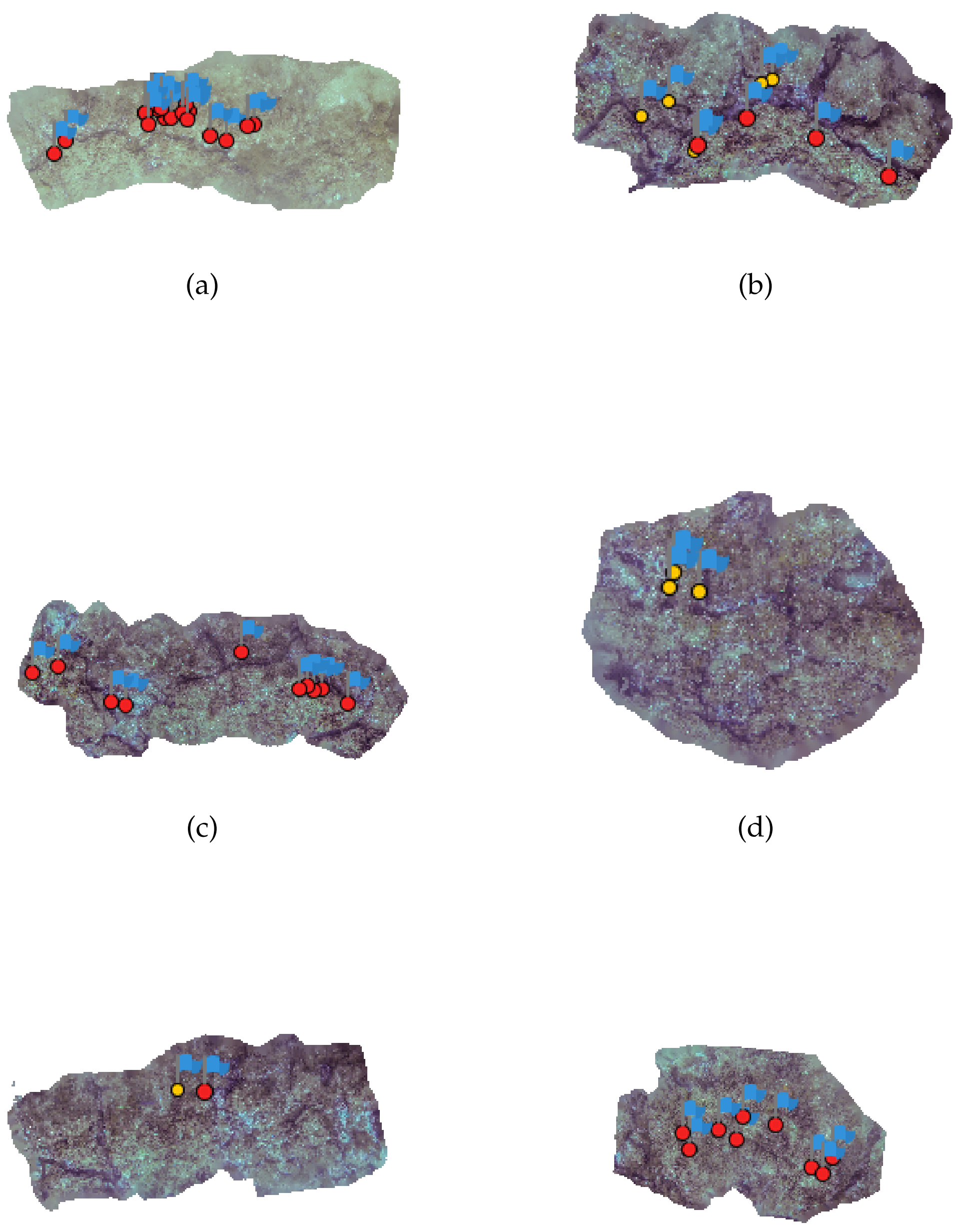
(f)

Figure 5.4: Images of the 3D models of different areas of Pedra da Cacela reef. The red markers show the positions of *Phorbas* sp., and the yellow markers the positions of *Spongia* sp.. Generated with Agisoft® Metashape.



(a) (b) (c) (d) (e) (f)

Figure 5.5: Images of the 3D models of different areas of Pedra do Lacém reef. The red markers show the positions of *Phorbas* sp., and the yellow markers the positions of *Spongia* sp.. Generated with Agisoft® Metashape.

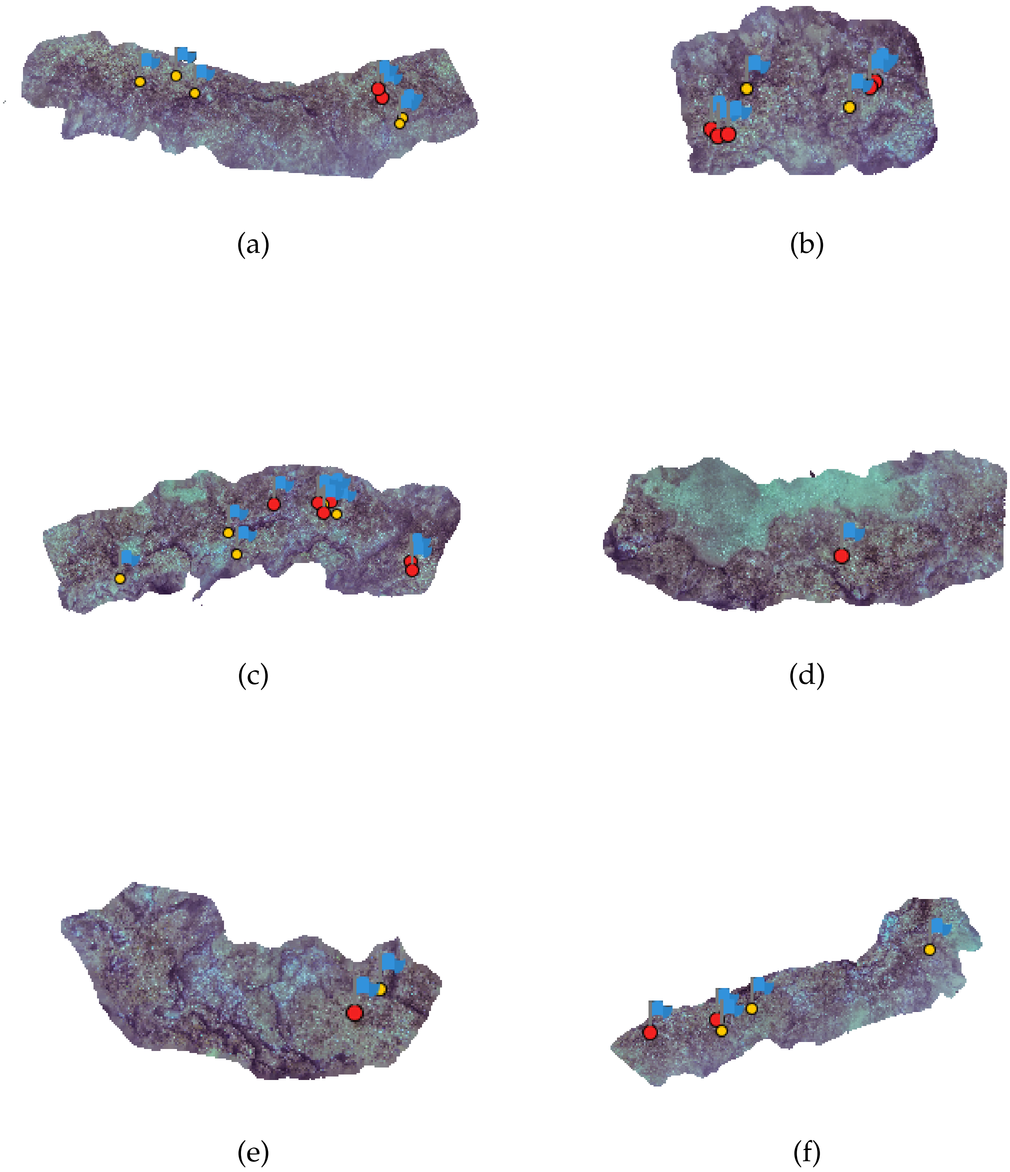


(a) (b)

(c) (d)

(e) (f)

Figure 5.6: Images of the 3D models of different areas of Pedra do Lacém reef. The red markers show the positions of *Phorbas* sp., and the yellow markers the positions of *Spongia* sp.. Generated with Agisoft® Metashape.



(a) (b) (c) (d) (e) (f)

Figure 5.7: Images of the 3D models of different areas of Pedra do Lacém reef. The red markers show the positions of *Phorbas* sp., and the yellow markers the positions of *Spongia* sp.. Generated with Agisoft® Metashape.

Appendix B - Tables

Table 5.1: Values of habitat complexity variables and sponge species found in each area analysed for Pedra da Cacela reef. Values of minimum distance between each sponge and the feature with high slope in the area (Distance (m)) and the standard deviations for rugosity (R_SD) and slope (S_SD) are also shown. The unidentified sponge species were identified by their colour (Blue - B, Yellow/Brown - YB, Yellow - Y).

Model	Area	Rugosity	R_SD	FD 1.8-0.6	FD 0.6-0.3	FD 0.3-0.15	Slope	S_SD	Distance (m)	Species
1	A1	0.740	0.057	2.034	2.149	2.085	36.535	22.152	-	-
	A2	0.745	0.078	2.075	2.043	2.097	36.458	20.929	-	-
	A3	0.863	0.052	2.009	2.043	2.076	31.137	19.095	-	-
	A4	0.734	0.068	2.062	2.058	2.138	41.109	21.125	-	-
	A5	0.805	0.056	2.029	2.085	2.097	35.925	20.502	0.500	*Spongia* sp.
									0.286	*Spongia* sp.
									1.631	*Spongia* sp.
									1.847	*Spongia* sp.
	A6	0.597	0.078	2.112	2.296	2.178	44.416	23.226	-	-
	A7	0.698	0.040	2.114	2.124	2.107	40.147	22.461	-	-
	A8	0.764	0.056	2.098	2.052	2.098	38.660	19.911	-	-
2	A1	0.729	0.058	2.009	2.109	2.119	23.773	22.033	-	-
	A2	0.860	0.134	2.072	2.035	2.043	24.076	18.354	-	-
	A3	0.785	0.090	2.036	2.138	2.100	32.266	21.902	-	-
	A4	0.890	0.074	2.015	2.047	2.055	22.098	18.507	-	-
	A5	0.769	0.103	2.035	2.143	2.144	34.753	20.506	1.516	*Spongia* sp.
									1.484	*Phorbas* sp.
	A6	0.766	0.069	2.011	2.044	2.099	36.368	20.170	-	-
	A7	0.717	0.047	2.072	2.092	2.161	38.467	20.497	-	-
	A8	0.755	0.137	2.021	2.064	2.103	35.717	21.020	-	-
3	A1	0.745	0.073	2.013	2.231	2.114	40.510	21.482	-	-
	A2	0.829	0.133	2.081	2.007	2.127	31.082	20.468	-	-
	A3	0.834	0.064	2.014	2.059	2.106	32.126	19.224	1.903	*Phorbas* sp.
	A4	0.794	0.162	2.034	2.124	2.152	35.275	18.984	2.131	*Spongia* sp.
									2.285	*Spongia* sp.
									1.815	*Spongia* sp.
									1.964	*Spongia* sp.
									1.423	*Phorbas* sp.
									1.291	*Phorbas* sp.
4	A1	0.882	0.044	2.012	2.034	2.050	29.729	17.859	0.772	*Spongia* sp.
									1.097	*Spongia* sp.
									1.233	*Spongia* sp.
									0.338	*Spongia* sp.
	A2	0.699	0.075	2.138	2.185	2.113	39.497	20.881	1.400	*Spongia* sp.
5	A1	0.713	0.131	2.053	2.076	2.182	37.587	20.332	0.799	*Phorbas* sp.
									0.930	*Phorbas* sp.
	A2	0.711	0.085	2.098	2.168	2.155	34.801	21.113	2.312	*Spongia* sp.
	A3	0.819	0.062	2.037	2.058	2.098	34.513	19.744	1.075	*Phorbas* sp.
6	A1	0.781	0.101	2.039	2.146	2.091	35.627	21.110	0.824	*Spongia* sp.
									1.953	*Spongia* sp.
	A2	0.592	0.096	2.209	2.076	2.146	36.056	24.152	1.922	*Spongia* sp.
7	A1	0.723	0.098	2.073	2.104	2.162	36.832	22.596	0.978	Y
	A2	0.794	0.052	2.036	2.072	2.112	32.888	21.200	-	-
	A3	0.699	0.063	2.059	2.095	2.099	42.308	21.394	0.925	YB
									1.163	*Spongia* sp.
8	A1	0.766	0.093	2.009	2.065	2.139	37.625	20.229	1.605	*Spongia* sp.
									1.197	*Phorbas* sp.
	A2	0.803	0.078	2.058	2.069	2.090	32.137	18.884	0.617	*Phorbas* sp.
									0.520	*Phorbas* sp.
	A3	0.779	0.071	2.032	2.074	2.122	35.075	19.383	-	-
	A4	0.778	0.065	2.056	2.033	2.090	39.898	21.394	-	-
	A5	0.748	0.077	2.055	2.139	2.137	36.042	20.004	0.526	YB
									1.835	*Spongia* sp.
									2.409	*Spongia* sp.
	A6	0.769	0.075	2.035	2.081	2.173	37.602	19.843	-	-

Table 5.2: Values of habitat complexity variables and sponge species found in each area analysed for Pedra da Cacela reef. Values of minimum distance between each sponge and the feature with high slope in the area (Distance (m)) and the standard deviations for rugosity (R_SD) and slope (S_SD) are also shown. The unidentified sponge species were identified by their colour (Blue - B, Yellow/Brown - YB, Yellow - Y).

Model	Area	Rugosity	R_SD	FD 1.8-0.6	FD 0.6-0.3	FD 0.3-0.15	Slope	S_SD	Distance (m)	Species
9	A1	0.702	0.117	2.055	2.081	2.180	36.762	20.127	1.296	YB
									1.494	*Phorbas* sp.
	A2	0.755	0.076	2.058	2.102	2.147	36.288	20.490	2.155	*Phorbas* sp.
	A3	0.672	0.061	2.046	2.137	2.178	39.373	21.073	-	-
10	A1	0.648	0.077	2.098	2.200	2.239	41.727	22.734	-	-
	A2	0.703	0.101	2.068	2.154	2.158	37.793	22.579	2.032	*Phorbas* sp.
									2.139	*Phorbas* sp.
	A3	0.741	0.097	2.024	2.123	2.179	36.463	20.720	0.075	*Phorbas* sp.
									0.459	*Phorbas* sp.
									1.017	*Phorbas* sp.
									1.692	*Phorbas* sp.
									2.111	*Phorbas* sp.
11	A1	0.848	0.059	2.030	2.037	2.066	34.587	18.551	1.642	*Spongia* sp.
									0.534	*Spongia* sp.
									1.510	*Phorbas* sp.
									1.488	*Phorbas* sp.
									0.870	*Phorbas* sp.
									0.964	*Phorbas* sp.
									1.003	*Phorbas* sp.
									1.182	*Phorbas* sp.
	A2	0.817	0.089	2.094	2.076	2.076	36.372	19.340	0.175	*Spongia* sp.
	A3	0.788	0.062	2.095	2.094	2.091	37.733	18.830	-	-
	A4	0.711	0.054	2.082	2.092	2.134	37.721	20.146	1.298	*Spongia* sp.
12	A1	0.745	0.132	2.129	2.116	2.131	39.496	23.175	-	-
	A2	0.656	0.079	2.055	2.173	2.198	45.266	21.066	-	-
	A3	0.648	0.070	2.034	2.212	2.192	45.868	21.145	2.137	*Spongia* sp.
									1.266	*Phorbas* sp.
									1.294	*Phorbas* sp.
									1.273	*Phorbas* sp.
	A4	0.695	0.178	2.174	2.230	2.099	32.805	23.432	-	-
	A5	0.660	0.076	2.075	2.278	2.292	41.255	24.330	-	-
13	A1	0.695	0.154	2.108	2.119	2.162	35.784	24.764	-	-
	A2	0.780	0.073	2.057	2.052	2.099	30.879	22.655	-	-
	A3	0.719	0.034	2.069	2.078	2.155	37.739	20.557	1.775	*Spongia* sp.
									2.106	*Spongia* sp.
									2.057	*Phorbas* sp.
14	A1	0.766	0.044	2.104	2.077	2.111	38.453	20.275	-	-
	A2	0.738	0.103	2.010	2.196	2.230	42.344	20.816	-	-
	A3	0.787	0.055	2.061	2.128	2.095	37.576	18.942	1.266	*Phorbas* sp.
									0.990	*Phorbas* sp.
	A4	0.771	0.040	2.015	2.178	2.156	36.789	19.959	-	-
	A5	0.760	0.125	2.141	2.138	2.136	39.629	21.994	1.734	*Phorbas* sp.
									1.367	*Phorbas* sp.
									1.591	*Phorbas* sp.
15	A1	0.711	0.075	2.075	2.158	2.096	42.663	21.021	1.980	*Phorbas* sp.
	A2	0.732	0.076	2.016	2.047	2.195	40.624	21.807	2.228	*Phorbas* sp.
									1.707	*Phorbas* sp.
16	A1	0.685	0.062	2.117	2.117	2.101	44.409	20.494	-	-
17	A1	0.862	0.050	2.016	2.016	2.056	32.841	18.851	0.645	*Phorbas* sp.
									0.526	*Phorbas* sp.
									0.955	*Phorbas* sp.
									0.328	*Phorbas* sp.
									1.821	*Phorbas* sp.
									1.951	*Phorbas* sp.
18	A1	0.716	0.095	2.119	2.158	2.169	36.458	21.801	1.186	*Phorbas* sp.
									1.352	*Phorbas* sp.
									1.688	*Phorbas* sp.
									1.862	*Phorbas* sp.
	A2	0.697	0.064	2.128	2.123	2.131	33.485	23.119	2.032	*Spongia* sp.

Table 5.3: Values of habitat complexity variables and sponge species found in each area analysed for Pedra da Cacela reef. Values of minimum distance between each sponge and the feature with high slope in the area (Distance (m)) and the standard deviations for rugosity (R_SD) and slope (S_SD) are also shown. The unidentified sponge species were identified by their colour (Blue - B, Yellow/Brown - YB, Yellow - Y).

Model	**Area**	**Rugosity**	**R_SD**	**FD 1.8-0.6**	**FD 0.6-0.3**	**FD 0.3-0.15**	**Slope**	**S_SD**	**Distance (m)**	**Species**
19	A1	0.716	0.115	2.080	2.146	2.140	35.895	22.065	-	-
	A2	0.751	0.069	2.080	2.100	2.092	31.915	21.150	1.748	*Spongia* sp.
20	A1	0.725	0.060	2.021	2.036	2.094	38.239	21.954	1.284	YB
									1.916	*Phorbas* sp.
									1.344	*Phorbas* sp.
									0.983	*Phorbas* sp.
									0.952	*Phorbas* sp.
	A2	0.739	0.053	2.014	2.158	2.086	40.827	19.876	1.655	*Spongia* sp.
									40.827	*Phorbas* sp.
21	A1	0.715	0.079	2.071	2.179	2.139	40.099	20.834	-	-
	A2	0.780	0.099	2.071	2.066	2.136	36.985	18.850	-	-
	A3	0.668	0.111	2.153	2.152	2.167	39.497	22.360	-	-
	A4	0.680	0.094	2.071	2.253	2.128	46.704	23.228	1.885	*Phorbas* sp.
	A5	0.643	0.062	2.122	2.186	2.157	45.289	23.191	-	-
	A6	0.759	0.066	2.102	2.120	2.088	42.796	21.044	-	-
	A7	0.675	0.157	2.075	2.296	2.251	44.651	21.490	1.925	*Phorbas* sp.
	A8	0.678	0.074	2.062	2.166	2.201	42.435	21.535	1.329	B
									0.753	*Phorbas* sp.
	A9	0.805	0.112	2.078	2.118	2.070	32.994	21.281	-	-
	A10	0.765	0.072	2.041	2.121	2.123	37.493	19.319	0.977	*Phorbas* sp.
									1.996	*Phorbas* sp.
22	A1	0.760	0.044	2.027	2.108	2.173	40.306	22.362	-	-
	A2	0.725	0.080	2.037	2.082	2.133	34.731	20.877	2.399	*Spongia* sp.
23	A1	0.774	0.077	2.028	2.066	2.115	35.119	18.777	1.120	*Phorbas* sp.
	A2	0.756	0.081	2.033	2.134	2.121	34.799	21.642	-	-
	A3	0.856	0.031	2.036	2.018	2.038	27.455	18.547	-	-
24	A1	0.844	0.048	2.030	2.018	2.077	31.242	19.107	1.189	*Phorbas* sp.
									1.246	*Phorbas* sp.
									1.430	*Phorbas* sp.
									1.469	*Phorbas* sp.
	A2	0.777	0.068	2.007	2.064	2.096	34.315	19.907	1.678	YB
									0.964	*Phorbas* sp.
25	A1	0.779	0.066	2.025	2.109	2.076	34.638	18.587	-	-
	A2	0.823	0.058	2.034	2.047	2.095	31.877	17.846	-	-

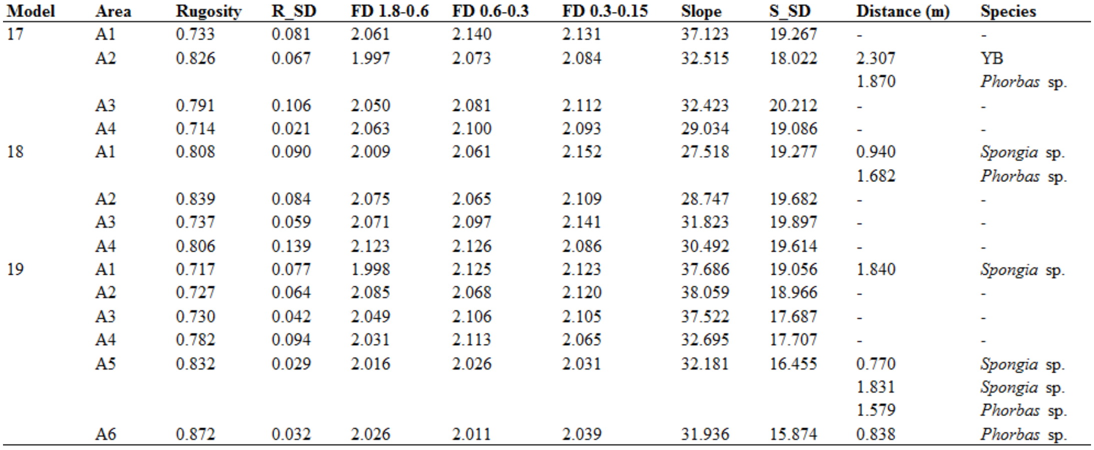
Table 5.4: Values of habitat complexity variables and sponge species found in each area analysed for Pedra do Lacém reef. Values of minimum distance between each sponge and the feature with high slope in the area (Distance (m)) and the standard deviations for rugosity (R_SD) and slope (S_SD) are also shown. The unidentified sponge species were identified by their colour (Blue - B, Yellow/Brown - YB, Yellow - Y).

Model	Area	Rugosity	R_SD	FD 1.8-0.6	FD 0.6-0.3	FD 0.3-0.15	Slope	S_SD	Distance (m)	Species
1	A1	0.885	0.045	2.013	2.053	2.058	28.171	17.622	-	-
	A2	0.780	0.060	2.048	2.195	2.093	34.429	18.852	1.622	*Spongia* sp.
									1.624	*Spongia* sp.
	A3	0.789	0.101	2.119	2.101	2.110	32.390	19.350	-	-
	A4	0.740	0.056	2.050	2.177	2.135	35.091	20.305	0.341	*Spongia* sp.
									0.661	*Phorbas* sp.
2	A1	0.784	0.039	2.071	2.077	2.153	36.470	18.979	-	-
	A2	0.921	0.066	2.023	2.053	2.059	25.411	16.821	-	-
	A3	0.770	0.042	2.023	2.109	2.140	37.056	18.220	-	-
	A4	0.823	0.044	2.045	2.104	2.060	32.869	18.305	-	-
	A5	0.821	0.064	2.106	2.053	2.074	32.504	18.800	-	-
3	A1	0.764	0.035	2.040	2.121	2.098	35.063	18.565	-	-
	A2	0.846	0.050	2.008	2.049	2.102	33.330	17.375	0.624	YB
	A3	0.836	0.022	2.016	2.064	2.078	30.842	17.777	0.958	YB
									0.497	*Spongia* sp.
									0.636	*Phorbas* sp.
									2.043	*Phorbas* sp.
4	A1	0.761	0.019	2.049	2.138	2.098	33.969	19.016	1.159	YB
									1.255	YB
									1.254	YB
									1.707	YB
									0.991	*Spongia* sp.
									0.392	*Spongia* sp.
									0.680	YB
	A2	0.774	0.143	2.074	2.089	2.099	29.420	19.326	1.306	*Spongia* sp.
									0.753	*Spongia* sp.
									1.055	*Spongia* sp.
5	A1	0.784	0.090	2.034	2.106	2.096	31.739	19.038	2.153	*Spongia* sp.
									2.483	*Spongia* sp.
	A2	0.769	0.095	2.038	2.123	2.109	30.359	19.238	-	-
	A3	0.869	0.066	2.031	2.103	2.083	30.210	19.847	-	-
6	A1	0.857	0.046	2.021	2.048	2.097	30.608	17.334	-	-
	A2	0.849	0.061	2.040	2.060	2.089	30.938	17.660	-	-
	A3	0.842	0.067	2.031	2.025	2.078	30.698	16.661	0.760	*Spongia* sp.
									1.663	*Phorbas* sp.
7	A1	0.831	0.070	2.028	2.046	2.078	30.371	17.379	1.938	Y
									0.906	Y
									1.411	Y
	A2	0.824	0.040	2.021	2.117	2.122	30.927	19.115	1.646	YB
	A3	0.813	0.065	2.104	2.104	2.151	33.865	20.661	-	-
	A4	0.817	0.058	2.066	2.081	2.147	31.511	19.627	0.547	*Phorbas* sp.
	A5	0.863	0.048	2.010	2.093	2.057	30.322	16.641	0.624	*Phorbas* sp.
	A6	0.836	0.046	2.043	2.111	2.065	31.931	16.217	1.845	*Phorbas* sp.
	A7	0.892	0.041	2.030	2.067	2.056	27.739	16.352	-	-
8	A1	0.881	0.049	2.024	2.050	2.048	29.719	16.811	-	-
	A2	0.862	0.032	2.068	2.026	2.065	30.242	17.433	1.349	*Phorbas* sp.
									1.530	*Phorbas* sp.
	A3	0.840	0.038	2.031	2.062	2.069	30.187	16.673	0.602	*Phorbas* sp.
									1.469	*Phorbas* sp.
									1.985	*Phorbas* sp.
									2.256	*Phorbas* sp.
									1.816	*Phorbas* sp.
									2.177	*Phorbas* sp.
									1.700	*Phorbas* sp.
									1.591	*Phorbas* sp.
									1.377	*Phorbas* sp.
	A4	0.819	0.043	2.044	2.075	2.072	30.723	18.509	2.063	*Phorbas* sp.

Table 5.5: Values of habitat complexity variables and sponge species found in each area analysed for Pedra do Lacém reef. Values of minimum distance between each sponge and the feature with high slope in the area (Distance (m)) and the standard deviations for rugosity (R_SD) and slope (S_SD) are also shown. The unidentified sponge species were identified by their colour (Blue - B, Yellow/Brown - YB, Yellow - Y).

Model	Area	Rugosity	R_SD	FD 1.8-0.6	FD 0.6-0.3	FD 0.3-0.15	Slope	S_SD	Distance (m)	Species
9	A1	0.689	0.124	2.101	2.096	2.184	34.094	19.579	2.052	*Phorbas* sp.
	A2	0.746	0.072	2.076	2.134	2.148	31.564	19.883	0.699	YB
									0.918	*Spongia* sp.
									1.435	*Spongia* sp.
									1.793	*Spongia* sp.
									0.280	*Phorbas* sp.
									0.831	*Phorbas* sp.
10	A1	0.753	0.044	2.078	2.051	2.126	33.194	20.085	1.291	YB
									0.786	*Phorbas* sp.
									1.264	*Phorbas* sp.
									1.426	*Phorbas* sp.
									1.563	*Phorbas* sp.
									1.722	*Phorbas* sp.
	A2	0.770	0.066	2.059	2.058	2.107	32.953	19.601	1.205	YB
									0.587	Y
									1.287	*Phorbas* sp.
									1.520	*Phorbas* sp.
11	A1	0.803	0.062	2.031	2.075	2.122	31.355	19.186	1.106	*Spongia* sp.
									1.268	*Spongia* sp.
									1.425	*Spongia* sp.
12	A1	0.848	0.097	2.017	2.047	2.068	32.667	18.902	-	-
	A2	0.767	0.094	2.079	2.102	2.111	34.199	19.770	-	-
	A3	0.763	0.090	2.112	2.091	2.124	38.376	19.924	1.675	*Spongia* sp.
									1.345	*Phorbas* sp.
	A4	0.845	0.041	2.009	2.032	2.036	33.865	17.567	-	-
	A5	0.800	0.071	2.046	2.114	2.118	37.228	20.054	-	-
13	A1	0.855	0.034	2.017	2.049	2.048	33.514	18.208	1.695	*Phorbas* sp.
									1.799	*Phorbas* sp.
									1.920	*Phorbas* sp.
									1.135	*Phorbas* sp.
									1.738	*Phorbas* sp.
									1.364	*Phorbas* sp.
									1.871	*Phorbas* sp.
14	A1	0.855	0.024	2.028	2.034	2.068	30.611	17.557	1.160	YB
									1.917	YB
									1.976	*Spongia* sp.
	A2	0.839	0.052	2.034	2.028	2.051	31.195	17.816	-	-
	A3	0.869	0.052	2.004	2.033	2.055	27.906	16.782	-	-
	A4	0.775	0.066	2.052	2.153	2.110	34.692	19.257	0.486	*Spongia* sp.
									0.689	*Spongia* sp.
	A5	0.772	0.059	2.008	2.088	2.093	37.335	19.904	-	-
15	A1	0.794	0.066	2.026	2.120	2.105	35.592	19.587	1.518	*Spongia* sp.
									0.790	*Phorbas* sp.
									0.925	*Phorbas* sp.
	A2	0.792	0.044	2.029	2.108	2.093	36.786	19.514	1.397	*Spongia* sp.
									2.500	*Phorbas* sp.
16	A1	0.628	0.060	2.125	2.144	2.188	43.195	22.769	-	-
	A2	0.778	0.068	2.035	2.145	2.110	32.375	19.616	1.273	*Spongia* sp.
									1.335	*Spongia* sp.
									1.425	*Spongia* sp.
									1.096	*Phorbas* sp.
									1.478	*Phorbas* sp.
									1.505	*Phorbas* sp.
	A3	0.736	0.097	2.069	2.179	2.132	34.727	19.226	0.873	*Phorbas* sp.
	A4	0.754	0.062	2.076	2.107	2.102	34.903	19.634	1.435	*Spongia* sp.
	A5	0.617	0.063	2.095	2.213	2.173	31.719	20.287	-	-
	A6	0.755	0.036	2.057	2.142	2.121	37.300	19.612	1.541	*Spongia* sp.

Table 5.6: Values of habitat complexity variables and sponge species found in each area analysed for Pedra do Lacém reef. Values of minimum distance between each sponge and the feature with high slope in the area (Distance (m)) and the standard deviations for rugosity (R_SD) and slope (S_SD) are also shown. The unidentified sponge species were identified by their colour (Blue - B, Yellow/Brown - YB, Yellow - Y).



Model	Area	Rugosity	R_SD	FD 1.8-0.6	FD 0.6-0.3	FD 0.3-0.15	Slope	S_SD	Distance (m)	Species
17	A1	0.733	0.081	2.061	2.140	2.131	37.123	19.267	-	-
	A2	0.826	0.067	1.997	2.073	2.084	32.515	18.022	2.307	YB
									1.870	*Phorbas* sp.
	A3	0.791	0.106	2.050	2.081	2.112	32.423	20.212	-	-
	A4	0.714	0.021	2.063	2.100	2.093	29.034	19.086	-	-
18	A1	0.808	0.090	2.009	2.061	2.152	27.518	19.277	0.940	*Spongia* sp.
									1.682	*Phorbas* sp.
	A2	0.839	0.084	2.075	2.065	2.109	28.747	19.682	-	-
	A3	0.737	0.059	2.071	2.097	2.141	31.823	19.897	-	-
	A4	0.806	0.139	2.123	2.126	2.086	30.492	19.614	-	-
19	A1	0.717	0.077	1.998	2.125	2.123	37.686	19.056	1.840	*Spongia* sp.
	A2	0.727	0.064	2.085	2.068	2.120	38.059	18.966	-	-
	A3	0.730	0.042	2.049	2.106	2.105	37.522	17.687	-	-
	A4	0.782	0.094	2.031	2.113	2.065	32.695	17.707	-	-
	A5	0.832	0.029	2.016	2.026	2.031	32.181	16.455	0.770	*Spongia* sp.
									1.831	*Spongia* sp.
									1.579	*Phorbas* sp.
	A6	0.872	0.032	2.026	2.011	2.039	31.936	15.874	0.838	*Phorbas* sp.