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### **Evaluating damselfish distribution patterns and benthic habitat complexity associations using SFM-Photogrammetry**

Frosin, Katrin

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# **Evaluating damselfish distribution patterns and benthic habitat complexity associations using SFM-Photogrammetry**

P R I F Y S G O L  
**BANGOR**  
U N I V E R S I T Y



A dissertation in partial fulfilment of the requirements for the degree of Master of Science by  
Research (MScRes) in Ocean Sciences.

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CAYMAN ISLANDS GOVERNMENT

## Declaration

This thesis is being submitted in partial fulfilment of the requirements for the degree of Master of Science by Research (MScRes) in Ocean Sciences, under supervisory agreement of its submission.

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references.

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed (Candidate)

31.01.2021

Date

\_\_\_\_\_

Signature

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This work is dedicated to my parents, my sister, and my brother - I always hoped you would be with us at the finishing line.

K.F.

## Abstract

Global coral reef habitats are in drastic decline in response to rising Ocean temperatures and prolonged heat waves which, alongside other stressors, are causing extensive coral bleaching events. Especially in the Caribbean, continuous coral mortality from bleaching episodes combined with the demise of branching *Acropora* coral spp. and the loss of the keystone herbivore *Diadema antillarum*, in the 1980's induced significant degradation of the physical reef structure. This region-wide "flattening" of the reef matrix equated to a loss of critical habitat for many species. Especially reef fish displaying high site fidelity such as territorial damselfishes are likely affected by long-term habitat alterations. These keystone algae-farmers depend on complex coral structures such as *Acropora* spp. and have been shown to undergo habitat shifts towards coral species potentially more susceptible to their gardening activities. They are known to exert positive and negative effects on coral and algal survival and likely play a significant role in future Caribbean reef resilience. This study evaluated the distribution of the territorial damselfishes *Stegastes planifrons* and *Stegastes diencaeus* in relation to environmental variables and structural reef complexity in the Cayman Islands. Differential structural metrics of micro-habitats were quantified to evaluate whether benthic complexity is of equal importance as a factor of habitat-quality. While both species are highly territorial, *S. planifrons* is regarded as a greater habitat specialist due to its strong preference for branching corals. Abundances were recorded and compared between northern (semi-exposed) and western (sheltered) shallow and deep reef terraces of Grand Cayman. High-resolution photogrammetric technology was utilized to rapidly capture the physical formation of reef sections and singular territories. Structural complexity metrics (fractal dimension (FD); two-dimensional surface area ( $m^2$ )) were then extracted from the re-constructed 3D-models. On the shallow reef terraces, correlations of abundances with transect complexity were explored. Finally, territories within shallow western transects were compared regarding home-range sizes and mean complexity values. Environmental variables such as exposure, depth and protection status significantly affected abundances of *S. planifrons* and *S. diencaeus* on the reef terrace scale, causing similar distribution patterns. Large abundance variations between sites similar in exposure and depth indicated that other factors are also at play in shaping observed distributions. Both species were positively correlated with transect complexity, yet this trend was less significant for *S. diencaeus*. On the microhabitat-scale, *S. planifrons* territories exhibited significantly higher mean complexity than those of *S. diencaeus*. Only *S. planifrons* home-range sizes were positively correlated to complexity, indicating that defence efforts increase with habitat quality.

These results demonstrated that the FD score can provide a useful metric to quantify habitat quality for *S. planifrons*. For *S. diencaeus*, different habitat metrics may be of greater importance for microhabitat distribution and defence. Based on the results from this study and similar trends observed elsewhere, this species may be able to adapt better to the less heterogenic communities of future coral reefs, while stronger habitat-specialists such as *S. planifrons* could display abundance reductions. Understanding how these species are associated to the reef-structure on different resolution-scales is essential in determining their significance in terms of future reef resilience. The modern mapping methodologies used in this study, in interrelation with fish population ecology, have become important tools for the continuous monitoring and management of these threatened ecosystems and will likely become common practice in marine landscape ecology.

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## List of Abbreviations

<b>AIC</b>	Akaike Information Criterion
<b>ANOVA</b>	Analysis of Variance
<b>CI</b>	Confidence Intervals
<b>DF</b>	Degree(s) of Freedom
<b>DoE</b>	Department of Environment
<b>DPC</b>	Dense Point Cloud
<b>EAN<sub>x</sub></b>	Enriched Air Nitrox (x=O <sub>2</sub> content)
<b>Eq.</b>	Equation
<b>FD</b>	Fractal Dimension
<b>GCP</b>	Ground Control Point
<b>GLM</b>	Generalized Linear Model
<b>GUI</b>	Graphical User Interface
<b>Ind.</b>	Individuals
<b>LiDAR</b>	Light Detection and Ranging
<b>LM</b>	Linear Model
<b>LN</b>	Natural Logarithm
<b>MPA</b>	Marine Protected Area
<b>NDZ</b>	No Dive Zone
<b>Pers. comm.</b>	Personal Communication
<b>S</b>	Slope
<b>SA</b>	Surface Area
<b>SCUBA</b>	Self-Contained Underwater Breathing Apparatus
<b>SD</b>	Standard Deviation
<b><i>S. diencaeus</i></b>	<i>Stegastes diencaeus</i>
<b>SE</b>	Standard Error
<b>SfM</b>	Structure from Motion
<b>Spp.</b>	Species
<b><i>S. planifrons</i></b>	<i>Stegastes planifrons</i>
<b>UVC</b>	Underwater Visual Census
<b>3D</b>	Three-Dimensional
<b>2D</b>	Two-Dimensional

## List of Symbols

$\alpha$	Alpha
$>$	Greater than
$<$	Lesser than
$\text{CaCO}_3$	Calcium Carbonate
$\text{cm}$	Centimetre(s)
$\text{ft}$	Feet
$\text{mm}$	Millimetre(s)
$\text{m}$	Metre(s)
$\text{m}^2$	Metre(s) squared
$\text{km}$	Kilometre(s)
$\text{km}^2$	Kilometre(s) squared
$n$	Sample Size
$\chi^2$	Chi-Squared
$\%$	Percentage
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# 1. Introduction

Coral reefs are widely accepted as among the most threatened ecosystems in the face of prevailing climate change projections (Bellwood *et al.*, 2004; Hughes *et al.*, 2017). Within the scientific community concerns prevail regarding the decline of these diverse habitats on a local and global scale. Reefs provide a range of ecosystem services for coastal nations, such as storm protection, resource provision for fisheries and income through rapidly growing tourism industries (Moberg and Folke, 1999; De Groot, Wilson and Boumans, 2002; Bellwood *et al.*, 2004). In the Caribbean, coral reefs have experienced extensive degradation over the last decades, mainly through the widespread loss of main reef-building corals (family Acroporidae) and following the epizootic event of the long-spined sea urchin (*Diadema antillarum*, Philippi, 1845), a keystone herbivore (Hughes, 1994; Aronson and Precht, 2001). In many regions the composition of reefs was re-shaped after phase shifts induced through the proliferation of algae and the demise of previously prominent branching corals, resulting in an overall decline of structural complexity (Hughes, 1994; Bellwood *et al.*, 2004; Alvarez-Filip *et al.*, 2009). Coral cover declined considerably throughout the entire region, increasingly threatening the systems' ability to sustain positive calcium carbonate (CaCO<sub>3</sub>) accretion rates (Gardner *et al.*, 2003; Alvarez-Filip *et al.*, 2009; Hughes and Tanner, 2013; Perry *et al.*, 2013). The degeneration of the overall reef matrix has been linked to drastic declines in diversity and abundance of coral reef fauna and forced expanses in research regarding coral reef conservation ecology and management (Gardner *et al.*, 2003; Bellwood *et al.*, 2004; Mumby, Hastings and Edwards, 2007; Alvarez-Filip *et al.*, 2009; Alvarez-filip *et al.*, 2015). Studies on spatial and temporal reef growth and topography have increasingly utilized terrestrial habitat mapping technologies, which are becoming increasingly more available for application within shallow marine ecosystems (Bayley and Mogg, 2018; D'Urban Jackson *et al.*, 2020). Such methods now present highly detailed, low-cost methods to rapidly capture and assess a range of measures of local bathymetry.

Caribbean reef degradation may especially affect benthic-pelagic species displaying high site fidelity such as territorial damselfishes of the family Pomacentridae, as they depend on complex scleractinian structures for food, shelter and reproductive purposes (Ceccarelli, Jones and Mccook, 2001). In the Caribbean, the most common damselfishes are six species of the genus *Stegastes*. They have been studied widely regarding their territorial behaviour and their role as key-stone species, by structuring the composition of their microhabitat through farming of algae-lawns (Hixon and Brostoff, 1983). They have been attributed both positive and negative



effects on reef communities, by promoting benthic diversity as well as limiting the growth and survival of coral and algae (Hixon and Brostoff, 1983; Gochfeld, 2009; Precht *et al.*, 2010; Casey, Choat and Connolly, 2015; Altman-Kurosaki *et al.*, 2018). Recent literature suggests that the loss of structural complexity in the last decades is forcing habitat shifts, facilitating species hybridization and reducing abundances of some *Stegastes* spp. (Precht *et al.*, 2010; Mullen *et al.*, 2012). Observed shifts onto secondary habitats have been found to have detrimental effects on the survival and growth of slower growing coral spp. (Precht *et al.*, 2010).

Understanding the environmental and physical factors influencing damselfish territory composition & distribution on multiple habitat scales can provide important insights into their role on continuously degrading Caribbean reef systems. This study aimed to investigate the distribution and abiotic microhabitat composition of two of the most territorial damselfish species in the Cayman Islands and examines the use of modern underwater mapping-technology to capture structural reef metrics, with specific focus on structure-from-motion (SFM) photogrammetry.

## **1.1 CORAL REEF COMPLEXITY**

Globally, healthy coral reefs undergo a constant process of recruitment and calcium-carbonate accretion and loss through disturbances and erosion (Fox and Bellwood, 2007). The ability of these dynamic systems to sustain positive carbonate accretion ( $\text{CaCO}_3$ ) rates and hence maintain the continuous growth and complexity of the reef matrix has been impacted by a range of natural and anthropogenic disturbances on a local, regional and global scale. The effects of disturbances such as pollution, overfishing, Ocean acidification, prolonged heat waves and hurricanes associated with climate change have been well documented (Bellwood *et al.*, 2004; Gardner *et al.*, 2005; Hughes and Tanner, 2013; Hughes *et al.*, 2017). With decreasing reef resilience, many reefs previously dominated by autogenic reef-building corals and coralline algae have been undergoing phase-shifts towards the dominance of fleshy macro algae (Done, 1992; Hughes, 1994; Bruno *et al.*, 2014).

Both globally and regionally, coral cover and recruitment has declined significantly and species prevalence shifted from complex branching coral morphologies to low relief massive and sub-massive species with often contrasting life history traits (Gardner *et al.*, 2003; Pandolfi *et al.*, 2003; Price *et al.*, 2019). Especially branching corals have seen extensive declines since the 1980s through disease outbreaks and bleaching events, though they showed declining trends

even prior to these disturbances (Aronson and Precht, 2001; Cramer *et al.*, 2020). Owing to their morphology providing shelter and favourable microhabitats, they are considered keystone structures on coral reefs (Richardson *et al.*, 2017; Wilson *et al.*, 2019). Reef complexity has been shown to be an important predictor of reef functional diversity and richness, as well as reef fauna abundance and biomass (Darling *et al.*, 2017; Richardson *et al.*, 2017; Aguilar-Medrano & Arias-González, 2018). Complex systems facilitate biodiversity by allowing co-existence and microhabitat partitioning of reef fauna and providing shelter from predation (Hixon and Beets, 1989; Graham and Nash, 2013). Considering this, changes in structural complexity through declines of complex coral species can strongly alter community structures and reef resilience and need to be considered in future management and conservation objectives (Graham and Nash, 2013; Komyakova *et al.*, 2018).

### **1.1.1 Caribbean coral reefs**

In the Caribbean, coral reef assemblages display low functional diversity compared to Indo-Pacific regions and have been described as functionally compromised assemblages (Bellwood and Hughes, 2001; Bellwood *et al.*, 2004; Roff and Mumby, 2012). Low trophic diversity decreases reef resilience and hence the system's ability to recover from disturbances, making it prone to phase shifts to alternative stable-states (Nyström, Folke and Moberg, 2000; Hughes *et al.*, 2003). Many of the previously coral-dominated reefs of this basin have undergone phase-shifts to lesser preferred macro-algae dominated states (Done, 1992; Hughes, 1994; Jackson *et al.*, 2012). Since the epizootic events of the primary keystone herbivore *Diadema antillarum* (Philippi, 1845) and the keystone reef structures formed by the Elkhorn and Staghorn corals (*Acropora palmata*; *Acropora cervicornis*; Lamarck, 1816), coral cover has significantly declined in the region (Alvarez-Filip *et al.*, 2009). This benthic transformation was enhanced by the history of disturbance events through hurricanes and the comparatively low grazing pressure to limit algae growth exerted by new primary herbivores such as parrotfishes (Carpenter, 1986; Hughes, Reed and Boyle, 1987; Mumby, Hastings and Edwards, 2007; Jackson *et al.*, 2012). Herbivores have long been recognized as a substantially important functional group in the Caribbean in terms of maintaining reef resilience, by controlling macro-algal abundance and thus limiting overgrowth and competition with coral colonies (Carpenter, 1986; Hughes *et al.*, 2007; Bruno *et al.*, 2014). As a result of these events, structural complexity has been substantially reduced throughout all depth ranges and sub-regions since at least the 1980's (Alvarez-Filip *et al.*, 2009). With projections of increasing stressors such as bleaching

events and ocean acidification and hurricanes, the resilience of Caribbean reefs is expected to continue to decline (Wilkinson and Souter, 2008; Micheli *et al.*, 2014). These changing community structures ask for previous research of the spatial and functional ecology of important trophic reef fauna such as herbivores to be reviewed and applied to modern coral reef systems (Williams *et al.*, 2019).

### **1.1.2 Cayman Islands coral reefs**

The Cayman Islands archipelago is a British overseas-territory, situated south of the coast of Cuba in the greater Caribbean. The islands harbour a total of 41 km<sup>2</sup> of coral reef habitat, extending along a narrow reef shelf around all three islands (McCoy, Dromard and Turner, 2010). The Caymanian nation has a long history of enforcement of their Marine Protected Areas (MPA) of over 35 years (McCoy, Dromard and Turner, 2010). The onset of strong growth of the tourism sector in the 1960's saw an increase of human related impacts on the marine environment and asked for an enactment of conservation measures (Ebanks and Bush, 1990). A system of marine park zonation with varying regulations is used to manage the local fishery and tourism industry such as recreational diving, whilst implementing protection measures for marine life (Appendix A). These MPAs have long been regarded as one of the Caribbean's best examples of well managed and enforced marine parks (Ebanks and Bush, 1990; Dixon, Fallon Scura and Van't Hof, 1993). Furthermore, coral reefs are of major economic value to the local tourism industry, which constitutes a substantial sector of the local economy (Austin and Tratalos, 2001).

Despite these protection measures, local reefs have been subject to a range of environmental stressors in the last decades that cannot be moderated through MPAs (Harper *et al.*, 2009; Turner *et al.*, 2013). The Island chain lays in the area of the Caribbean frequently affected by hurricanes. On average, a hurricane may strike land every 10 years, with the most recent causing significant submarine damage being hurricane Ivan in 2004 and another two category 4 hurricanes in 2008 (Turner *et al.*, 2013; McCoy, 2018). Storm damage has been established as a major contributor to reef degradation and phase shifts, with reefs losing an average of 17% of live coral cover per storm (Gardner *et al.*, 2005). Bleaching events have also become more frequent, significantly impacting the survival and persistence of live coral cover around the Islands. Bleaching was first noted in 1983, with recent episodes in 2005 and severely in 2009 (Hooideonk *et al.*, 2012; Turner *et al.*, 2013; Eakin *et al.*, 2018; McCoy, 2018). The global

bleaching episode spanning 2014-2017 reportedly did not largely affect the reefs around the islands (Mccoy, 2018). In Grand Cayman, the northern shallow reef terrace has been especially affected by hurricane damage, resulting in a loss of the previously abundant *Acropora* spp. within the fringing reef section (Mccoy, 2018).

In terms of anthropogenic stressors, the diving and fishing industries show the most notable impacts on coral reefs (Austin and Tratalos, 2001). Fisheries in the Cayman Islands have historically been described as being small-scale, yet the extent of artisanal and recreational fishing has been found to be substantial (Harper *et al.*, 2009; Henshall, 2009). Besides these disturbances, Caymanian reefs still exhibit moderately high coral cover of 12-30% when compared to other Caribbean nations (Mccoy, 2018).

## **1.2 DIGITAL HABITAT MAPPING**

### **1.2.1 Habitat mapping history**

The degree of complexity of physical reef structures has long been regarded as an important indicator of the diversity, health and resilience of reef communities (Carleton and Sammarco, 1987; Tews *et al.*, 2004; Darling *et al.*, 2017). The index of “rugosity” has been widely used to capture small-scale changes in topographic elevations of a surface. This measure aims to capture the roughness of a surface by using a single metric for simplification purposes (Stahl, 1962). Traditionally, rugosity was measured in shallow marine habitats via the “chain-and-tape” method (Risk, 1972), in which a chain of a known dimension is laid linearly across the benthos that is measured by a transect tape, and the ratio between the linear and actual length calculated (Risk, 1972; McCormick, 1994). Alternative methods use a grading system via visual census or depth measurements at several points for quantifications of complexity (Polunin and Roberts, 1993; Wilson, Graham and Polunin, 2007; Dustan, Doherty and Pardede, 2013; Darling *et al.*, 2017). Though they are useful for broad assessments of reef complexity measures, there are various limitations and problematics associated to the use of these methods and the resulting data in marine habitats (Wilson, Graham and Polunin, 2007). These include observer bias, measurement differences resulting from variations of chain-link sizes and the time-intensive efforts of data collection and limited survey dive times (Knudby and LeDrew, 2007; Zawada and Brock, 2009; Leon *et al.*, 2015). Additionally, they fail to capture the variety of benthic structural metrics different species may associate to (González-Rivero *et al.*, 2017).

Finally, rugosity considers elevation changes on a singular, coarse scale, whereas reef fauna usually responds to changes in complexity on a range of scales due to differences in body sizes and habitat utilization (Harborne, Mumby and Ferrari, 2012; Nash *et al.*, 2013; Young *et al.*, 2017). More extensive modes of habitat mapping such as LiDAR (Light Detection and Ranging) have been restricted in their wide-scale application in coral reef studies due to high operational & logistical costs and problematics as well as required technical expertise (Zawada and Brock, 2009; Höfle and Rutzinger, 2011).

### **1.2.2 Recent technological advances**

Derived from previous application in terrestrial mapping, Structure-From-Motion (SFM) short-range photogrammetry has become increasingly utilized within marine habitats in recent years (Westoby *et al.*, 2012; Leon *et al.*, 2015; Bayley and Mogg, 2018). This method of capturing benthic topography uses a series of overlapping photographs to generate three-dimensional (3D) models. It has gained popularity due to its low-cost, non-invasive nature and rapid collection yielding large quantities of highly detailed resolution data (Westoby *et al.*, 2012; Guo *et al.*, 2016; Bayley and Mogg, 2018; Bayley *et al.*, 2019). Simultaneously, affordable open-source software packages handling large quantities of imagery data have become more widely available (Remondino *et al.*, 2012). Several biotic and abiotic metrics can be extracted from the resulting models, hence greatly reducing in-situ data collection time. As the data is archivable and can be replicated within the same reef section at several resolutions, it has been used for monitoring purposes and temporal studies of topographic reef growth & degradation (Eltner *et al.*, 2017; Bayley *et al.*, 2019).

There is a great variety of different variables aiming to describe surface complexity characteristics which can be extracted from 3D generated models, such as volume ( $m^3$ ), 3D surface area ( $m^2$ ) or the tortuosity index (Bertuzzi, Rauws and Courault, 1990; Shepard *et al.*, 2001). The overarching problem of many structural variables is their scale-dependence and usual exclusion of other complexity attributes (Du Preez, 2015). A metric that has gained more popularity in the field of ecology in recent years is the fractal dimension (FD) score. First proposed by Mandelbrot in 1983, it presents a scale-invariant approach to measurements of surface roughness and is hence widely applicable over a range of habitat types and scales (Mandelbrot and Wheeler, 1983; Zawada and Brock, 2009; Bayley *et al.*, 2019). The concept of FD measures the degree to which any given object fills the space in which it resides, with

several 2D and 3D based methods available for its calculation (Mandelbrot and Wheeler, 1983; Davies and Hall, 1999; Zawada and Brock, 2009; Reichert *et al.*, 2017). It has been found to present an accurate metric when derived via SFM-Photogrammetry in calculating complexity parameters from the highly irregular bathymetry of coral reefs in comparison to traditional approaches (Zawada and Brock, 2009; Zawada, Piniak and Hearn, 2010; Burns *et al.*, 2015; Leon *et al.*, 2015). Image-based 3D reconstruction now presents a powerful new tool to deepen scientific knowledge of the ecological associations between structural components and reef communities and will likely become a standard method in the field of tropical marine landscape ecology (D’Urban Jackson *et al.*, 2020).

### **1.3 DAMSELFISH FUNCTIONS AND DISTRIBUTION**

#### **1.3.1 Ecological significance of territoriality**

The developments of marine habitat mapping allowed recent studies to utilize SFM-Photogrammetry methods to start investigating the specific microhabitat attributes affecting distributions of important benthic-associated reef fish in the Caribbean in greater detail (González-Rivero *et al.*, 2017). Similarly, this study focusses on the benthic association of damselfishes, which are part of a diverse group of reef fishes within the family Pomacentridae and commonly found throughout the Caribbean region. Due to their high prevalence and easy accessibility on shallow reefs they have been prominent subjects of a wide array of ecological studies. Members of the genus *Stegastes* have been investigated intensely, primarily due to their characteristic territorial behaviour (Waldner and Robertson, 1980; Sammarco and Williams, 1982; Ceccarelli, 2007; Vermeij *et al.*, 2015). Previous research has focussed greatly on the ecological effects of the most abundant territorial *Stegastes* spp., summarized by reviews such as that of Ceccarelli *et al.*, (2001). Damselfishes are known to maintain small algal “gardens” through the direct exclusion of other herbivores via active defence and removal, selective weeding of benthic species, and by killing live coral for space to farm algae (Thresher, 1976; Ceccarelli, 2007; Catano *et al.*, 2014). Territories are suggested to serve many functions such as shelter from predation, areas for reproductive purposes as well as food supply from either algae, crypto fauna or detritus (Itzkowitz, 1985, 1991; Zeller, 1988; Dromard *et al.*, 2013; Vermeij *et al.*, 2015). Whilst all *Stegastes* spp. are at least partially herbivorous, the degree of farming behaviour and resulting benthic alterations vary. The exact effects of such activities on the benthic community structure deviate between studies and regions, yet higher displays of

territoriality seemingly exert greater effects (Ceccarelli *et al.*, 2001). Selective weeding behaviour has both positive and negative effects on coral and algae survival and diversity and the severity of such activities seem to depend on environmental variables such as predator abundance (Hixon and Brostoff, 1983; Ceccarelli, Jones and Mccook, 2001; Ceccarelli, 2007; Gochfeld, 2009; Vermeij *et al.*, 2015). As such, damselfish can enhance algal successional states towards macro-algal dominance on different reef systems, yet studies deviate between regions in their quantification of these ecological effects (Solandt, Campbell and Haley, 2003; Chong-Seng *et al.*, 2011; Catano, Shantz and Burkepile, 2014; Casey, Choat and Connolly, 2015; Schopmeyer and Lirman, 2015; Vermeij *et al.*, 2015; Blanchette *et al.*, 2019; Randazzo Eisemann *et al.*, 2019).

Despite of their small body size, *Stegastes* spp. are prominent members of the Caribbean reef community. Previous studies estimated territories to cover significant proportions of benthos on coral reefs, illustrating the potentially disproportional effects of farming activities (Solandt, Campbell and Haley, 2003; Di Iulio Ilarri *et al.*, 2008; Carvalho *et al.*, 2012). The two species of focus in this study are the three-spot damselfish *Stegastes planifrons* (Cuvier, 1830) and the longfin damselfish *Stegastes diencaeus* (Jordan & Rutter, 1897). Both species are highly territorial herbivores known to exert strong effects on benthic communities and are commonly found around the coral reefs of the Cayman Islands (Ceccarelli, Jones and Mccook, 2001; Pattengill-Semmens and Semmens, 2003; Vermeij *et al.*, 2015).

### **1.3.2 Benthic association and distribution patterns**

Damselfish in the Caribbean have been traditionally associated with relatively sheltered shallow reef habitats, with high densities associated with back- and fringing reefs. As reef systems have undergone extensive changes in the last decades, the population dynamics of coral reef communities have been significantly altered. To identify potential effects on damselfish populations, recent focus has shifted onto microhabitat distribution and composition of different species on progressively degraded reef systems (Solandt, Campbell and Haley, 2003; Carvalho *et al.*, 2012). As habitat-specialists, *S. planifrons* and *S. diencaeus* are prone to display changes in abundances and distributions in response to shifts in benthic composition, diversity and complexity (Jones *et al.*, 2004; Alvarez-filip *et al.*, 2015). Despite some disparity, recent studies identified habitat complexity as the main factor driving some damselfish distributions, outweighing predation pressure (Precht *et al.*, 2010; Carvalho *et al.*, 2012; Vermeij *et al.*, 2015; Boström-Einarsson *et al.*, 2018). *S. planifrons* has been historically associated to branching A.

*cervicornis* thickets and relatively sheltered reef habitats and is among the most-habitat-specialized damselfishes (Tolimieri, 1998; Ceccarelli, Jones and Mccook, 2001; Wilkes *et al.*, 2008; Carvalho *et al.*, 2012). A recent study surveying several locations in the Caribbean observed a shift of this species onto secondary habitats mostly consisting of *Orbicella annularis* after the loss of its preferred habitat type (Precht *et al.*, 2010). Owing to their life history traits such as slow growth, the effects of damselfish farming activities may have substantial detrimental effects to the survival of such coral species (Precht *et al.*, 2010).

However, consequences of reef complexity loss may not have negative implications for the abundance and distribution of all *Stegastes* spp. *S. diencaeus* habitat preferences were originally described as rock, rubble and back-reef environments by Itzkowitz in 1977, yet studies assessing these preferences have been comparatively sparse (Itzkowitz, 1977; Solandt, Campbell and Haley, 2003). In Jamaica, where back-reefs have significantly changed since the 1970's, Solandt *et al.* (2003) found a significant increase of *S. diencaeus* abundances on the fore-reef after extensive coral cover loss (Solandt, Campbell and Haley, 2003). Within this habitat, the study further noted significantly higher abundances in areas of higher coral cover and diversity compared to algae-dominated substrata. Such differences in associations to habitat attributes may allow some habitat-specialists to better adapt and persist on the changing environments of Caribbean reef habitats.

Previous studies measuring distributions on the reef scale suggest environmental gradients such as wave-energy and light availability to be the driving forces causing spatial patterns of similar trophic groups of reef fish (Huston, 1985; Floeter *et al.*, 2007). Yet, while similar patterns of damselfish distributions may be observed on a larger spatial scale, studies suggest factors on the micro-habitat scale such as competition and niche separation to cause differential benthic distribution patterns within habitats (Meadows, 2001; Dromard, Bouchon-Navaro, Cordonnier, Harmelin-Vivien, *et al.*, 2013; Jacob G. Eurich, McCormick and Jones, 2018). At the microhabitat scale, factors such as habitat fragmentation, quality as well as interspecific competition have been related to changes in the defended size of *S. planifrons* home-ranges and distribution (Meadows, 2001; Dromard, *et al.*, 2013). In comparison, *S. diencaeus* territory sizes stay more uniform, whilst other parameters such as the availability of nesting sites are found to be more important in habitat choice and defence (Cheney and Cote, 2003). Understanding the structural complexity measures different damselfish associate with on progressively degrading Caribbean reef systems is becoming of ever greater importance to predict their future distributions and ecological roles in affecting communities and reef resilience.



## 1.4. STUDY RATIONALE

In many regions of the Caribbean, only few recent studies have examined potential habitat shifts and abundance changes of damselfishes. This makes interpretations of current and future farming activities and their effects on reef communities and resilience problematic. Generalising distribution trends on different reef habitats from studies finding habitat shifts, such as those of Kaufman (1983) and Precht *et al.* (2010) is difficult, considering that reef health, bathymetry and community structures vary greatly between locations in response to a range of biological and environmental factors. In the Cayman Islands, there have been long-term monitoring efforts of the floral and faunal diversity, health and status of coral reefs as part of local MPA management (Dromard, McCoy and Turner, 2011). Whilst biomass and distributions of larger primary herbivores such as parrotfishes have been investigated intensely, less attention has been given to the distribution and ecological significance of smaller herbivores such as damselfishes. There is a particular lack of a comprehensive quantitative assessment of *Stegastes* spp. distributions around the islands, limiting interpretations of the extend of ecological significance of their territorial activities on local reefs. Previous assessments of trophic assemblages often summarized territorial damselfishes as one category of the genus *Stegastes*, with the prevalence and abundance of individual species less quantified. One comprehensive assessment of reef fish communities conducted in 1999 did state *S. planifrons* and *S. diencaeus* as amongst the 25 most frequently sighted fish species on Caymanian coral reefs, inferring considerable previous densities (Pattengill-Semmens and Semmens, 2003). The sheltered and semi-exposed western and northern reef terraces of Grand Cayman present a good study location to examine local damselfish distribution patterns. The western terraces have been protected by MPAs for decades and present a preferable sheltered habitat. The northern terraces are more exposed, with a documented loss of *Acropora* spp. and benthic disturbance in shallow waters, making examinations of distribution patterns and habitat associations with regards to different environmental and biological variables on the reef and microhabitat scale possible.

This study aims to present a new assessment of distribution patterns of the two damselfishes *Stegastes planifrons* and *Stegastes diencaeus* on the reef systems around Grand Cayman. Specifically, this study set out to investigate: i) the importance of environmental variables such as aspect, depth and structural complexity in structuring similar distribution patterns of both species on the reef terrace scale; ii) whether less complexity-associated damselfish such as *S. diencaeus* are more successful in persisting within a range of benthic reef habitats; iii) the

differential association of both species to structural benthic attributes on a microhabitat scale. Understanding current factors influencing abundance patterns and differential adaptation abilities of damselfishes within changing microhabitats can provide important information in determining their modern ecological roles in terms of future reef resilience and local MPA management efforts around the islands.

This study applies 3D habitat mapping technology as a faster, highly detailed method to assess small scale reef bathymetry and tests its ability to accurately measure the structural attributes damselfish may associate to on the reef terrace- and territory scale. To our knowledge, only few other studies have previously used SFM-photogrammetry to map the exact home-ranges of these species and examine their variations in complexity components. The 3D models of shallow coral reef terraces generated during this study also aim to present a baseline for local authorities, facilitating future monitoring of the benthic biotic and abiotic components of Caymanian reefs through the use of this high resolution method.

## 1.5 HYPOTHESES

The following four hypotheses were tested during this study:

**H<sub>1</sub>:** Abundances of *Stegastes planifrons* & *Stegastes diencaeus* will be significantly higher on Western reef terraces than on Northern reef terraces.

**H<sub>2</sub>:** Abundances of *Stegastes planifrons* & *Stegastes diencaeus* will be positively correlated to fractal dimension scores on shallow reef terraces.

**H<sub>3</sub>:** Fractal dimension scores and the defended two-dimensional (m<sup>2</sup>) area of *S. planifrons* territories will be significantly more correlated than those of *S. diencaeus*.

**H<sub>4</sub>:** Within Sites, *Stegastes planifrons* will associate significantly more to territories of higher fractal dimension scores than does *Stegastes diencaeus*.

## 2. Methodology

### 2.1 OBJECTIVES

For the purpose of testing each hypothesis, the following three objectives were framed. For simplification within this study, “habitat quality” is referring to territory complexity as measured via the fractal dimension (FD) score.

**Objective 1:** Investigate potential effects of exposure and depth on population abundances of *Stegastes planifrons* & *Stegastes diencaeus* on the fore-reef terraces of Grand Cayman.

- Use underwater visual census (UVC) to count individual population abundances between 22 corresponding shallow (5-15 m.) and deep (15-30 m.) reef terraces within the northern and western aspects of Grand Cayman using 4 x 100 m<sup>2</sup> belt-transect surveys per site.
- Assess whether abundance variations are influenced by the environmental variables exposure and depth, by investigating whether there are significant differences in abundances with reef aspect and depth on abundances between the northern and western survey sites.
- Investigate whether complexity varies significantly with exposure on local shallow reef terraces by comparing mean fractal dimension scores of 15 transects within five survey sites per aspect.

**Objective 2:** Investigate the differences in population abundances of *Stegastes planifrons* & *Stegastes diencaeus* in response to a changing complexity gradient on shallow reef terraces.

- Quantify the abundance of both species along the shallow reef terraces of five survey sites, each including 3 x 100 m<sup>2</sup> belt transects per northern and western aspects using UVC.
- Explore the correlation of individual transect abundances with the fractal dimension scores derived from three-dimensional (3D) models generated from SFM-photogrammetry for each of the 3 x 100 m<sup>2</sup> belt transects per site.

**Objective 3:** Investigate the variations in territory complexity and home-range size of *Stegastes planifrons* & *Stegastes diencaeus* within the shallow western reef terrace.

- Quantify variations in the home-range and habitat quality of individual species through observations of habitat boundaries and generation of digital elevation models (DEM) and 3D models via SFM-Photogrammetry of nine territories per species per survey site.
- Explore the relationship of extracted fractal dimension scores and two-dimensional (2D) surface area of individual species' territories to assess whether increasing availability of complex habitat affects defended home-ranges and hence exerted energy towards habitat defence.
- Compare mean fractal dimension scores and 2D surface area of territories of both species to investigate whether there are significant differences in their association to habitat complexity and hence habitat defence efforts.

## 2.2 SURVEY AREA

This study was undertaken in the archipelago of the Cayman Islands, a British overseas territory comprising three islands within the Greater Antilles of the Caribbean region. All surveys were conducted on Grand Cayman (19°18'41.1"N, 81°15'26.5"W) (Figure 1), the main and largest island of the island chain. The islands are part of the Cayman ridge, which is bordered by abyssal waters (>2000 m.) either side, with the Cayman Trench laying in the South and the Yucatan Basin in the North-West (McCoy, Dromard and Turner, 2010; Logan, 2013). They exhibit a distinct submarine topography with a narrow shelf running outwards at an average width of 500 m., surrounding all three islands. There are two distinct reef terraces, with the shallow terrace ranging from the fringing reef to ~15 m. depth, and a deep terrace within depths of ~15 – 30 m. (Figure 2) (McCoy, Dromard and Turner, 2010; Logan, 2013). From the deep terrace, the shelf falls sharply into abyssal depths. Survey sites were chosen along the northern and western reef terraces of Grand Cayman, due to their low (western) and moderate (northern) exposure owing to prevailing North-Eastern trade winds. Local reefs exhibit a spur and groove formation, presenting more pronounced with increasing exposure (Figure 2) (McCoy, Dromard and Turner, 2010; Turner *et al.*, 2013; McCoy, 2018). Northern, shallow terraces have a documented historic abundance of *Acropora cervicornis*, having substantially declined and mostly disappeared over the last decades (McCoy, 2018). Northern deep reef terraces are described as significantly more developed than western deep reef terraces (McCoy, 2018). The islands' MPA zones lay almost exclusively within the western shoreline and encompass 9 km<sup>2</sup> (Figure 1, 3).

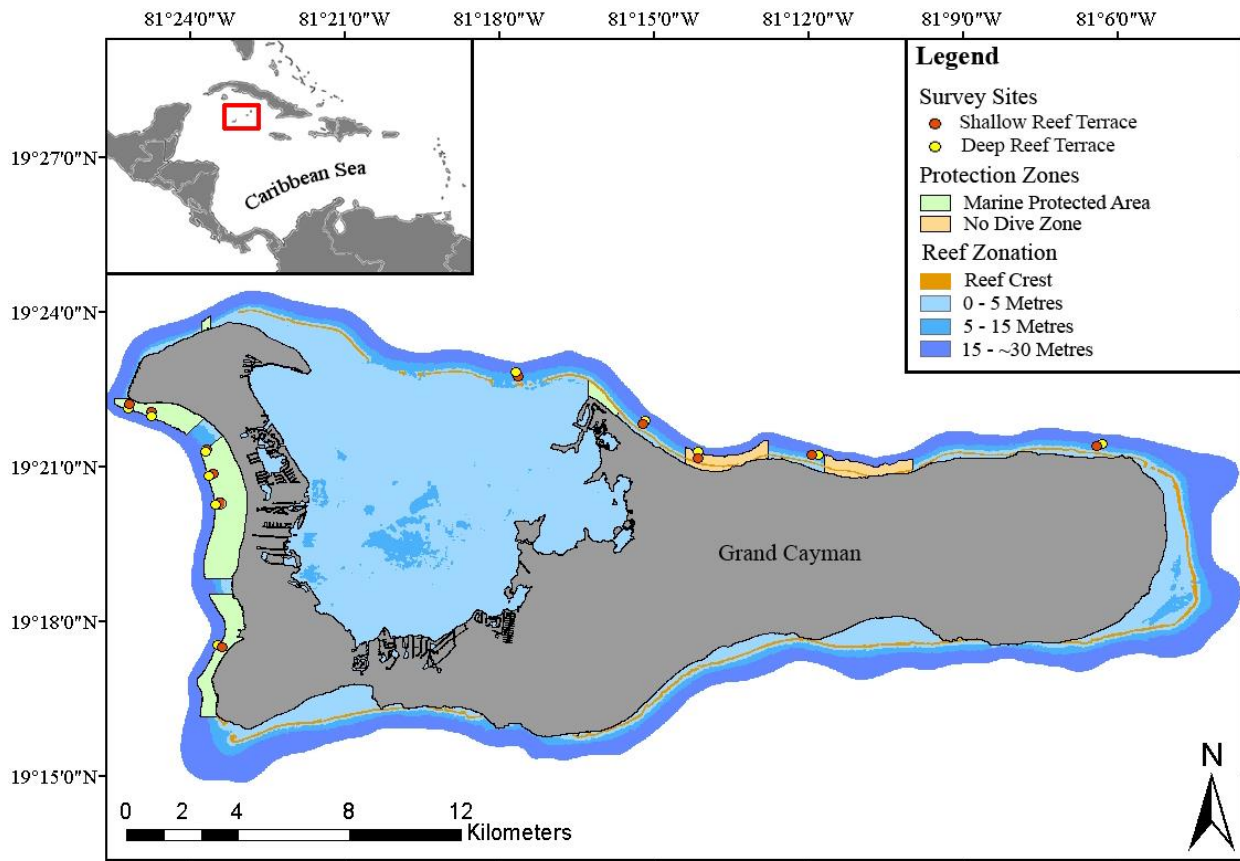
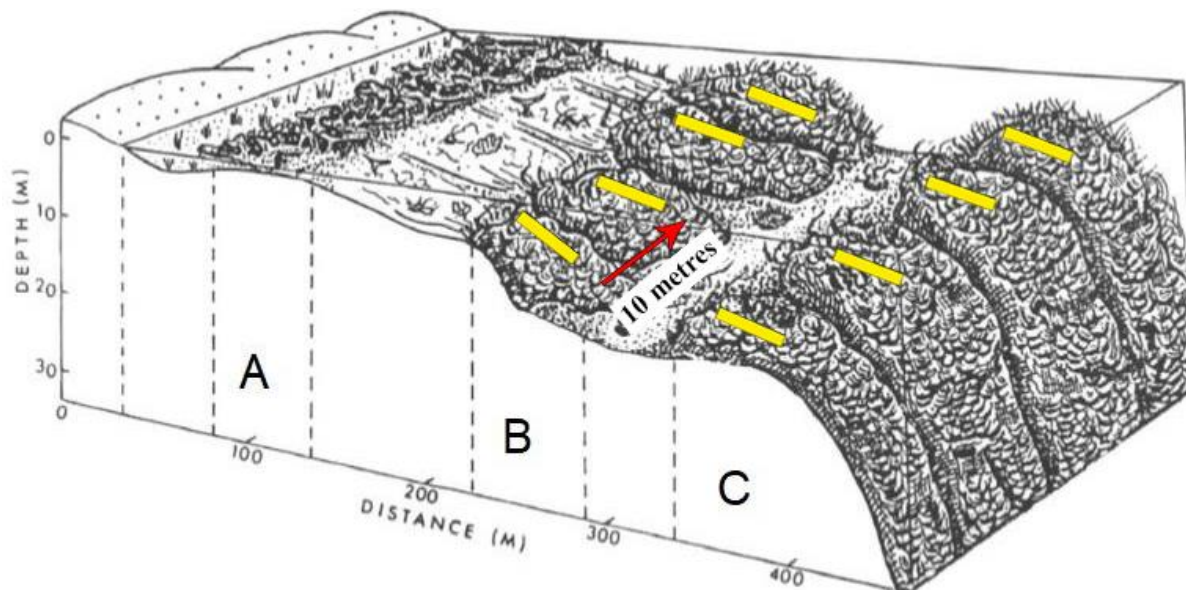


Figure 1: The location of corresponding survey sites on shallow (5-15m.) and deep (15-30 m.) reef terraces along the northern and western aspects of Grand Cayman, Cayman Islands. MPAs and No Dive Zones are displayed. Insert: Caribbean region. The red rectangle illustrates the location of the Cayman Islands archipelago (Coordinates provided in Appendix B; Map generated via ArcMap ('ArcGIS Desktop', 2020)).

## 2.3 STUDY SPECIES

This study focussed on two of the six prominent members of the genus *Stegastes* on Caribbean coral reefs, *Stegastes planifrons* and *Stegastes diencaeus*. They were chosen as adequate study species as both damselfish species are known to share similar trophic classifications and usually occupy single-owner territories, which they defended highly aggressively (Table 1). Furthermore, they were previously recorded in high abundances within similar habitat ranges in the Cayman Islands, as reported by surveys between 1994 – 2001 during a comprehensive assessment of local reef fish diversity (Pattengill-Semmens and Semmens, 2003). Prior to data collection for this study, a preliminary survey within deep and shallow survey sites revealed similar trends of higher abundances of these two species in comparison to very low abundances of other members of the genus within similar habitats.



*Figure 2: Generalised topography of the reef shelf around the Cayman Islands, spanning from the fringing reef (A) to the shallow reef terrace (B) and the deep reef terrace (C) by the sharp drop-off to abyssal depths. Yellow lines outline the positioning of transects along the spurs of the reefs, with a gap of a minimum of 10 m. (Sourced and adapted from Logan, 1994, 2013).*

Only adults were selected for data collection, due to the differences in territorial and habitat-specific behaviour between juvenile and adult individuals (Ceccarelli, Jones and Mccook, 2001). Due to these characteristics, individuals were assumed to exhibit bold behaviours to defend home-ranges, making it possible to standardise efforts of territorial boundary identification. Identification and differentiation on the species level was undertaken via observations of distinct colouration patterns and morphological characteristics such as the size of the anal fin following descriptions of a reef fish identification guide (Humann and Deloach, 2014).

## **2.4 SURVEY DESIGN**

### **2.4.1 Logistics, equipment and health & safety**

All data collection and dive operation management was undertaken in collaboration with the Cayman Islands Department of Environment (DoE) using SCUBA. Surveys were conducted between March and May of 2019, using selected long-term monitoring sites previously established by the DoE (Appendix B; Figure 2, 3). All dive operations were executed under the health & safety diving policy of both the DoE and Bangor University. The utilized breathing gas was Enriched Air Nitrox (EANx) with a mixture of 32-34% O<sub>2</sub> content, to assure an adequate safety margin for the undertaking of consecutive dives during the fieldwork period.

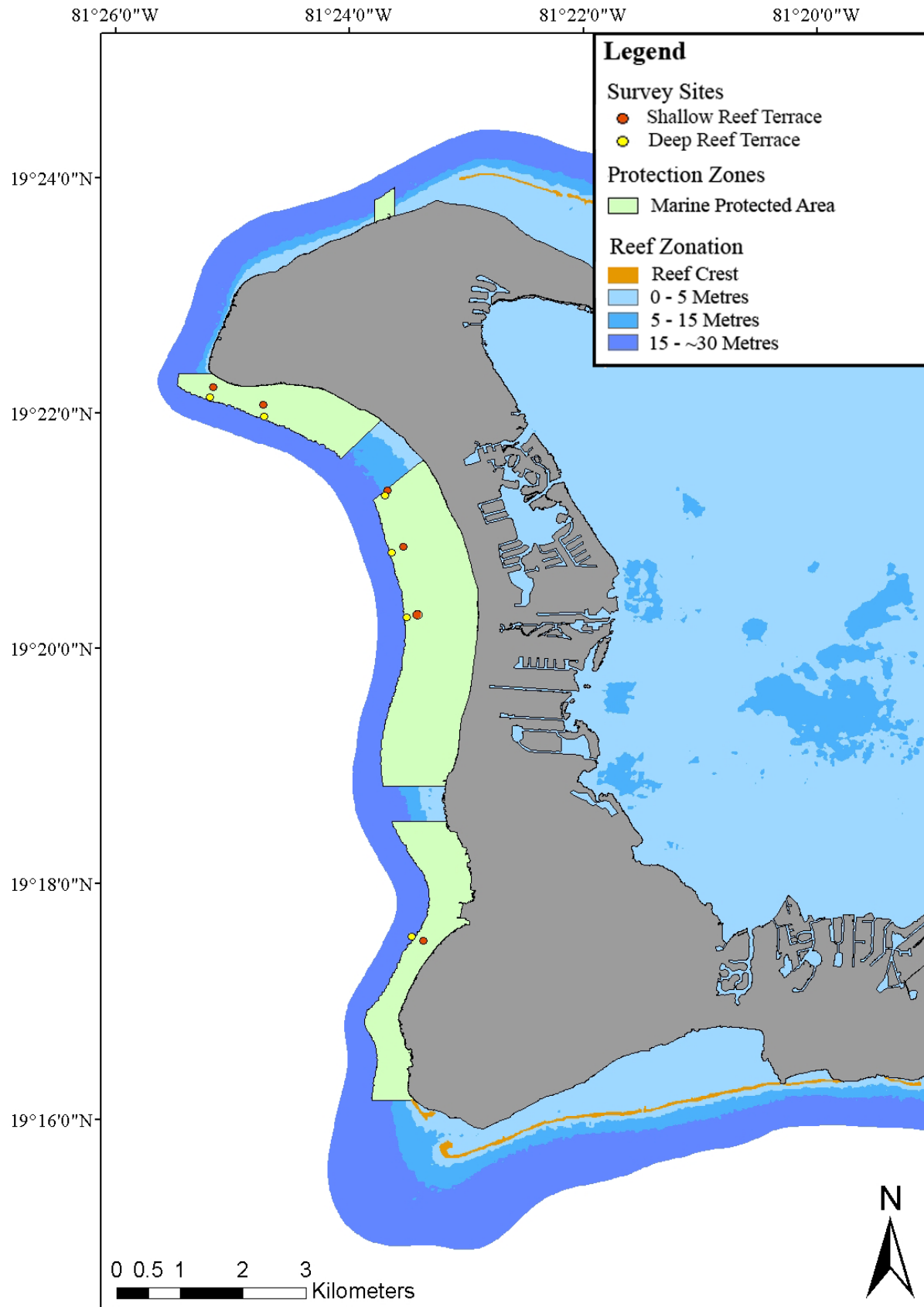


Figure 3: The location of corresponding survey sites on shallow (5-15m.) and deep (15-30 m.) reef terraces inside the designated MPAs of the western aspect of Grand Cayman (Coordinates provided in Appendix B; Map generated via ArcMap (ESRI (2020)).

Table 1: Species characteristics, historic habitat preferences and trophic association derived from pervious literature of the two damselfish species of focus: *Stegastes planifrons* & *Stegastes diencaeus* (Table sourced & adapted from: González-Rivero et al., 2017).

Species	Trophic Classification	Common Name	Associated Substrate	Reef Habitat	Territoriality	Ref.
<i>Stegastes planifrons</i>	Herbivorous	Three-spot damselfish	Live & dead <i>Acropora</i> spp; <i>Porites</i> spp. <i>Orbicella</i> spp. & rubble	Back-reef environment, patch reefs	Strongly aggressive, single owner territories	Itzkowitz, 1977; Sammarco and Williams, 1982; Precht et al., 2010; Dromard et al., 2013
<i>Stegastes diencaeus</i>	Herbivorous	Longfin damselfish	Rock, large rubble, >40 cm	Back-reef environment	Strongly aggressive, single owner territories	Itzkowitz, 1977; Draud and Itzkowitz, 1995; Cheney and Cote, 2003

#### 2.4.2 Abundance surveys

A total of 10 survey sites were chosen with an approximately even spread in the Northern aspect and 12 in the Western aspect (Figure 1). Each shallow (5 - 15 m.) site has a corresponding deep (15 - 30 m.) site on the reef shelf, allowing for a balanced experimental design (Table 2). Within each site, 4 belt-transects were placed using measuring tapes to collect count data on *S. planifrons* and *S. diencaeus* adults. All transects were placed on the reef spurs perpendicular to the shoreline, at a minimum of 10 m. distance to assure independence of observations (Figure 2). Each transect measured 20 m. in length and 5 m. in width, covering a reef section of 100 m<sup>2</sup> and standardising abundance counts for comparison. In total, 400 m<sup>2</sup> of reef benthos were surveyed per survey site, amounting to a total survey coverage of 8.8 km<sup>2</sup>. After the tape was rolled out onto the reef, a period of ~5 minutes was allowed before the start of the survey to minimize observational errors due fish disturbances previously observed in the presence of



divers (Di Iulio Ilarri *et al.*, 2008). Following, underwater visual census (UVC) was utilized to record fish abundances, with observation times per transect being standardised to 10 minute intervals. All counts were undertaken by the same diver who had undergone trials prior to data collection, to train in species identification and increase observational accuracy of abundances. All sampling efforts were undertaken between 11 am – 3 pm, so as to minimize biases due to diurnal behavioural changes of territoriality and density differences of damselfishes (McDougall and Kramer, 2007).

#### **2.4.3 Reef-scale structural complexity surveys**

For the purpose of investigating structural complexity differences on the shallow reef terrace scale, three of the four belt-transects used for the previous abundance counts on the shallow survey sites were chosen at random (Figure 4). For each transect, SFM-photogrammetric technology was utilized to capture the physical formation of the underlying reef section. The nature of this methodology means that images have to be taken in overlapping patterns from several angles. This can increase the time spent photographing large complex stretches of coral reefs of varying vertical relief when using one camera (Westoby *et al.*, 2012; Bryson *et al.*, 2017). A custom built system incorporating three mounted cameras (Model= GoPro Hero 5 black) was used in order to photograph the benthos from several angles simultaneously, thus aiming to include a larger proportion of overhanging surfaces, whilst concurrently decreasing survey time (Figure 5.1). To accurately scale the resulting 3D models during later post-processing, ground control points (GCP) of known dimensions were positioned within the reef section (Figure 6). Scale bars and spirit-levels mounted onto an adjustable tripod were the chosen GCPs used as scaling references.

#### **2.4.4 Territory-scale structural complexity surveys**

In order to investigate the physical complexity variables of individual territories of *S. planifrons* and *S. diencaeus*, data collection focussed on the selected five survey sites of the shallow western terrace (Figure 3). Within each site, the same transects previously surveyed via SFM-photogrammetry to capture general site complexity were chosen, following a spatially nested sampling design (Figure 4). Levelling the spirit level is an important step in 3D regeneration to accurately orientate the resulting model via measurements of the flat surface.

*Table 2: The GPS position, protection and location with aspect of the long-term monitoring sites surveyed around Grand Cayman during this study.*

Site Name	Corr. Site Nr.	Latitude	Longitude	Protection	Aspect	Depth
<b>Dragons Hole</b>	3	19,3663	-81,41227	MPA	West	Deep
<b>Rainbow Reef</b>	3	19,36797	-81,41238	MPA	West	Shallow
<b>Victorias' Secret Wall</b>	2	19,34700	-81,39400	MPA	West	Deep
<b>Victorias' Secret Reef</b>	2	19,35578	-81,39467	MPA	West	Shallow
<b>Holiday Inn</b>	1	19,33777	-81,39185	MPA	West	Deep
<b>Oro Verde</b>	1	19,3382	-81,39038	MPA	West	Shallow
<b>Sea View Wall</b>	4	19,2926	-81,39117	MPA	West	Deep
<b>Sea View Reef</b>	4	19,29196	-81,38953	MPA	West	Shallow
<b>North West Point</b>	5	19,369	-81,42	MPA	West	Deep
<b>Bonnies Arch</b>	5	19,37038	-81,41950	MPA	West	Shallow
<b>Big Tunnels</b>	11	19,35510	-81,39500	MPA	West	Deep
<b>Bolero</b>	11	19,34785	-81,39240	MPA	West	Shallow
<b>Andes Wall</b>	6	19,36485	-81,25288	Non-MPA	North	Deep
<b>Andes Reef</b>	6	19,36397	-81,2538	Non-MPA	North	Shallow
<b>Black Rock</b>	7	19,3576	-81,10542	Non-MPA	North	Deep
<b>Fish Tank</b>	7	19,35675	-81,10697	Non-MPA	North	Shallow
<b>Haunted House</b>	8	19,38055	-81,29473	Non-MPA	North	Deep
<b>Pinnacles Reef</b>	8	19,37942	-81,2939	Non-MPA	North	Shallow
<b>Apollo</b>	9	19,35395	-81,19702	Non-MPA	North	Deep
<b>Apollo</b>	9	19,35383	-81,19901	Non-MPA	North	Shallow
<b>No Dive Zone</b>	10	19,3550	-81,2360	NDZ	North	Deep
<b>No Dive Zone</b>	10	19,3530	-81,2360	NDZ	North	Shallow

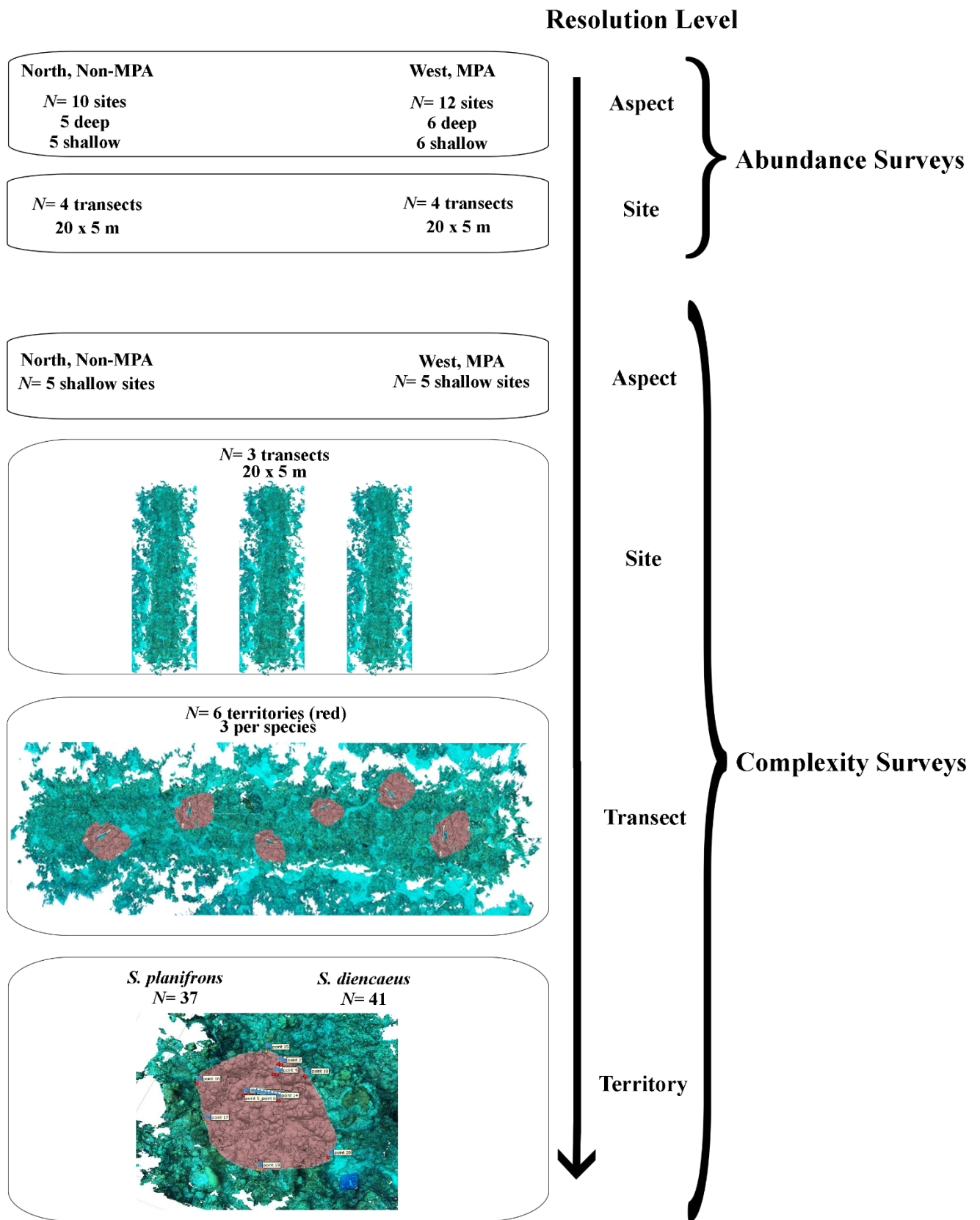


Figure 4: Flowchart of the spatially nested sampling design incorporating different resolution levels, which was used to undertake abundance and complexity surveys on the northern and western reef terraces of Grand Cayman.

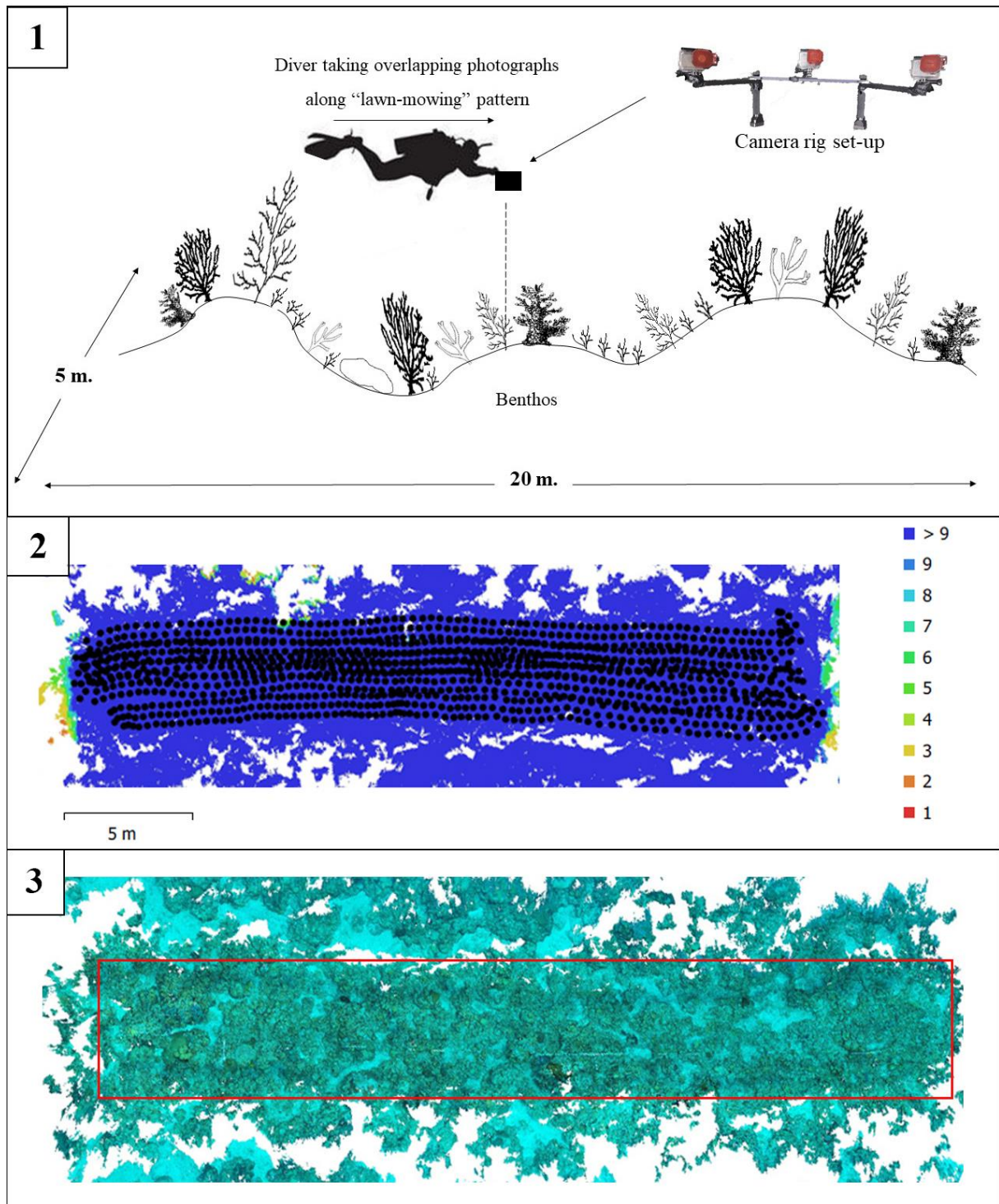


Figure 5: Image acquisition for photogrammetric 3D model reconstruction of the reef benthos within the established 20 x 5 m. transect. **1:** Visualisation of positioning of a SCUBA diver above the transect, swimming at 1-2 m. distance above the reef at a slow, constant swimming speed. **2:** Birds-eye view of the captured reef area over the 20 x 5 m. transect. Black dots illustrate the calculated position of the camera during each image, outlining the "lawn-mowing" pattern to achieve adequate image overlap. Colours illustrate the extend of image overlap for each area. **3:** Birds-eye view of the resulting DPC. The red rectangle outlines the 100 m<sup>2</sup> transect area, which was then cropped to size for further analysis.

Preliminary trials testing the system were conducted on shallow reefs to identify potential projection, occlusion (from shadows) and resolution errors associated to the use of this method in submarine terrain. A diver moved the camera rig across the transect area in a “lawn-mowing pattern” in perpendicular lines, to assure adequate overlap (>60%) of photographs (Figure 5.2). Images were taken at an interval of 1 frame per second, whilst keeping a constant distance of ~2 m. from the substrate at an adjusted swimming speed. Within each transect, three territories of adult specimen of each of the two species were identified, totalling six territories per transect. Throughout data collection, logistical and environmental factors contributed to a slightly imbalanced experimental design of territories surveyed per species within each transect. In total, 78 territories were surveyed and 3D reconstructed (*S. planifrons*  $N=37$ ; *S. diencaeus*  $N=41$ ).

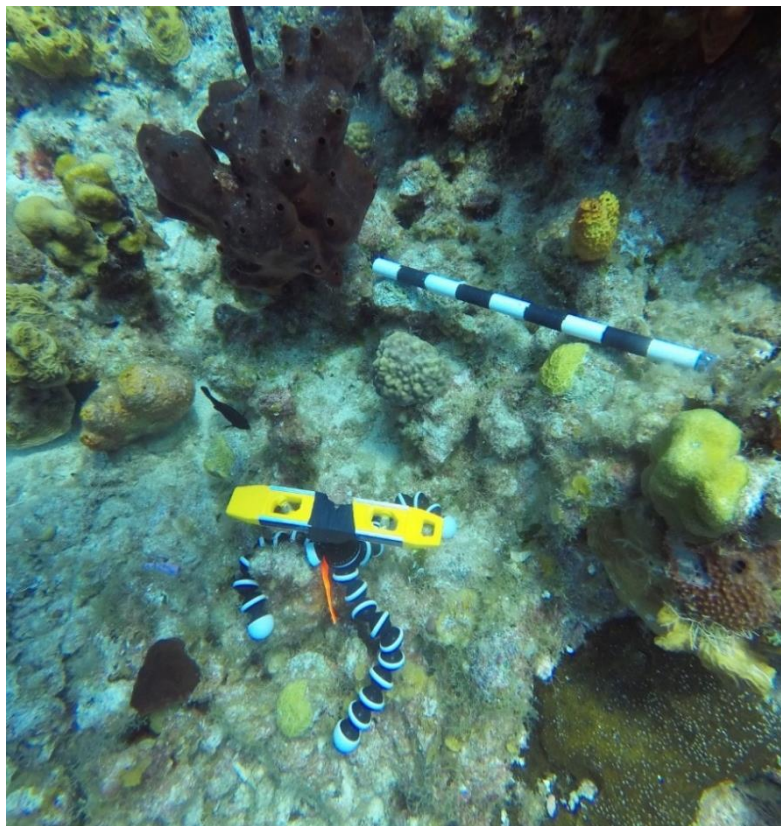
All chosen territories were at least one home-range (~2 m.) apart, to allow for independence of observations. Only territories defended by one solitary (non-courting) damselfish were chosen for sampling. The diver established territorial boundaries by observing each fish’s agonistic behaviour, identified by the aggressive defence and maintenance of the habitat. To quantify habitat boundaries of damselfish, a similar method as applied by Dromard *et al.* (2013) (adapted from Odum and Kuenzler, 1955) as well as Ceccarelli (2007) was used. When fish chased intruders, the area where chasing efforts discontinued was marked with a pink led weight (Figure 7.1), with a total of six markers placed per territory. Similarly, areas where browsing and farming behaviour stopped were observed and accounted for when marking the boundary. The number of markers was found to be sufficient in outlining the size of territories during preliminary trials. Each individual was observed for 5 min. to standardise observation time. The spirit-level and scale bar were then positioned on the benthos. Finally, the camera system was moved over the area in a “grid” pattern, taking photographs from ~1 m. distance at an interval of one frame/second.

## **2.5 3D DIGITAL BENTHIC RECONSTRUCTION**

Each resulting series of photographs was transferred onto a computer of adequate processing power for digital 3D reconstruction of the captured reef matrix. Access to required processing power was provided by the DoE during the period of data collection. Further access was then provided within Bangor University, through a partnership with Supercomputing-Wales (SCW) ([www.supercomputing.wales](http://www.supercomputing.wales)), facilitated by a collaboration between Welsh Universities and the Welsh Government. The cluster, based in Cardiff, Wales, was utilized for model generation via remote access using secure shell (SSH) connections via programs such as the MobaXterm®



Unix terminal (Mobatek, 2020). Full transect surveys resulted in ~1800 photographs each, whilst singular territories resulted in between 300-400 photographs. All 3D model generation was undertaken using the professional edition of the program Agisoft® Metashape (previously named Agisoft® Photoscan; Agisoft LLC., 2020). Photographs were uploaded into the program in separate chunks. A standardised workflow was selected to generate the dense point cloud (DPC), digital elevation model (DEM) and mesh (3D model) for later data-extraction (Figure 8). Further program specifications can be found in Appendix C. The chosen parameters were derived in part from the recommendations of the Agisoft Metashape manual, whilst also maximising processing time and achieving adequate resolution of the resulting models (Agisoft-LLC, 2020). For full transect models, the DPCs were transferred into the open source 3D point-cloud processing software CloudCompare and cut to 100 m<sup>2</sup> using the “cross-section” tool (Figure 5.3, CloudCompare, 2020) This allowed for an overlap of the abundance counts and complexity measurements for each reef section. For territory models, the boundary markers were used to crop the models to the exact size of each individual’s home-range (Figure 7.2). All DEMs were standardised to the same resolution of 2 mm, whilst all generated meshes had a scaling error <1cm.



*Figure 6: Image showing the positioning of the spirit level on an adjustable tripod mount, as well as a scale bar of known dimensions placed onto the reef for later scaling of the 3D generated model*

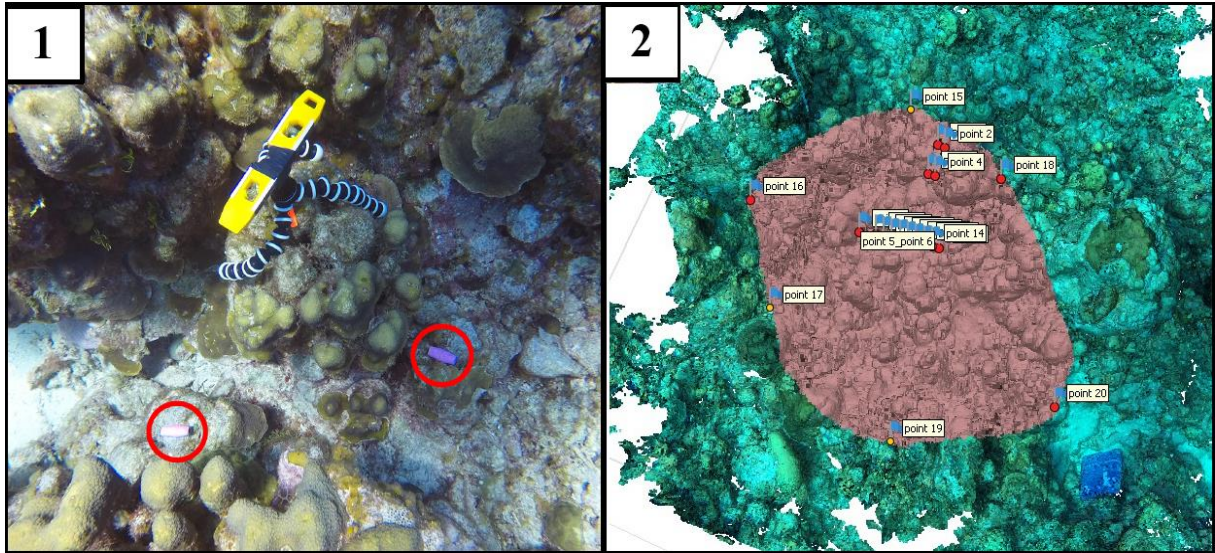


Figure 7: **1:** Image showing the positioning of the spirit level on an adjustable tripod. Red circles outline the pink led weights positioned on the outer boundaries of individual territories. **2:** The 3D reconstructed dense point cloud of a territory, with markers showing the positions of the led weights. The red area illustrates the total reef section encompassed in the territory, which is then cropped to size.

## 2.6 DATA EXTRACTION

In order to derive 2D surface area in  $\text{m}^2$  (SA), the DEM was generated from the DPC for each model. 2D SA was then calculated via the DEM measurement tool in Agisoft Metashape, using the polygon function. The measurement of the 2D area defended by damselfish was chosen as to establish home-range sizes as has previously been used as a successful measure and could be calculated at a high accuracy from derived DEMs (Ceccarelli, 2007; Dromard *et al.*, 2013).

In order to extract fractal dimension (FD) values, the meshes were extracted from Agisoft Metashape. The fractal dimension tool box, which was developed during a recent study by Reichert *et al.*, (2017) on the power of 3D fractal dimension estimates to analyse stony corals, was utilized to extract FD scores (Backes, 2017; Reichert *et al.*, 2017). It uses the Boulingard-Minkowski variation method, to extract FD values from meshes (Mandelbrot and Wheeler, 1983; Dubuc *et al.*, 1989). This method was chosen as it has been established as being highly accurate and has previously been successfully applied to measure the irregularity of coral reef substrates (Tricot, 1995; Zawada and Brock, 2009; Leon *et al.*, 2015; Reichert *et al.*, 2017). The resulting outputs were then plotted as  $x=\log(\text{Dilation\_Radius})$  and  $y=(\log(\text{Influence\_Volume}))$  using the statistical computing language R via its graphical user



interface (GUI), R studio (R Core Team, 2020). The slope (S) of the line of best fit was then derived and FD calculated via the function:

$$\text{Eq. 1} = \text{FD} = 3 - S$$

Calculated values of FD lay on a scale of 0 – 3, with 3 signifying the most complex topography.

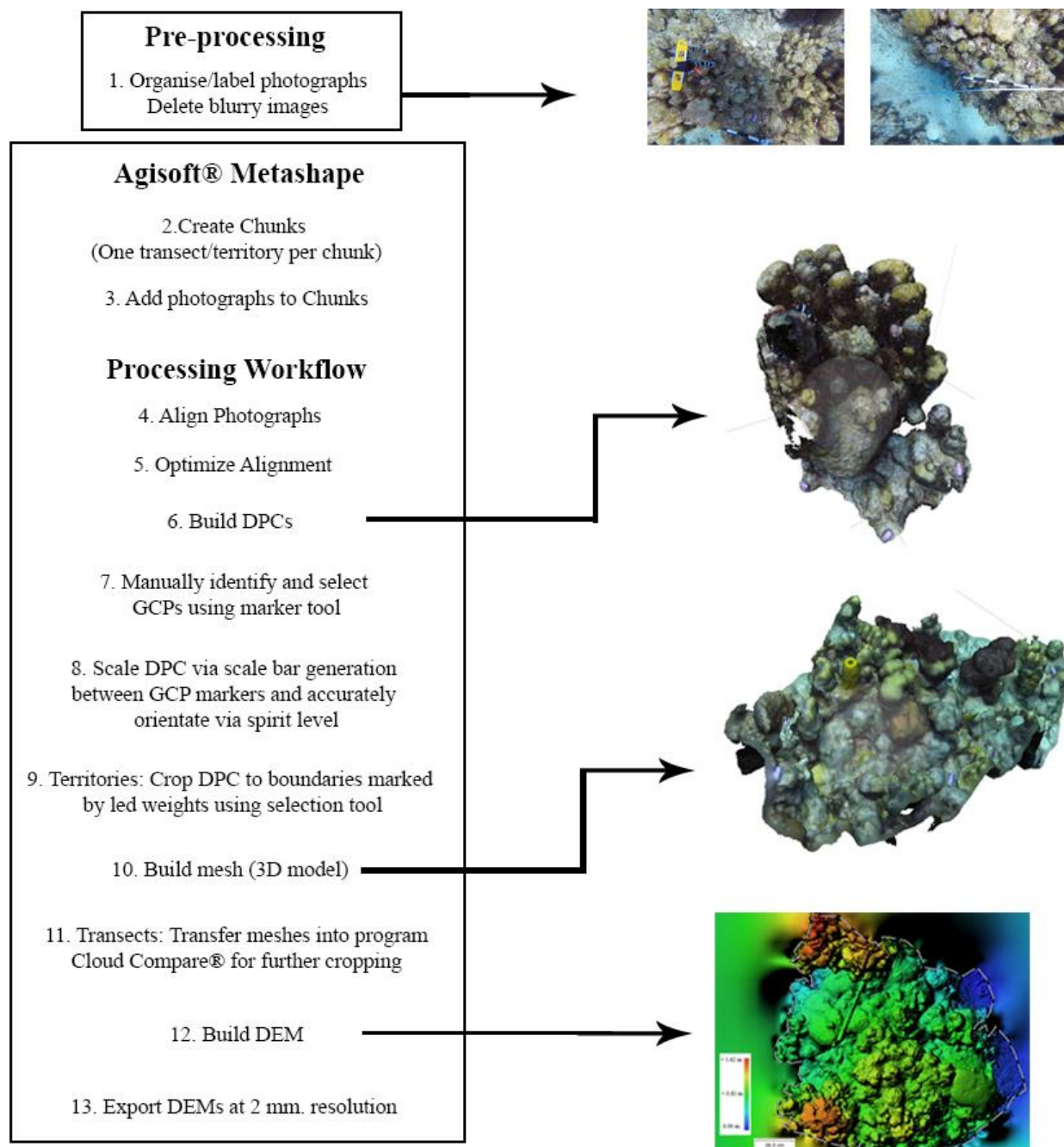


Figure 8: Standardised workflow to generate dense point clouds, DEMs and meshes (3D models from photographs of the reef benthos for later data extraction using the program Agisoft® Metashape).



## 2.7 STATISTICAL ANALYSIS

All data collation and organisation was undertaken within the program Microsoft Excel and then transferred into the GUI R studio where all further analysis was undertaken. For all analysis, to meet assumptions of the appropriate statistical tests, Levene's tests of variance were performed to assess homoscedasticity and Shapiro Wilk's tests were performed to assess whether the data followed a normal distribution. Where assumptions of normal distribution were violated, quasi-poisson and negative binominal distributions were fitted, or a log-transformation ( $\log()$  function, natural logarithm (LN)) applied where appropriate. Models of best fit were chosen via an assessment and comparison of degrees of freedom, residual spread, histogram & QQ-plots and Akaike information criterion (AIC) (Akaike, 1974) scores of different linear models (LM) and generalized linear models (GLM). For all analysis statistical significance ( $\alpha$ ) was set to  $<0.05$ .

### 2.7.1 Reef-scale distribution patterns

The highly variable abundance counts of *S. planifrons* and *S. dienciaeus* both followed a pattern of over dispersion of residuals often found when handling data sets of such nature (White and Bennetts, 1996). As the two species did not display similar data distributions, this great inflation of lower count values was accounted for by using GLMs with a negative binominal distribution for *S. planifrons* count data and a quasi-Poisson distribution for *S. dienciaeus* count data (Bliss and Fisher, 1953; Wedderburn, 1974; White and Bennetts, 1996). With assumptions of homoscedasticity and normal distribution met, a two-way analysis of variance (ANOVA) was performed to investigate whether there is an effect of aspect and depth on distribution patterns of each species and whether there is a detectable interaction between them. Each model included species abundance (dependent variable) and an interaction of the fixed effects of depth and aspect (independent variables). An approach including a mixed effect model with the random effect of survey site was excluded, as it did not score lower AICs. Following, sub-set GLMs were fitted as a *post-hoc* method to investigate where significant differences in abundances lie between shallow and deep reef terraces within and between aspects. In order to investigate whether there was a significant difference in FD scores between northern and western shallow reef terraces, a Welch's two-sample t-test was performed.

To assess whether shallow reef terrace complexity has an effect on damselfish distributions the presence and strength of a relationship between FD scores and individual species abundances was investigated. As *S. planifrons* data did not meet statistical assumptions, a GLM with a negative-binominal distribution was chosen to account for over dispersion. For *S. diencaeus* a GLM model with a Poisson distribution was fitted to account for the nature of count data not allowing negative values, as is assumed by a normal (Gaussian) distribution. Both models included species abundance (dependent variable) and the fixed effects of FD and aspect (independent variables). An interaction between FD and aspect was excluded from the GLMs following results of preliminary tests.

### **2.7.2 Territory-scale habitat characteristics**

In order to assess whether a change in habitat quality has an effect on the size of the home range defended by the two damselfish species, the presence and strength of a relationship between FD scores and the 2D area (m<sup>2</sup>) of individual territories was investigated. Data was log-transformed (LN) to meet statistical assumptions. LMs were then fitted including 2D area (dependent variable) and FD scores (independent variable).

To investigate whether *S. planifrons* associates with territorial areas of significantly higher benthic complexity than *S. diencaeus* and whether they differ in their efforts of habitat defence within the same habitat, FD scores and 2D area measurements of all territories were pooled. Significant differences in FD scores and respective 2D areas between both species were then detected via two-sample t-tests. The 2D area data was log-transformed (LN) to meet statistical assumptions.

### 3. Results

#### 3.1 REEF SCALE DISTRIBUTION PATTERNS

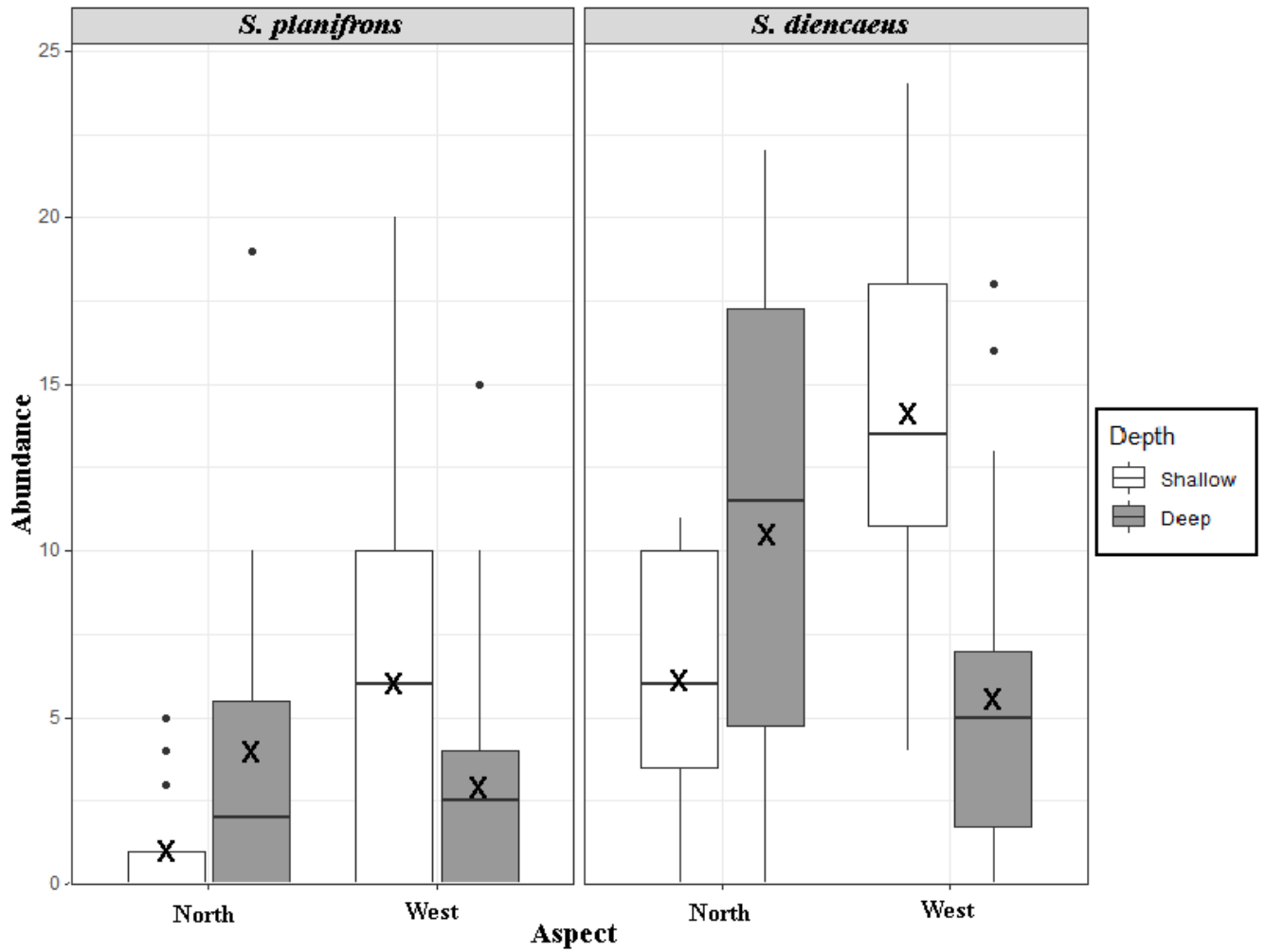
##### 3.1.1 Effects of aspect and depth

Abundances of *S. planifrons* and *S. dienciaeus* appeared to follow similar trends when comparing their distributions on shallow and deep reef terraces across northern and western survey sites (Figure 9). The ANOVA analysis found an interaction of the effects of depth and aspect variables on distributions of both species (Table 3). Mean abundances of *S. planifrons* were highest on shallow Western terraces ( $5.95 \pm 1.15$ ) with marginally non-significantly lower mean abundances on deep terraces ( $2.92 \pm 0.73$ ; GLM,  $z=1.93$ ,  $P=0.05$ ,  $n=48$ ). Inversely, Northern mean abundances were significantly lower on shallow ( $0.9 \pm 0.35$ ; GLM,  $z=-2.89$ ,  $P<0.01$ ,  $n=40$ ) than deep terraces ( $3.85 \pm 1.09$ ; GLM,  $z=1.93$ ,  $P=0.05$ ,  $n=48$ ). For *S. dienciaeus*, mean abundances were also highest on shallow Western terraces ( $14.20 \pm 0.98$ ), whilst being significantly lower on deep terraces ( $5.63 \pm 0.98$ ; GLM,  $z=5.55$ ,  $P<0.001$ ,  $n=40$ ). Within Northern survey sites, the same inversed trend as observed for *S. planifrons* was seen, with significantly lower mean abundances on shallow reef terraces ( $6.15 \pm 0.79$ ) than deep reef terraces ( $10.6 \pm 1.58$ ; GLM,  $z=-2.21$ ,  $P=0.03$ ,  $n=40$ ).

When comparing shallow terraces, western *S. planifrons* abundances were significantly higher than northern abundances (GLM,  $z=4.03$ ,  $P<0.001$ ,  $n=44$ ), as were abundances of *S. dienciaeus* (GLM;  $z=6.24$ ,  $P<0.001$ ,  $n=44$ ). There was no significant difference in *S. planifrons* abundances on the deep reef terraces between aspects (GLM,  $z=-0.71$ ,  $P=0.48$ ;  $n=44$ ) whilst *S. dienciaeus* abundances were significantly higher on northern deep terraces (GLM,  $z=-2.29$ ,  $P=0.02$ ,  $n=44$ ). Throughout all sites, recorded pooled mean abundances of *S. dienciaeus* were higher within both aspects and depth ranges than those of *S. planifrons* (Figure 9).

##### 3.1.2 Effect of structural complexity

When pooling and comparing the mean fractal dimension scores for shallow northern and western reef terraces, the t-test reported no significant difference ( $t(22.68)=-1.24$ ,  $P=0.23$ ). There was a large amount of variation of scores between different sites, displaying no clear trend of higher complexity for either aspect (Figure 10).



**Figure 9:** Boxplots displaying abundances *S. planifrons* and *S. diencaeus* across all combined survey sites ( $n=22$ ) of deep and shallow reef terraces within the northern ( $n=10$ ) and western ( $n=12$ ) aspects of Grand Cayman. “X” symbols represent pooled mean abundances.

**Table 3:** ANOVA analysis outputs testing for significant effects of explanatory variables on abundances of *S. planifrons* and *S. diencaeus* and interactions between them. Significant values are indicated via “\*” in **bold**.

Species	Variable(s)	DF	$\chi^2$	P
<i>S. planifrons</i>	Depth	1	0.11	0.75
	Aspect	1	4.63	<b>0.03*</b>
	Depth : Aspect	1	12.48	<b>&lt; 0.001*</b>
<i>S. diencaeus</i>	Depth	1	16.94	<b>0.02*</b>
	Aspect	1	5.66	0.18
	Depth : Aspect	1	99.16	<b>&lt;0.001*</b>

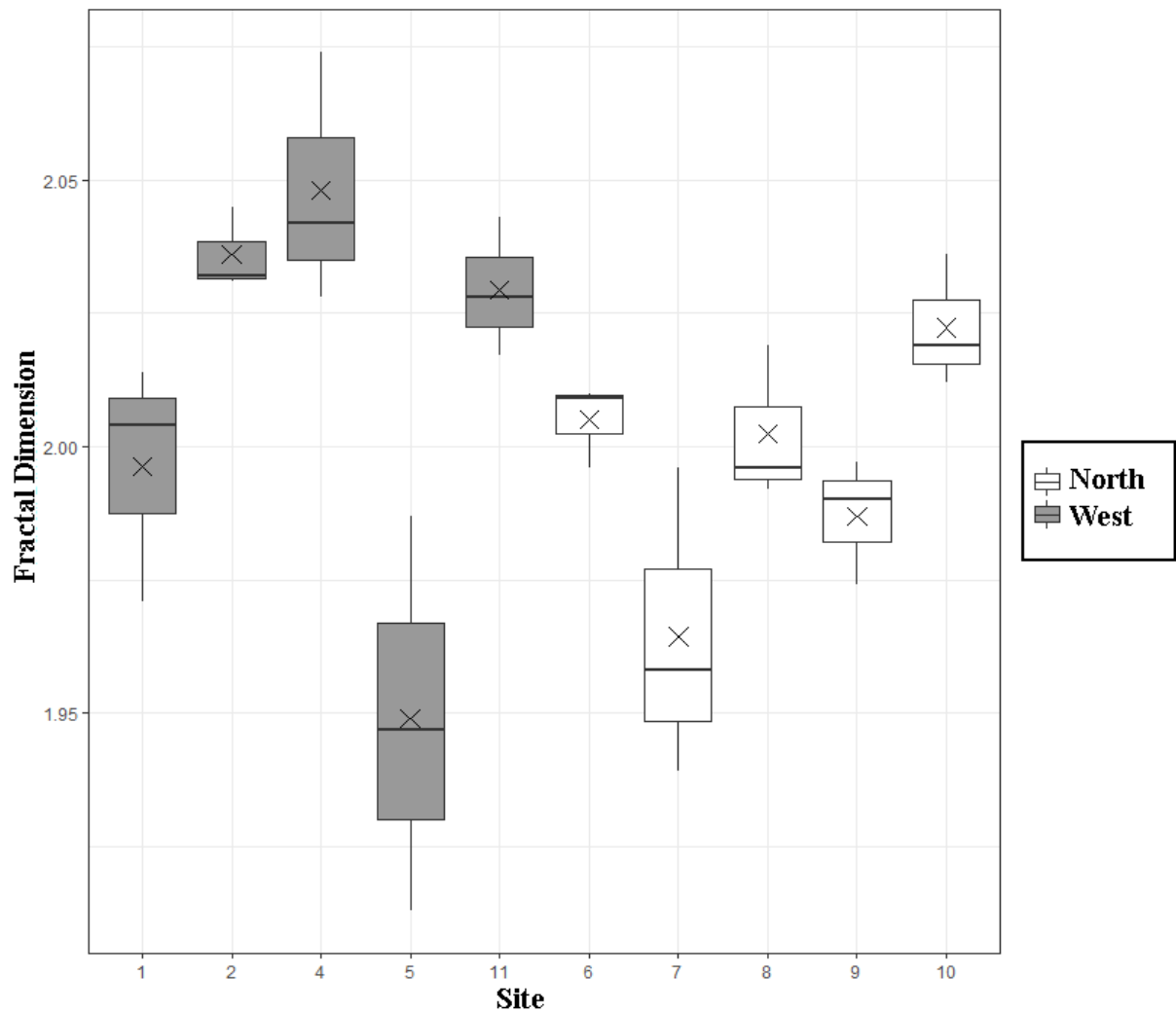


Figure 10: Boxplots displaying fractal dimension scores for transects of shallow survey sites ( $n=3$ ) in the northern and western Aspects of Grand Cayman. “X” symbols represent mean FD scores.

When investigating the relationship between shallow reef terrace abundances and FD scores for each species, fitted models showed significant effects of FD scores on abundances of both species. This effect appeared stronger for *S. planifrons* abundances (GLM,  $z=2.87$ ,  $P<0.005$ ,  $n=30$ ) than for *S. diemaeus* abundances (GLM,  $z=2.19$ ,  $P=0.03$ ,  $n=30$ ), though both were statistically significant. Models further predicted that for each species, aspect had a strongly significant effect on the strength of these relationships (Figure 11). *S. planifrons*, the relationship between abundances and FD scores was significant for both western and northern observations (West: GLM,  $z=4.09$ ,  $P<0.001$ ,  $n=15$ ; North: GLM,  $z=-2.91$ ,  $P<0.005$ ,  $n=15$ ). For *S. diemaeus*, only the western observations showed a significant relationship (West: GLM,  $z=5.72$ ,  $P<0.001$ ,  $n=15$ ; North: GLM,  $z=-1.65$ ,  $P=0.1$ ,  $n=15$ ).

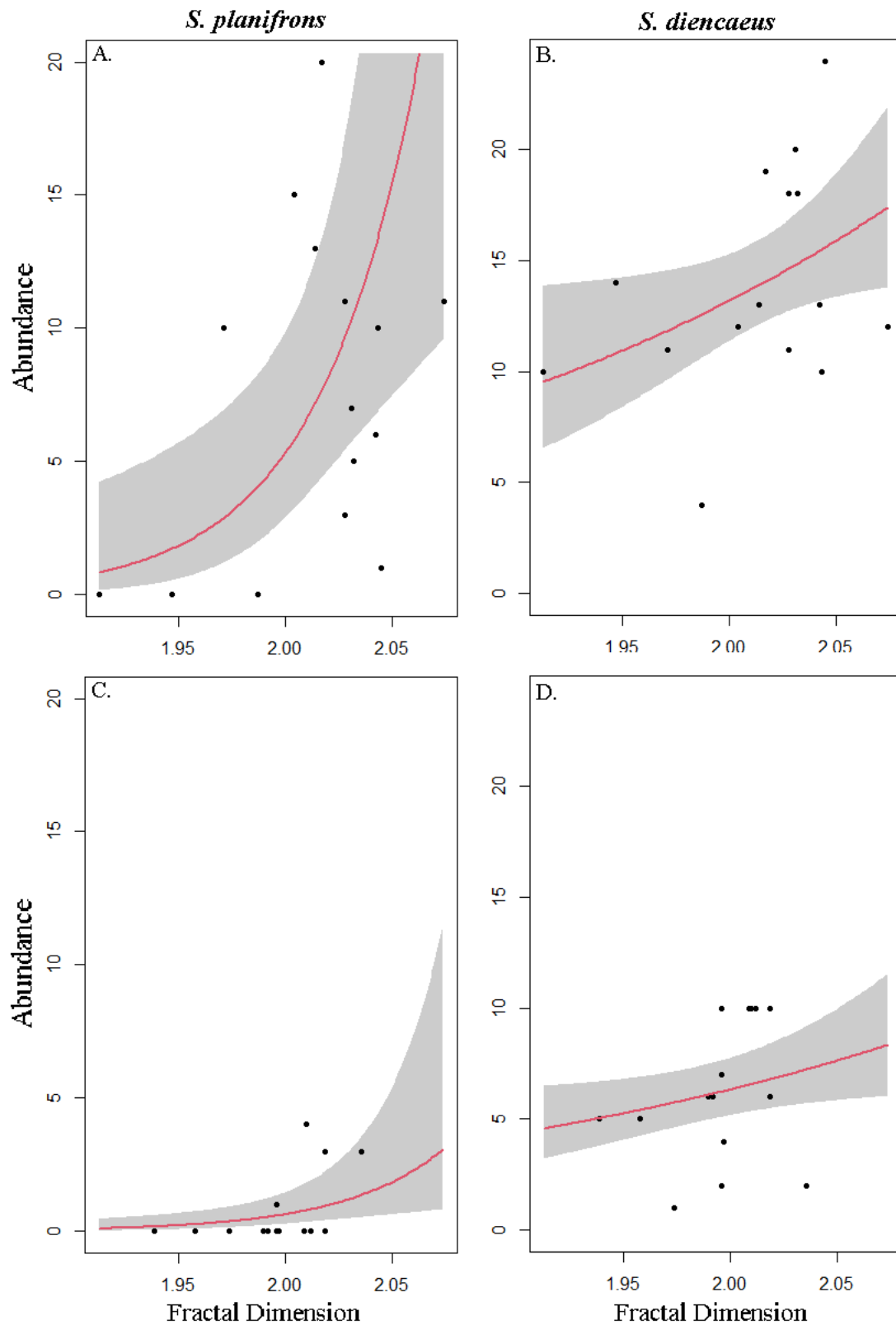


Figure 11: Regression plots displaying abundances of *S. planifrons* and *S. diencaeus* as a function of fractal dimension scores per transect across all shallow survey sites (transect  $n=30$ ) in the Western (A.; B.) and Northern (C.; D.) Aspects of Grand Cayman. Red lines represent the GLM predicted fit of the relationship. Grey areas represent upper and lower 95% confidence intervals (CI).

## 3.2 TERRITORY SCALE HABITAT AND HOME-RANGE CHARACTERISTICS

### 3.2.1 Effects of habitat quality on home-range size

Analyses of linear models predicting the relationship between the 2D area of the defended home-range and its associated complexity revealed different trends for the two species. *S. planifrons* territories exhibited a weak but significant positive correlation, with the size of the 2D area of the home range increasing with increasing FD scores (Table 4, Figure 12). *S. diencaeus* showed no significant relationship, with overall trends showing a slight decrease of the 2D area of home ranges with increasing FD scores and large variation of data points (Table 4, Figure 12).

Table 4: Regression analysis outputs testing for a relationship between the 2D surface area ( $m^2$ ) and FD scores of territories of *S. planifrons* and *S. diencaeus*. Significant values are indicated via “\*” in **bold**.

Species	F	P	Multiple R <sup>2</sup>	Equation
<i>S. planifrons</i>	10.17	<b>&lt;0.005*</b>	0.23	$y = -12.01 + 5.78x$
<i>S. diencaeus</i>	1.12	0.1	0.03	$Y = 3.89 - 1.64x$

### 3.2.2. Differences in habitat quality and habitat defence

When comparing territorial characteristics of *S. planifrons* and *S. diencaeus* within the same habitat on shallow western terraces, significant differences in the mean FD and 2D area of home-ranges were found. T-tests revealed significantly higher mean FD scores of *S. planifrons* territories ( $2.08 \pm 0.005$ ) when compared to *S. diencaeus* ( $2.09 \pm 0.005$ ;  $t(75.82) = 2.3$ ,  $P = 0.02$ ; Figure 13: A., C.). Simultaneously, the mean 2D home-range area of *S. planifrons* ( $1.17 m^2 \pm 0.07$ ) was significantly smaller ( $t(74.05) = 5.03$ ,  $P < 0.001$ ) than that of *S. diencaeus* ( $1.71 m^2 \pm 0.55$ ; Figure 13: B., D.). This trend was consistent within all individual survey sites (Figure 13). Within all survey sites, mean FD scores of both species’ territories were higher than mean survey site scores (Figure 14).

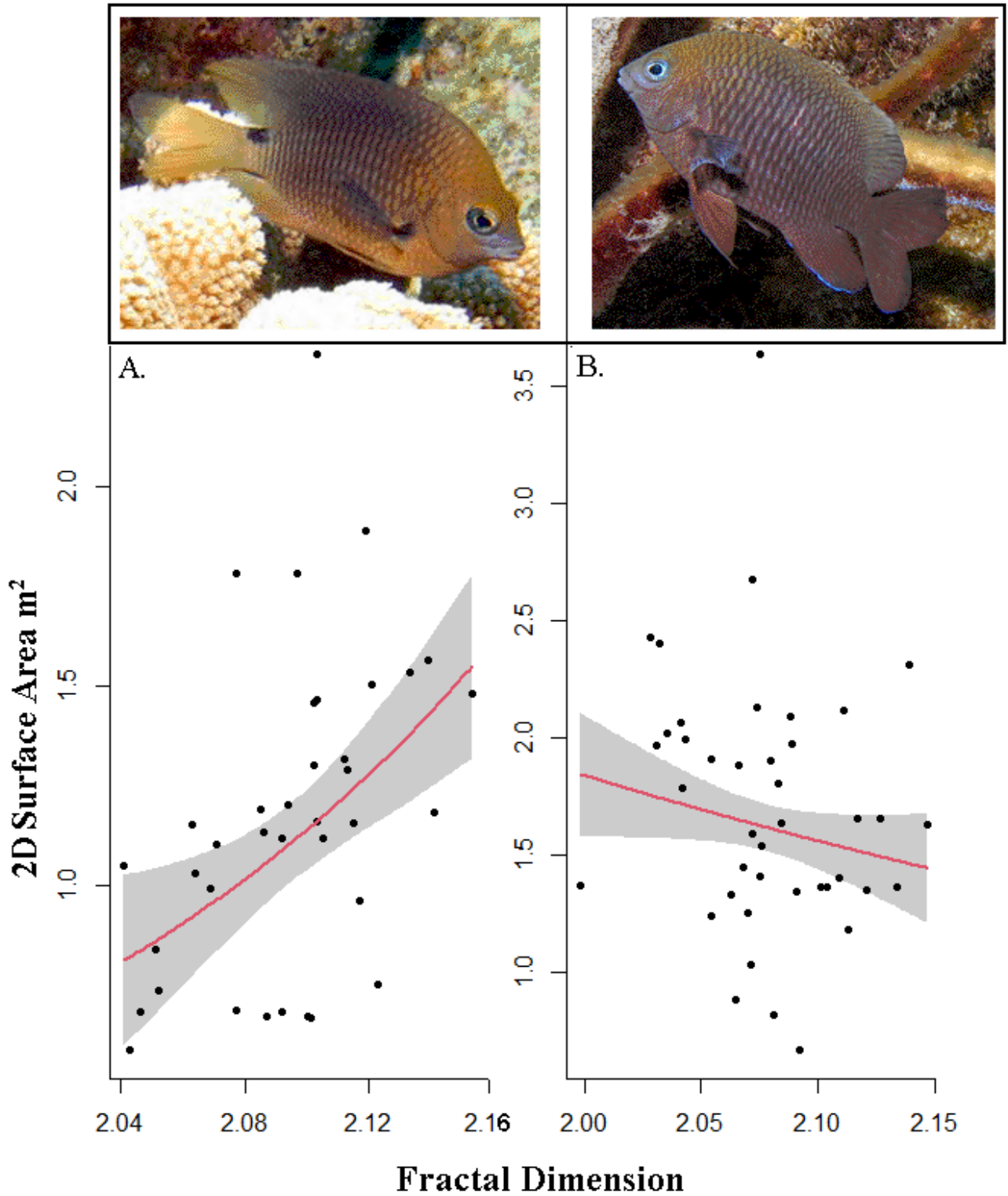


Figure 12: Regression plots displaying the 2D surface area ( $m^2$ ) as a function of FD scores of individual territories of *S. planifrons* (A.;  $n=37$ ) and *S. diencaeus* (B;  $n=41$ ) within western shallow survey sites. Red lines represent the LM predicted fit of the relationship. Grey areas represent upper and lower 95% confidence intervals (CI) (Images: © Florent Chaplin, 2020 a, b).



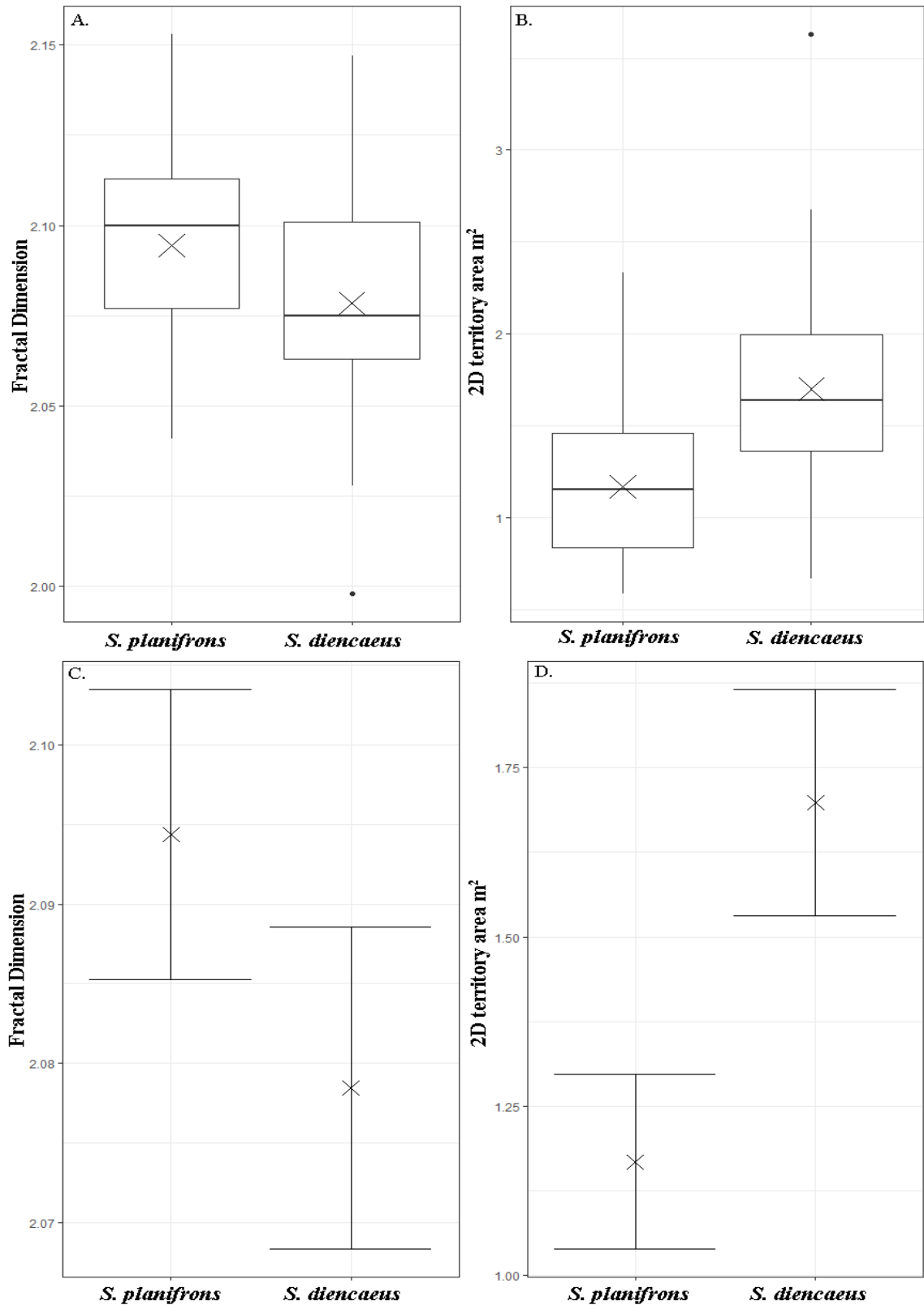


Figure 13: First row: Boxplots displaying the FD scores (A.) and 2D surface area ( $m^2$ ) (B.) of *S. planifrons* and *S. diencaeus* territories. Second Row: Plotted upper and lower 95% confidence Intervals around the mean FD scores (C.) and 2D surface area ( $m^2$ ) (D.) of all pooled territories per species. “X” symbols represent mean values. Data was collected within the shallow western survey sites of Grand Cayman.

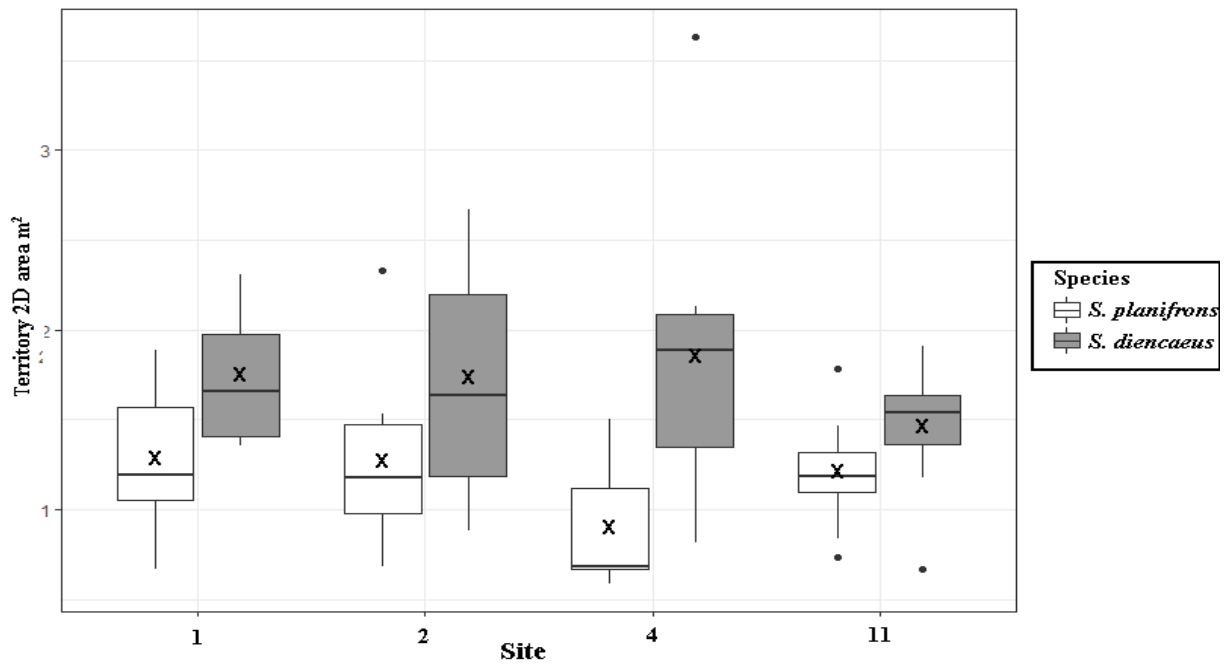


Figure 14: Boxplots displaying the 2D territory area ( $\text{m}^2$ ) of territories of *S. planifrons* and *S. diencaeus* across four shallow survey sites in the western aspect of Grand Cayman. “X” symbols represent pooled mean FD scores

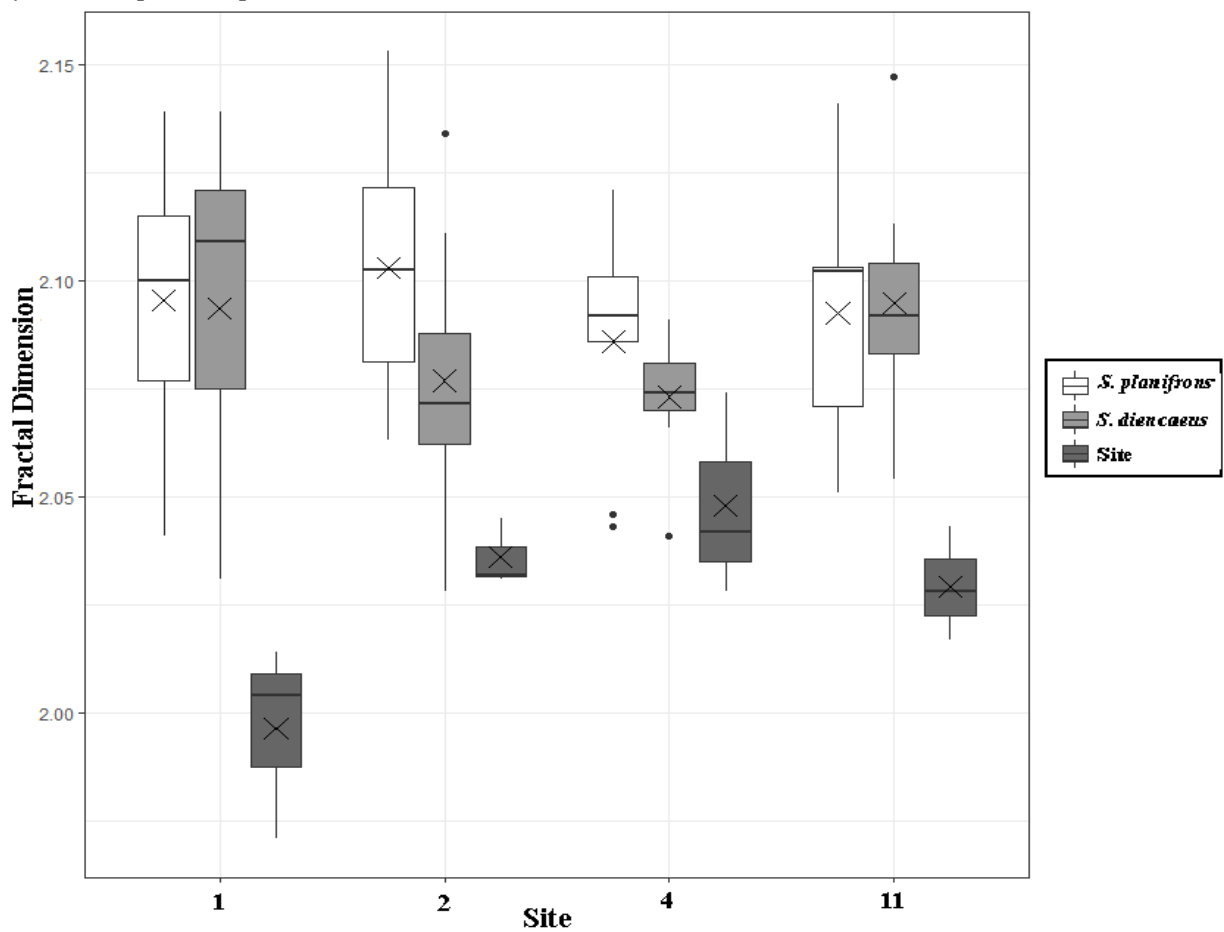


Figure 15: Boxplot displaying FD scores measured of *S. planifrons* & *S. diencaeus* territories and the overlapping reef sections across four shallow survey sites in the western aspect of Grand Cayman. “X” symbols represent pooled mean FD scores.

## 4. Discussion

### 4.1 REEF-SCALE DISTRIBUTION PATTERNS

#### 4.1.1 Distributions with exposure and depth

On the surveyed reefs around Grand Cayman, distributions of *S. planifrons* and *S. diencaeus* followed similar patterns with depth and exposure, suggesting that, on the reef terrace scale, a combination of these factors is partially structuring damselfish population abundances. Mean population abundances were significantly highest on the shallow western reef terrace. These findings showed that in Grand Cayman, the sheltered and shallow reef habitat range for these species was similar to descriptions in previous studies (Waldner and Robertson, 1980; Solandt, Campbell and Haley, 2003; Floeter *et al.*, 2007). The western aspect of Grand Cayman presents the most sheltered coastal stretch and harbors all MPA zones situated around the island. Wave exposure is known to be an important force structuring both benthic- and reef fish communities (Huston, 1985; Fulton, Bellwood and Wainwright, 2005; Mumby, 2012). Habitat specialized herbivores have been found to associate with more sheltered environments in comparison to herbivores with larger home-ranges and morphological adaptations to enhance swimming abilities (Floeter *et al.*, 2007; Bejarano *et al.*, 2017). Previous assessments on the effectiveness of MPAs on reef fish population distributions and biomass as part of DoE monitoring programs detected an increase of herbivore biomass inside shallow terrace MPAs on Grand Cayman, suggesting a positive effect of protection efforts under the absence of fishing pressure (Dromard, McCoy and Turner, 2011; Hughes, 2017; McCoy, 2018). Whilst the western reef terrace is less developed compared to the northern reef terrace with reduced overall vertical relief of the spur-and-groove zone, it presents a similar benthic composition of coral diversity and cover including *Orbicella* spp. favored by *S. planifrons*. However, neither *S. diencaeus* or *S. planifrons* showed a strong preference for low exposure and greater protection in deeper waters. *S. diencaeus* even exhibited the lowest mean abundance values recorded during this study. This is possibly due to the availability of favorable shallow reef habitats, allowing both damselfishes to exist within their common depth ranges, though damselfishes are not purely restricted to shallower waters (Robertson, 1984; Ceccarelli, Jones and Mccook, 2001). Whilst there are no major biotic or abiotic differences in shallow and deeper western reefs, there is a history of destruction from cruise ship anchoring on the outer reef shelf. The submarine topography of a narrow shelf dropping sharply to abyssal depths has limited the ability of cruise ships to anchor further off-shore, significantly reducing reef structures on the deeper terrace off

George Town, where a proportion of survey sites were located (Turner *et al.*, 2013). Due to the lack of quantitative data on damselfish densities in previous decades, it is not possible to clearly interpret these distribution patterns as a direct result of habitat degradation and such anthropogenic disturbances. Previous studies have associated *S. diencaeus* to large rocks and rubble and described its ability to persist in degrading environments. Yet, despite the species being less associated to complex coral structures, it still positively associates to live coral cover and habitat metrics providing favorable conditions for nesting sites, which are potentially more common within shallow reef communities (Solandt, Campbell and Haley, 2003).

Interestingly, an inversed distribution trend was found on the northern aspect of Grand Cayman, with abundances of species being significantly lower on the shallow reef terrace in comparison to the corresponding deep reef terrace. Considering that shallow abundances were also significantly reduced in comparison to western shallow reefs, this suggests that this reef section presents an overall less favorable habitat for these damselfishes. Especially *S. planifrons* showed the lowest recorded abundances compared to any other depth and aspect during this study. As mentioned before, northern reefs were previously comprised a previous abundance of complex coral structures such as *Acropora* spp. dominating the reef crest, which have mostly disappeared in the last decades. Northern reefs have additionally been specifically affected by previous hurricane damage and experienced subsequent coral cover loss. Though patterns of recovery and relatively stable benthic community structures have been monitored since, these factors likely contributed to the disappearance of suitable habitat for both damselfish species (Mccoy, 2018). In addition, the loss of branching corals and consequent lack of shelter provided against the higher degree of wave energy forcing in the semi-exposed aspect may also be a contributing factor to the low recorded abundances.

Both species displayed significantly higher abundances on the deeper northern reef terrace. The northern deep reef environment has been described as substantially more developed than its western counterpart, and *Orbicella* spp. such as *Orbicella annularis* are the dominant coral types (Turner *et al.*, 2013; Mccoy, 2018). This benthic community may provide a secondary habitat for *S. planifrons* and *S. diencaeus* populations in comparison to the potentially less heterogeneous shallower waters. Similar patterns were observed by a study monitoring relocation and recruitment patterns of *S. planifrons* after hurricane damage to the branching corals of the shallow reef habitat in Jamaica in 1980 (Kaufman, 1983). A shift towards deeper reef habitats was measured, which remained persistent after the disturbance event and were interpreted as a direct result of habitat loss in shallower waters. Due to the increasing degree of

degradation and stressors experienced in shallow reef systems, recent studies have focused on the potential refuge deeper reef habitats may provide for coral associated fish groups such as damselfish (Jankowski, Graham and Jones, 2015; MacDonald, Bridge and Jones, 2016; Goldstein, D'Alessandro and Sponaugle, 2017). Though no temporal comparisons can be made, the observed inversed distribution patterns with aspect in this study could imply a habitat shift towards deeper waters, where shallow waters have become less favorable. Considering the high respective northern abundance of *S. diencaeus*, the low abundances found within deeper western waters may be influenced more strongly by other environmental factors decoupled from depth and shallow water complexity. Similar interpretations were made by a study examining the spatial distribution of the common bi-colour damselfish (*Stegastes partitus*) along depth gradients (Goldstein, D'Alessandro and Sponaugle, 2017).

There was a lot of variability of mean abundances per site, suggesting that on the site level, there may be a variety of other variables at play in structuring distributions. Reef systems are highly dynamic and heterogeneous habitats and their spatial and trophic composition is affected by a range of environmental gradients as well as biological factors (Huston, 1985; McGehee, 1995; Williams *et al.*, 2013). Considering this, settlement preferences and predation pressure are probably additional factors shaping distributions around Grand Cayman. Predation pressure, though deemed less significant than benthic composition factors for damselfish abundances, may partially structure recruitment survival as well as adult distributions (Precht *et al.*, 2010). This may be more significant for *S. planifrons* due to its smaller body-size in comparison to *S. diencaeus*, which seems to be less affected by the risk of predation (McDougall and Kramer, 2007). Previous studies identified behavioral changes as well as a reduction in abundances of *S. planifrons* in response to predator presence (Vermeij *et al.*, 2015). Additionally, Precht *et al.* (2010) found that this effect was dependent on the availability of structurally complex habitats facilitating shelter. Effects of predation may also be mediated by shifts in trophic structures through differential fishing regulations. In Belize, a reduction of larger-bodied predators through fishing pressure caused a marked increase in meso-scale predators and a subsequent reduction of *S. planifrons* densities (Mumby *et al.*, 2012). Another predator that is known to exert significant predation pressure on benthic fish recruits and adults including Pomacentridae is the invasive lionfish (*Pterois volitans*) (Morris and Akins, 2009). Like many other reef fish, *S. planifrons* has been shown to have minimal avoidance responses to the presence of *P. volitans* and hence has the potential to suffer higher mortality through predation pressure (Kindinger, 2015; Davis, 2018; Haines and Côté, 2019). There are culling efforts in place in the Cayman Islands to manage local populations, yet there have been reports of higher densities

and larger specimen of *P. volitans* on deeper reefs, potentially as a result of avoidance of culling activities in shallower waters (Gunn, 2017). This could explain the respectively lower abundances of *S. planifrons* in comparison to *S. diencaeus* on deeper reef terraces. The prevalence of coral cover could be another factor specifically affecting recruitment processes, as damselfish, like many other reef fish, prefer live coral for larval settlement (Jones *et al.*, 2004; Precht *et al.*, 2010).

The higher prevalence of *S. diencaeus* in comparison to *S. planifrons* throughout all study sites could be an indication of better adaptation capabilities of this species to a range of habitats and environmental stressors. Being less bound to specific benthic components may allow this species to flourish in a greater range of environments. Yet, in the surveys undertaken in 1999 in the Cayman Islands, *S. diencaeus* was already more prevalent than *S. planifrons* (Pattengill-Semmens and Semmens, 2003). Without consistent temporal comparisons a full interpretation of such deviations of abundance is not possible. The loss of habitat specialists recorded throughout the Caribbean region combined with observations of similar patterns in distribution changes elsewhere, suggest that local populations could be prone to such habitat shifts (Kaufman, 1983; Solandt, Campbell and Haley, 2003; Alvarez-Filip *et al.*, 2009; Precht *et al.*, 2010).

#### **4.1.2 Distributions with shallow reef complexity**

The quantification of habitat complexity on shallow reef terraces found that the northern and western reef terraces did not differ significantly in their overall complexity when comparing pooled aspects alone. This resulted from variations of complexity measurements between all survey sites regardless of aspect. These variations of fractal dimension values also ranged on a relatively small scale. This indicated that there are exposure-related factors influencing shallow reef distributions that are decoupled from reef complexity and emphasized the relative homogeneity of reef habitats between these aspects. Hence, reef complexity was found to have no measurable effect on distributions on the reef terrace scale as a factor of exposure gradients. Yet, as hypothesized transect complexity significantly affected abundances of *S. planifrons* and *S. diencaeus*, with the strength of this effect varying with aspect. Within the western aspect, both species were positively associated to increasing complexity, with the trend being stronger for *S. planifrons*. This was expected, following the well-established concept of a positive relationship between habitat complexity and abundance and diversity of reef fauna (Harborne, Mumby and Ferrari, 2012; Graham and Nash, 2013). The findings further strengthen the

hypothesis that a structurally complex habitat is of greater importance to this species' distribution than that of *S. diencaeus*. Only *S. planifrons* abundances had a positive association to reef complexity within the northern aspect, though this relationship was weaker than in the western aspect. Many transects recorded no counts of this species, with the only sightings being recorded in transects of slightly higher complexity. This suggests that even in lesser preferred habitats, any settling individuals still correlate with increased benthic complexity. Similar patterns have been observed in other studies comparing *S. planifrons* densities on remaining favoured habitats to surrounding coral rubble (Wilkes *et al.*, 2008). For *S. diencaeus*, previously discussed factors aside site complexity may be stronger variables causing its distribution on northern reefs, hence resulting in no detectable relationship to benthic complexity. For both species, northern transects also showed a smaller range of FD values than western transects, which may indicate slightly greater habitat homogeneity. This, coupled with recorded low abundances on this reef terrace, may have led to a decreased ability to detect relationships in this environment. Competition is unlikely to be a factor in the lacking relationship of complexity and *S. diencaeus* abundances, as this species is among the most territorial and largest damselfishes and it has not been observed to be reduced in abundances through high inter- or intra- specific densities (Robertson, 1996). Overall, these findings suggest that even though exposure does not significantly affect general shallow reef terrace complexity and distribution patterns, variations of transect complexity have significant effects on damselfish abundances, though this may also be dependent on other environmental stressors.

Both species abundance counts showed noteworthy spreads around the GLM-predicted lines of best fit. This presented another indicator that general benthic complexity is not the sole metric determining the distribution of these fish on shallow reef terraces. There is a range of benthic variables that may play a biological role in structuring reef fish communities, which may not be captured in generalized complexity measurements. FD described the degree to which a given object fills the space which it occupies, presenting a useful and precise indicator of the overall degree of complexity of a given benthos. It does not necessarily include components of the reef structure such as crevices and holes, which have been shown to be of biological importance in providing shelter and nesting grounds (Hixon and Beets, 1989; Hixon, 1991; Nemeth, 1998). In a study undertaken by Almany (2004), the presence of shelter holes of adequate sizes significantly affected recruitment and survival rates of damselfishes in the presence of predators. The scale on which complexity attributes are measured is a critical factor in understanding how structural metrics influence damselfish distribution on different spatial scales. A study by Harbone *et al.* (2012) compared reef fish correlations to seven different

rugosity metrics on a meso-scale on a Belizean fore-reef and found differential correlations of fish groups to different metrics, varying between e.g. mean coral height and coral abundance (Harborne, Mumby and Ferrari, 2012). Due to their strong benthic reliance, structural attributes on the micro-habitat scale have been suggested to have greater effects on the distribution of damselfishes than factors measured on a meso-scale (Tolimieri, 1998). Overall, seeing as neither general complexity, exposure or depth gradients seem to fully explain the observed distribution patterns, the previously discussed factors such as predator abundance and differential benthic components should be considered in future studies to better understand the environmental and anthropogenic stressors affecting damselfish community structures around Caymanian coral reefs.

## **4.2 MICROHABITAT-SCALE COMPLEXITY ASSOCIATIONS**

Investigations of the strength of different metrics affecting distributions of *S. planifrons* and *S. diencaeus* on the microhabitat-scale showed differing relationships between the defended home-range size and territorial complexity. *S. planifrons* home-range sizes were positively correlated to microhabitat complexity, whereas *S. diencaeus* showed no correlation trend within similar habitats. This underpins the hypothesis that *S. planifrons* abundances correlate with habitats of higher general complexity more than those of *S. diencaeus* and will exert more energy towards defending a larger home-range. The findings of this study indicate that home-range size, interpreted as function of defence efforts, is maximised towards areas of higher complexity in *S. planifrons*. This was further strengthened by the findings that *S. planifrons* territories were also of significantly higher overall complexity, whilst their defended home-ranges were significantly smaller than those of *S. diencaeus*. *S. planifrons* home-ranges were consistently lower irrespective of survey sites. This follows the trend of optimal territory-size models stating that the territory size increases proportionally to the benefits of intruder exclusion, as has been found for *S. planifrons* (Thresher, 1976; Davies and Houston, 1984). In previous studies, habitat quality was described as a function of the availability of food, shelter and nesting holes (Thresher, 1976; Meadows, 2001; Cheney and Cote, 2003). The same concept can be seen when using FD as a general measure of habitat quality in this study. Conversely, a study by Cheney and Cote (2003) assessing territorial compositions of *S. diencaeus* found that territory size remained uniform throughout territories of varying benthic components. Furthermore, this study found that variables such as rugosity had no significant effect on recolonization speed, whilst the presence of nesting sites did. As previously discussed, habitat



characteristics such as nesting sites and coral cover and species are not specifically captured via metrics of general complexity, potentially explaining the lack of a correlation of defence efforts in this study. Conversely to the findings of Cheney and Cote (2003), this study observed *S. diencaeus* home-ranges on shallow western reef terraces to show variations in 2D size between  $>2.5 \text{ m}^2$  and  $<1 \text{ m}^2$ . A factor that has been found to potentially affect the defended territory size of this species is the relocation to other territories, which seems to increase energetic costs and hence decrease home-range sizes (McDougall and Kramer, 2007). Yet, frequency with which individuals re-locate to adjacent habitats and how strongly this affects variations in territory size remains less clear. *S. diencaeus* may also exhibit sex-specific distribution patterns, as males have been found to generally defend larger territories than females (Cheney and Cote, 2003). The significant differences in overall territory sizes between species may also be explained by the larger maximum body size of *S. diencaeus*. In the genus *Stegastes*, the degree of territoriality has been linked to body size, with larger individuals having the ability to defend larger territories (Ceccarelli, Jones and Mccook, 2001). The final observation of this study was that, throughout all survey sites, the mean complexity scores of *S. planifrons* and *S. diencaeus* territories were consistently higher than those of the respective sites within which they were found. This pattern strengthens the assumptions that, while both species associate to higher general complexity on a site-scale, this is not necessarily true for the micro-habitat scale.

Despite the significant correlation of habitat defence and complexity found for *S. planifrons*, only 23% of observed home-range variations were explained by this relationship. This may stem from the range of ecological factors affecting territorial defence in damselfishes such as inter- and intra-specific competition. Whether inter-specific competition is a significant force acting between the two species on Caymanian reefs is debateable. Previously, investigations of the ecological overlap of different damselfish found no association *S. planifrons* and *S. diencaeus* abundances, implying no competitive interactions (Robertson, 1996). Whether potential habitat shifts in recent years have led to inter-specific competition within increasingly overlapping habitats remains less clear. Like many reef fish, damselfish exhibit patterns of niche-separation, allowing them to co-exist within similar habitat ranges (Waldner and Robertson, 1980; Ebersole, 1985; Dromard *et al.*, 2013; Eurich, McCormick and Jones, 2018). Hence, the differential associations to benthic attributes on a micro-habitat scale may be the structuring force allowing both species to co-exist on within similar ranges on Caymanian reefs. If competitive interactions are having an effect, the ecology of both these damselfish coupled with the loss of structural habitat, observed differences in home-range sizes and mean

abundances would suggest that *S. diencaeus* is partially outcompeting *S. planifrons* within shared habitat ranges. This is only indicated within this study and would need further evaluation through future research. Overall, available evidence from the literature indicates that in interference-competition with other damselfish, both species seem to out-compete congeners (Ebersole, 1985; Draud and Itzkowitz, 1995; Ceccarelli, Jones and Mccook, 2001; Dromard *et al.*, 2013). Conversely, intra-specific competition within similar habitats has previously been found to influence spatial patterns and behavioural changes of both species. In a study of *S. planifrons* distributions, the relative spatial position of individuals in a territorial cluster on a patch-reef caused variations in defended home-range sizes and fitness (Meadows, 2001). This so-called centre-edge effect may cause variations in microhabitat attributes if patterns of clustering are also in effect on these fore-reef environments. Additionally, the stressors of predation affect the gardening activities of *S. planifrons*, with reductions of their territorial effects being correlated with increased predator presence (Vermeij *et al.*, 2015). Little is known about the extent to which predation pressure affects *S. diencaeus* territoriality, yet it has been observed to extend territories in habitats of lower quality due to lower densities and competition with con-specifics, and subsequently defended smaller territorial areas among higher densities (Solandt, Campbell and Haley, 2003). Such trade-offs of territorial efforts and habitat quality have also been observed in other territorial herbivores such as the dusky damselfish (*Stegastes adustus*, Troschel, 1865) following the loss of coral cover (Di Santo *et al.*, 2020). These findings may have important implications for the distribution and hence strength of ecological effects of damselfish territories in Caribbean coral reef communities, which are projected to experience continuous benthic degradation and alterations.

#### 4.3 LIMITATIONS

As is common with studies of ecological nature in tropical coral reef systems, time as well as funding constraints regarding in-situ data collection during fieldwork periods can cause certain limitations. Firstly, assessing populations during a singular, short time-frame of two months creates a “snapshot” of local populations in time, but does not allow temporal comparisons of seasonal damselfish distribution trends that may follow natural fluctuations of these dynamic systems. Hence this study did not aim to present a fully comprehensive assessment of local populations of *S. planifrons* and *S. diencaeus* on Caymanian coral reefs, but instead provided a first updated assessment of their current status and distribution trends. Secondly, limited fieldwork constrains replication efforts, leading to relatively low sample sizes

of e.g. territorial quantifications. Increasing such replication would potentially have enhanced the observed correlations of territorial complexity and home-range sizes and would allow assessments of the effects of inter- and intra-specific competition on these habitat characteristics. Thirdly, the limited time spent within the Cayman Islands meant that natural factors, such as unfavourable weather conditions often found in the exposed southern aspect of Grand Cayman, limited the ability to survey all aspects and lead to unequal replication in some areas. Finally, the use of photogrammetric technology is time limited underwater, which did not allow surveys to measure structural complexity on deeper reefs whilst staying within diving safety margins.

Even though the methodological design accounted for the disturbance of damselfish in response to the positioning of transect tapes by leaving a resting period before starting UVC, the presence of divers is still a potential factor that could have influenced sheltering behaviour and lead to biases in perceived abundances. The presence of divers observing territorial behaviour seemed to have limited effect on the territorial defence of individuals, as both species exhibited consistently bold behaviour throughout the sampling period.

Photogrammetry yields a variety of benefits in comparison to traditional methodologies to capture structural metrics of a given benthos. Yet, it is also associated with limitations in coral reef environments that had to be accounted for in the context of this study. Light availability and visibility are major factors contributing to the resolution of 3D generated models and greatly vary within coral reefs depending on turbulence and depth. Whilst the application of filters can aid against the rapid absorption of colours of longer wavelengths such as red, the loss of light in combination with decreased diving time made reef-scale surveys on deeper reef terraces difficult. In shallower waters, turbulent water can significantly decrease one's ability to accurately capture the reef benthos due to image distortion caused by increased movement of the diver. Additionally, this technology is restricted to re-constructing only still objects and hard substrates, excluding any objects prone to movement such as sea-fans and algae. While this method creates a great variety of high resolution data, the high associated processing time to generate different parts of the 3D models and required computational power limited data extraction within the time-constraints of the production of this thesis. Yet, the archivable nature of this data allows future extractions of a range of metrics to answer questions regarding changing reef community composition and complexity on both spatial and temporal scales.

## 5. Conclusions and recommendations

This study found that environmental variables such as exposure, depth and protection efforts significantly affect abundances of *S. planifrons* and *S. diencaeus* on the reef terrace scale, causing similar distribution patterns. These distributions also indicated a potential shift of habitat types following decadal simplification of the preferred structurally complex reef matrix. It was shown that species associations to reef complexity vary depending on the spatial scales of measurements. The results demonstrated that general complexity, as measured via the fractal dimension score using the method of SFM-photogrammetry, can provide a useful metric to quantify habitat quality for *S. planifrons*. It was also established that for *S. diencaeus*, different habitat metrics may be of greater importance in structuring microhabitat-scale distributions and habitat defence efforts. Based on the results from this study and similar trends observed in other regions, this species may be able to adapt better to the less heterogenic communities of future coral reefs, while stronger habitat-specialists such as *S. planifrons* could display reductions in abundances.

Measuring the effect of several environmental variables on reef fish distributions over a range of spatial scales can answer important question about the degree to which different factors are contributing to community compositions between habitats (Harborne, Mumby and Ferrari, 2012; Williams *et al.*, 2013). As such, it is an important focus of modern coral reef landscape ecology. The observed distribution patterns within this study open up a range of research questions that should be explored. The inversed abundances within northern and western reef terraces suggest that other environmental variables are interplaying in shaping distribution patterns, such as secondary effects from fishing pressure and predator and herbivore abundances. Considering that competition and predation may be increasingly significant factors affecting damselfishes on degrading coral reefs, their effects on local populations should be quantified. The degree to which microhabitat attributes shape reef-scale distributions of territorial herbivores has not been well established on changing reefs, and studies utilizing modern mapping technology to investigate individual microhabitats are rare. Although it is recognized that traditional methods to extract complexity values have proven effective as rough measures of complexity, the methodology of this study provided a high resolution data-set using a metric that is comparable on several scales and can quantify the degree of heterogeneity of entire reef sections in greater detail. As such, it simultaneously enables the future use of the collected models to extract a range of structural attributes on several resolutions and to monitor and explore correlations to reef fish abundances.

There is room to expand the methodological approach of this study to extract several specific benthic metrics on the reef- and microhabitat scale that different reef fish may correlate with. As 3D reconstruction technologies continue to develop, the quantification of a range of variables is becoming more affordable and broadly available. Such methodological advancements could present valuable tools in the Cayman Islands by decreasing survey times and increasing the resolution of local monitoring efforts of coral reef communities on temporal and spatial scales. Increasing benthic coverage and replication by mapping survey sites and microhabitats along all depth and exposure gradients around Grand Cayman would aid in further enhancing the understanding of which environmental factors influence the observed damselfish distribution patterns on a range of spatial scales. It may be difficult to project the results of such surveys onto the sister islands, Cayman Brac and Little Cayman, as they can differ from the main island in their benthic and fish community structures (Mccoy, 2018). Extending survey efforts onto these islands would therefore aid in fully understanding the role of damselfishes on different Caymanian reef habitats and their future significance in terms of local reef resilience. Fast monitoring methods are also essential in documenting and responding to future bleaching events and disease outbreaks, such as the rapidly spreading stony coral tissue loss disease, which reached Caymanian reefs in July 2020 (Croy McCoy, pers. comm.). Considering the variety of different biotic and abiotic components that presented methods can capture, they can be applied to a range of shallow water ecosystems and will likely become commonplace in marine landscape ecology on a global scale.

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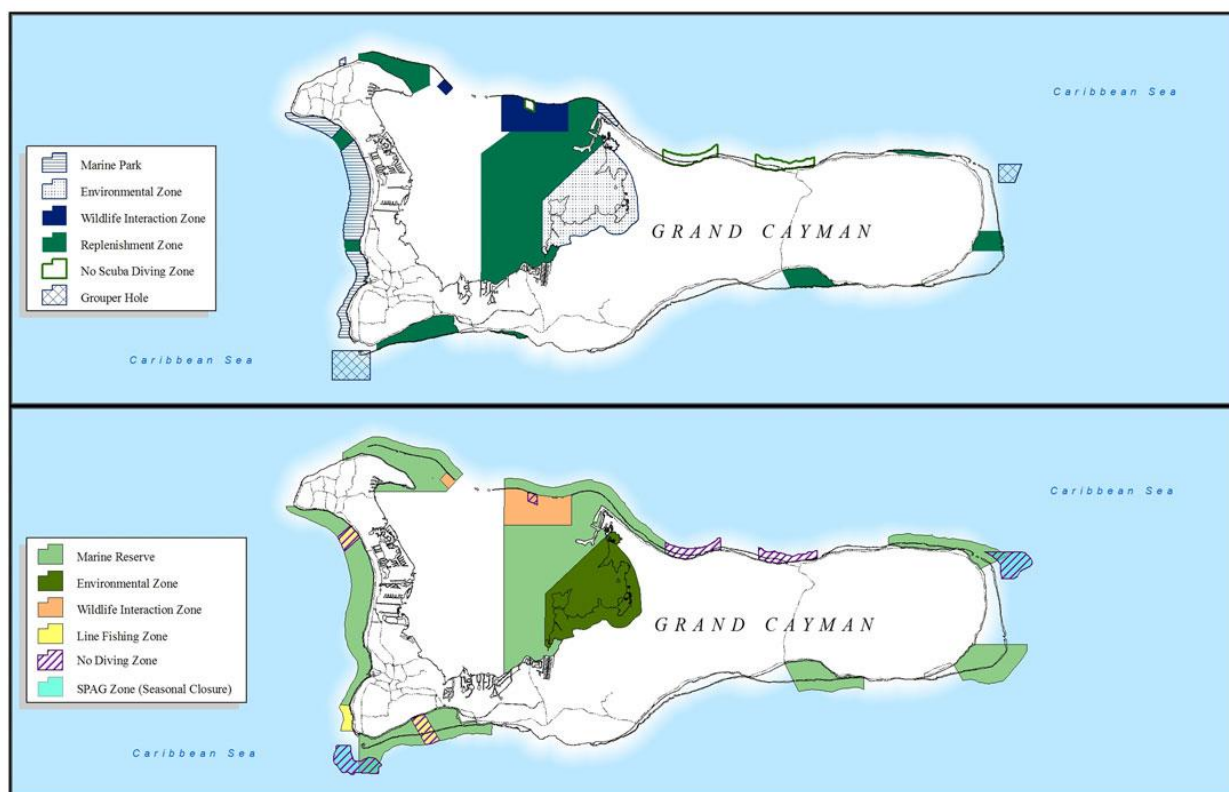
## Appendices

### APPENDIX A: MARINE PROTECTION LAWS IN THE CAYMAN ISLANDS

**Table a1:** Regulations regarding all different protection zones established within Caymanian waters through the Marine Conservation Law. Information is courtesy of the Department of Environment of the Cayman Islands.

<b>Marine Park Zone</b>	<ul style="list-style-type: none"> <li>➤ No taking of any marine life alive or dead, except: <ul style="list-style-type: none"> <li>• Line fishing from shore is permitted</li> <li>• Line fishing at depths of 80 ft or greater is permitted</li> <li>• Taking fry and sprat with a fry or cast net is permitted.</li> </ul> <p>Note: fish traps, spear guns, pole spears and other nets are prohibited</p> </li> <li>➤ No anchoring – use of fixed moorings only, except: <ul style="list-style-type: none"> <li>• boats of 60 ft or less may anchor in sand, so long as no grappling hook is used, and neither the anchor nor the rope or chain will impact coral;</li> <li>• anchoring permitted in designated Port anchorage areas – contact Port Security on VHF channel 16;</li> <li>• anchoring prohibitions suspended during emergencies and by permission of Port Director</li> </ul> </li> </ul>
<b>Environmental Zone</b>	<ul style="list-style-type: none"> <li>➤ No taking of any marine life, alive or dead with no exceptions. <ul style="list-style-type: none"> <li>➤ No in-water activities.</li> </ul> </li> <li>➤ Public may access only at speeds of 5 mph or less. <ul style="list-style-type: none"> <li>➤ No anchoring of any boat.</li> </ul> </li> <li>➤ NOTE: Line fishing, fish traps, nets, spear guns and strikers are totally prohibited</li> </ul>
<b>Replenishment Zone</b>	<ul style="list-style-type: none"> <li>➤ No taking of conch or lobster by any means. <ul style="list-style-type: none"> <li>➤ Line fishing and anchoring permitted.</li> <li>➤ Anchor, chain or line must not impact coral.</li> </ul> </li> <li>➤ Spear guns, pole spears, fish traps and nets prohibited, except that fry and sprat may be taken with a fry or cast net.</li> </ul>
<b>No Diving Zone</b>	<ul style="list-style-type: none"> <li>➤ No SCUBA diving</li> </ul>
<b>Prohibited Diving Zone</b>	<ul style="list-style-type: none"> <li>➤ No SCUBA diving within this zone unless licensed to do so by the National Conservation Council</li> </ul>

<p><b>Wildlife Interaction Zone</b></p>	<ul style="list-style-type: none"> <li>➤ No taking of any marine life by any means <ul style="list-style-type: none"> <li>➤ No selling of fish food from boats</li> </ul> </li> <li>➤ No removing of any marine life from the water</li> <li>➤ No anchoring in water shallower than three ft or so that the anchor or boat is within 20 ft of any reef structure</li> <li>➤ No feeding of any marine life with food of any kind or amount other than that approved by the National Conservation Council</li> <li>➤ Fish feeding is prohibited anywhere in Cayman waters outside of a designated WIZ unless licensed by the National Conservation Council</li> <li>➤ No wearing of any footwear in water shallower than four ft</li> <li>➤ Special conditions apply to commercial boats who must have a license issued by the National Conservation Council and clearly displayed on the boat to enter this area</li> </ul>
<p><b>Designated SPAG-zone (Grouper Spawning Area)</b></p>	<ul style="list-style-type: none"> <li>➤ East Cost and West End of Cayman Brac, Little Cayman and Twelve Mile Bank, Coxswain Bank and South West point Grand Cayman</li> <li>➤ No fish pots, spear fishing, or net fishing within designated Grouper Spawning Areas</li> </ul>



**Figure a1:** Current (top) and proposed extensions (bottom) to the marine protection zonation around Grand Cayman.

## APPENDIX B: AGISOFT METASHAPE PROCESSING SPECIFICATIONS

**Table b1:** Specifications for the processing of photographs and creation of different parts of 3D models using the Agisoft Metashape software.

Workflow Job Type	Settings	Value
Align Photos	Accuracy	High
	Key point limit	40.000
	Tie point limit	4.000
Optimize Alignment	Default Settings	-
Build Dense Cloud	Quality	High
	Depth Filtering	Aggressive
	Calculate point colours	Yes
Build Mesh	Surface type	Arbitrary
	Depth Maps Quality	High
	Custom Face count	200.000
	Interpolation	Enabled
Build Tiled Model	Source data	Dense Cloud
	Depth Maps Quality	High
	Face Count	High
Build DEM	Source data	Dense Cloud
	Interpolation	Enabled
	Point classes	All

## APPENDIX C: ABUNDANCE AND COMPLEXITY DATA SETS

**Table c1:** Averaged abundance counts of *S. planifrons* and *S. diencaeus* within deep and shallow survey sites on northern and western reef terraces around Grand Cayman.

Site	Site Nr.	Aspect	Depth	Species	N	Abundance	SD	±SE	CI
Andes Reef	6	North	Shallow	<i>S. diencaeus</i>	4	10.25	0.5	0.25	0.81
Andes Reef	6	North	Shallow	<i>S. planifrons</i>	4	1.5	1.73	0.87	2.76
Andes Wall	6	North	Deep	<i>S. diencaeus</i>	4	14.75	2.22	1.11	3.53
Andes Wall	6	North	Deep	<i>S. planifrons</i>	4	3.75	4.79	2.39	7.62
Bonnies Arch	5	West	Shallow	<i>S. diencaeus</i>	4	9.25	4.11	2.06	6.54
Bonnies Arch	5	West	Shallow	<i>S. planifrons</i>	4	0	0	0	0
Apollo	9	North	Deep	<i>S. diencaeus</i>	4	12.75	4.11	2.06	6.55
Apollo	9	North	Deep	<i>S. planifrons</i>	4	0.75	0.5	0.25	0.81
Apollo	9	North	Shallow	<i>S. diencaeus</i>	4	4.25	2.36	1.18	3.76
Apollo	9	North	Shallow	<i>S. planifrons</i>	4	0	0	0	0
Big Tunnels	11	West	Deep	<i>S. diencaeus</i>	4	5.5	2.08	1.04	3.31
Big Tunnels	11	West	Deep	<i>S. planifrons</i>	4	1.25	1.89	0.96	3.01
Black Rock	7	North	Deep	<i>S. diencaeus</i>	4	0.25	0.5	0.25	0.81
Black Rock	7	North	Deep	<i>S. planifrons</i>	4	7.5	8.19	4.09	13.02
Bolero	11	West	Shallow	<i>S. diencaeus</i>	4	15.25	4.11	2.06	6.55
Bolero	11	West	Shallow	<i>S. planifrons</i>	4	11.75	5.91	2.96	9.40
Dragons Hole	3	West	Deep	<i>S. diencaeus</i>	4	6.75	5.32	2.66	8.46
Dragons Hole	3	West	Deep	<i>S. planifrons</i>	4	1.25	1.89	0.95	3.01
Fish Tank	7	North	Shallow	<i>S. diencaeus</i>	4	3.5	1.73	0.87	2.76
Fish Tank	7	North	Shallow	<i>S. planifrons</i>	4	0.25	0.5	0.25	0.81
Haunted House	8	North	Deep	<i>S. diencaeus</i>	4	6.5	2.38	1.190	3.79
Haunted House	8	North	Deep	<i>S. planifrons</i>	4	4.5	3.11	1.55	4.95
Holiday Inn	1	West	Deep	<i>S. diencaeus</i>	4	5.75	0.96	0.48	1.52

Holiday Inn	1	West	Deep	<i>S. planifrons</i>	4	3	1.41	0.71	2.25
No Dive Zone	10	North	Deep	<i>S. diencaeus</i>	4	18.75	2.22	1.11	3.53
No Dive Zone	10	North	Deep	<i>S. planifrons</i>	4	2.75	4.27	2.14	6.81
No Dive Zone	10	North	Shallow	<i>S. diencaeus</i>	4	8	4	2	6.36
No Dive Zone	10	North	Shallow	<i>S. planifrons</i>	4	2.75	2.06	1.03	3.28
North West Point	5	West	Deep	<i>S. diencaeus</i>	4	1.25	1.26	0.63	2
North West Point	5	West	Deep	<i>S. planifrons</i>	4	0.5	1	0.5	1.59
Oro verde	1	West	Shallow	<i>S. diencaeus</i>	4	14.75	5.56	2.78	8.85
Oro verde	1	West	Shallow	<i>S. planifrons</i>	4	11.25	3.5	1.75	5.57
Pinnacles Reef	8	North	Shallow	<i>S. diencaeus</i>	4	4.75	3.2	1.6	5.09
Pinnacles Reef	8	North	Shallow	<i>S. planifrons</i>	4	0	0	0	0
Rainbow Reef	3	West	Shallow	<i>S. diencaeus</i>	4	15	3.56	1.78	5.66
Rainbow Reef	3	West	Shallow	<i>S. planifrons</i>	4	0.25	0.5	0.25	0.81
Sea View Wall	4	West	Deep	<i>S. diencaeus</i>	4	2.25	2.63	1.32	4.19
Sea View Wall	4	West	Deep	<i>S. planifrons</i>	4	3.25	2.22	1.11	3.53
Sew View Reef	4	West	Shallow	<i>S. diencaeus</i>	4	11.25	1.71	0.85	2.72
Sew View Reef	4	West	Shallow	<i>S. planifrons</i>	4	7.25	3.5	1.75	5.57
Victorias' Secret Reef	2	West	Shallow	<i>S. diencaeus</i>	4	19.75	3.1	1.55	4.93
Victorias' Secret Reef	2	West	Shallow	<i>S. planifrons</i>	4	5.25	3.1	1.55	4.93
Victorias' Secret Wall	2	West	Deep	<i>S. diencaeus</i>	4	12.25	5.91	2.96	9.4
Victorias' Secret Wall	2	West	Deep	<i>S. planifrons</i>	4	8.25	5.38	2.69	8.56

**Table c2:** Total abundance counts per transect as well as averaged fractal dimension (FD) scores and two-dimensional (2D) measurements of home-range sizes of *S. planifrons* and *S. dienciaeus* territories surveyed on the western shallow reef terrace of Grand Cayman.

Species	Site Nr.	Site	Transect Nr.	Abundance	FD	2D (m <sup>2</sup> )
<i>S. planifrons</i>	11	Bolero	11.1	11	2.108	1.199
<i>S. planifrons</i>	11	Bolero	11.2	10	2.085	1.201
<i>S. planifrons</i>	11	Bolero	11.3	20	2.084	1.225
<i>S. dienciaeus</i>	11	Bolero	11.1	18	2.083	1.338
<i>S. dienciaeus</i>	11	Bolero	11.2	10	2.09	1.485
<i>S. dienciaeus</i>	11	Bolero	11.3	19	2.111	1.543
<i>S. planifrons</i>	1	Oro Verde	1.1	13	2.111	1.746
<i>S. planifrons</i>	1	Oro Verde	1.2	10	2.1	1.004
<i>S. planifrons</i>	1	Oro Verde	1.3	15	2.074	1.109
<i>S. dienciaeus</i>	1	Oro Verde	1.1	13	2.122	1.789
<i>S. dienciaeus</i>	1	Oro Verde	1.2	11	2.097	1.68
<i>S. dienciaeus</i>	1	Oro Verde	1.3	12	2.062	1.781
<i>S. planifrons</i>	4	Sea View Reef	4.1	6	2.097	0.972
<i>S. planifrons</i>	4	Sea View Reef	4.3	11	2.1	1.097
<i>S. planifrons</i>	4	Sea View Reef	4.4	9	2.060	0.648
<i>S. dienciaeus</i>	4	Sea View Reef	4.1	13	2.084	1.476
<i>S. dienciaeus</i>	4	Sea View Reef	4.3	12	2.072	2.549
<i>S. dienciaeus</i>	4	Sea View Reef	4.4	9	2.064	1.381
<i>S. dienciaeus</i>	5	Bonnies Arch	5.1	4	2.041	1.723
<i>S. planifrons</i>	2	Bonnies Arch	2.1	1	2.064	1.029
<i>S. planifrons</i>	2	Bonnies Arch	2.2	5	2.097	1.222
<i>S. planifrons</i>	2	Bonnies Arch	2.3	7	2.126	1.406
<i>S. dienciaeus</i>	2	Bonnies Arch	2.1	24	2.067	1.899
<i>S. dienciaeus</i>	2	Bonnies Arch	2.3	20	2.093	1.385

**Table c3:** Fractal dimension (FD) scores of each of three transects per survey site on the northern and western shallow reef terraces around Grand Cayman.

Aspect	Site Nr.	Site	Transect Nr.	Abundance	FD
North	6	Andes Reef	6.1	10	1.996
North	6	Andes Reef	6.2	10	2.01
North	6	Andes Reef	6.3	10	2.009
North	9	Apollo	9.1	1	1.974
North	9	Apollo	9.2	4	1.997
North	9	Apollo	9.3	6	1.99
North	7	Fish Tank	7.1	2	1.996
North	7	Fish Tank	7.2	5	1.958
North	7	Fish Tank	7.3	5	1.939
North	10	No Dive Zone	10.1	2	2.036
North	10	No Dive Zone	10.2	10	2.012
North	10	No Dive Zone	10.3	10	2.019
North	8	Pinnacles Reef	8.1	6	2.019
North	8	Pinnacles Reef	8.2	6	1.992
North	8	Pinnacles Reef	8.3	7	1.996
West	5	Annies Arch	5.1	4	1.987
West	5	Annies Arch	5.2	10	1.913
West	5	Annies Arch	5.3	14	1.947
West	11	Bolero	11.1	18	2.028
West	11	Bolero	11.2	10	2.043
West	11	Bolero	11.3	19	2.017
West	1	Oro verde	1.1	13	2.014
West	1	Oro verde	1.2	11	1.971
West	1	Oro verde	1.3	12	2.004
West	4	Sea View Reef	4.1	13	2.042
West	4	Sea View Reef	4.2	11	2.028
West	4	Sea View Reef	4.3	12	2.074
West	2	Victorias' Secret Reef	2.1	24	2.045
West	2	Victorias' Secret Reef	2.2	18	2.032
West	2	Victorias' Secret Reef	2.3	20	2.031