

Reef fish associations with benthic habitats at a remote protected coral reef ecosystem in the Western Indian Ocean ~ Aldabra Atoll, Seychelles

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DECLARATIONS

The following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author unless otherwise stated.

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A tribute to Aldabra

Aldabra is a large, pristine and remote atoll in the vastness of the Indian Ocean. It is over a thousand kilometres from Mahé, the capital of the Seychelles, more than 400 km from Madagascar and over 600 km from Africa. Not only is Aldabra far away from everywhere, but it is isolated from humans. Months go by only interacting with the 15 to 25 staff working and living there. Piracy in the region stymied even the most adventurous sailors from coming to the atoll while I was on Aldabra. The human population here is outnumbered by most, if not all, species inhabiting the atoll. I experienced coral reefs bursting with life, groupers larger than a fully-grown man and aggregations of sharks patrolling the reefs. Scores of green turtles nest on the beaches every night, and if you are lucky, you may see the elusive dugong feeding on seagrass beds in the lagoon. In the air, frigate birds swoop overhead, cutting the air with their magnificently large boomerang wings at hair-raising speed as they chase red-footed boobies returning with their bounty of silver from a days' fishing at sea. The white-throated rail, endemic to Aldabra, did not evolve a fear for humans and will boldly peck at your toes out of sheer curiosity. They are companions to over 100 000 giant tortoises lumbering everywhere imaginable, and everywhere unimaginable, on the atoll. Aldabra, a tropical coral atoll with an intact ecosystem, exemplifies a place where nature thrives! Aldabra filled me with true marvel for nature which enriched and humbled me with a new understanding of what the natural world was once like, and indeed with optimism for what it could be. In the quiet isolation, far away from the world disrupted by man's long history of destruction, can one still hear the voice of nature, and her urgent plight to protect what is left. There is so much to be gained!

ABSTRACT

The aim of the thesis is to develop an understanding of the associations between reef fish and benthic habitats and assess the modifying effects of environmental processes on these relationships at Aldabra, a pristine atoll in the Western Indian Ocean (WIO). Conducting research in pristine, or reference coral reef ecosystem, removes the impact of direct anthropogenic disturbances and provides essential information on natural ecosystem structure and functioning.

Three primary hypotheses were tested: 1) Environmental drivers such as depth and exposure to wave energy determine the spatial distribution of benthic habitats; 2) The reef fish assemblage structure is explained by habitat at multiple scales and modified by the effects of environmental drivers such as depth, wave energy and cyclical temporal drivers such as time and tides; 3) The reef fish assemblage at Aldabra represents a pristine reef fish assemblage, comprising high levels of herbivores and predators. The research focussed on the benthic habitat on the seaward reefs between the shoreline and 50 m depth. The first objective was to characterise the benthic habitats on Aldabra Atoll's seaward reefs and map their spatial distributions using remotely sensed imagery and ground truthing data. The second was to assess the influence of depth and exposure to wave energy on the distribution of benthic habitats. The third was to identify the most suitable standardised method to survey the reef fish assemblage structure on Aldabra's, and fourth to determine the effect of tide and time of day on the reef fish assemblage. The fifth objective was to establish the association between reef fish assemblage structure and benthic habitats and to test how species-size influenced the scale of habitat at which the associations were most apparent.

Four categories of geomorphic reef zones (reef flats (19.2 km²), top of the forereef slope (7.8 km²), deep forereef slope (11.6 km²), and reef platform (14.3 km²)) were manually delineated following the visual outlines of reef features from satellite imagery. The six broad-scale and twelve fine-scale benthic habitats were mapped using a supervised maximum likelihood classification and the spatial coverage of each determined. The broad-scale habitats were 1) Epilithic algal matrix, 2) Hard and soft (coral, 3) Rubble, 4) Macroalgae, 5) Seagrass and 6) Sand. Similarly, twelve fine-scale benthic habitats were characterised and mapped, for example, Hard coral (19 %) including massive and submassive forms with *Millepora* and *Rhytisma*. The broad-scale benthic habitat map had an overall producer accuracy of 54 % and fine-scale habitat map 29 %, which was consistent with studies using similar habitat classification methods.

The prevailing wave energy, depth and the directional orientation of coral reefs (aspect) significantly influenced the probability of occurrence of each of the broad-scale benthic habitats, and there was a shift in peak probability of occurrence of all habitat categories to a greater depth with an increase in wave energy. The strong relationship of benthic habitats with depth and wave energy suggests that the distributions of benthic habitats are likely to change with sea-level rise and increased intensity and frequency of storms in future.

Overall, 338 fish species from 51 families, including 14 species of elasmobranch were recorded using Baited Remote Underwater Video systems (BRUVs) and unbaited Remote Underwater Video systems (RUVs) from 231 samples. Fish were significantly more abundant when observed using BRUVs (119 ± 7) relative to RUVs (92 ± 7), and the assemblage structures were significantly different between the two sampling methods. Abundance and species richness of generalist carnivores and piscivores were significantly greater in BRUVs, while RUVs recorded significantly greater numbers of herbivores and more species of herbivore and corallivore. The results suggest that BRUVs are better suited when studying predatory fish which may not be detected without bait. However, when surveying a taxonomically and functionally diverse assemblage of fishes at a pristine reef, RUVs may provide a more accurate estimate of natural reef fish assemblage structure.

Reef fish assemblages observed using RUVs were significantly different between morning-high-tide, midday-low-tide and evening-high-tide for all trophic groups. However, the reef fish assemblage structure observed using BRUVs was insensitive to change in tide and time of day, which may be explained by the attraction effect of bait dampening the effect of tide and time of day. While RUVs appear better to detect more subtle variations in fish assemblage structure, care needs to be taken when designing research programmes that use RUVs, as the sampling design should account for tide and time of day to avoid misinterpreting the cyclical variation, which may confound results.

Reef fish assemblages were significantly different among habitats within geomorphic reef zones, broad-scale and fine-scale habitats. Species turnover rates were significantly different for all Actinopterygii size-class categories between the three scales of habitat. No marked differences in species turnover rates among habitats were detected for the majority of Elasmobranch size-class categories. The strong habitat dependency over various spatial scales indicates that effective conservation of Actinopterygii fish at Aldabra, and elsewhere in similar ecosystems requires protection of representative sets of benthic habitats. However, Elasmobranch conservation requires sufficiently large areas as these species utilise multiple habitats, over multiple scales, which are likely to exceed the confines of Aldabra's reef.

Aldabra's hard coral dominated reefs, diverse fish assemblages with an abundance of herbivores, large groupers and reef sharks, and the presence of very large sharks indicate an intact coral reef. The intact benthic habitats and reef fish assemblage structure recorded in this study provided ecological reference points from which to inform management strategies for the more degraded reefs in the WIO and highlights the value in sustained protection of remote and coral reefs ecosystems.

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Chapter 1. General introduction



Lunar fusiliers over a healthy hard-coral-rich reef at Aldabra Atoll. Credit: Pristine Seas Survey, National Geographic.

1.1. OVERARCHING THESIS AIM

The overarching aim of the thesis is to build on the understanding of reef fish associations with benthic habitats from coral reef ecosystems and the role that environmental drivers play in altering the distribution of habitat and the structure of fish assemblages. The thesis sets out to investigate these relationships at multiple scales over which coral reef habitats can be defined. The research was conducted at a location considered to be near pristine allowing natural patterns that are unaltered by anthropogenic pressures to be identified.

1.2. VALUE OF TROPICAL CORAL REEF ECOSYSTEMS

Tropical coral reef ecosystems are exceptionally diverse, harbouring between 25 % and 30 % of all known marine life, despite occupying only 0.2 % of the ocean floor surface (Connell 1978; Knowlton 2001; Reaka-Kudla 2001; Roberts et al. 2002). Coral reefs form complex three-dimensional habitat which supports the ecological functioning of these biodiverse ecosystems (Moberg and Folke 1999; Spalding 2001). The structural framework of coral reef habitat creates sheltered sandy terraces and lagoon environments, where other benthic habitat types such as seagrass beds and mangroves occur as part of this ecosystem. The connectivity between these habitats, including coral reefs, seagrass beds, mangroves, as well as the pelagic and deep-water environments, provides a range of feeding opportunities and refuges (Hixon and Beets 1989, 1993). These linked habitats provide the critical niches to support different life-stages of many fish and invertebrate species (Nagelkerken et al. 2002; Mumby 2006; McMahon et al. 2012).

In addition to the ecological value, coral reefs and associated ecosystems provide a variety of ecosystems goods and services on which people depend (Moberg and Folke 1999; Koch et al. 2009). For example, fringing coral reefs protect the coast from destructive wave energy, mangroves prevent coastal erosion and saltwater intrusion, and seagrass beds absorb nutrient outflows (Moberg and Folke 1999; Barbier et al. 2008; Koch et al. 2009). Millions of people from over 100 countries rely on coral reef fisheries as their main source of protein and livelihood (Jennings and Polunin 1996; Cinner et al. 2012) with ecosystem service values from coral reefs estimated at \$ 352,249/ha/year (de Groot et al. 2012; Costanza et al. 2014).

1.3. THREATS TO CORAL REEF ECOSYSTEM

Coral reef ecosystems are under a multitude of severe threats, which continuously erode their biodiversity, habitat complexity, ecological functioning and valuable ecosystems services (Roberts et al. 2002; Pandolfi et al. 2003; Bellwood et al. 2004, 2006; Munday 2004; Nyström 2006; Hughes et al. 2007; Carpenter et al. 2008; Graham et al. 2008; Cinner et al. 2012).

Prominent in recent history, global-scale coral bleaching events, the first in 1998 and most recently between 2015 and 2017, caused significant loss of coral reefs worldwide (Goreau et al. 2000; Hoegh-Guldberg et al. 2017; Hughes et al. 2017; Albright 2018; Hughes et al. 2018). Before 1998, coral bleaching was only observed on a small scale, with early observations starting in the 1980s (Goreau et al. 2000). In 1998, coral reefs suffered unprecedented mortality at a scale that had never previously been recorded (Goreau et al. 2000). After the 1998 mass-bleaching event, a period of recovery followed, with the amount of hard-coral coverage increasing to a varying degree at a number of sites in the Indian Ocean (e.g. Turner et al. 2000a; Sheppard et al. 2002; Stobart et al. 2005; McClanahan et al. 2011). Since 1998 there have been frequent coral-bleaching events affecting regional or localised reef complexes (e.g. Berkelmans et al. 2004; Krishnan et al. 2011). Following 1998, the next global bleaching began in 2015 (Donner et al. 2017) and again caused large-scale mortality in reefs worldwide, and for the first time recurred the subsequent year (Ainsworth et al. 2016; Sheppard et al. 2017). There is a strong correlation between the occurrence of mass coral bleaching events and El Niño Southern Oscillation (ENSO) events (Coffroth et al. 1990; Brown 1997). El Niño Southern Oscillation events have been predicted to increase in frequency as a result of global climate change (Spencer et al. 2000; Loya et al. 2001; Bellwood et al. 2004, 2006; Balvanera et al. 2006; Nyström 2006; Hughes et al. 2010; Hooper et al. 2012; Kemp et al. 2014). As such, the degradation of coral reef ecosystems is likely to continue, and the state of this ecosystem is predicted to become critical due to the increased frequency, intensity and duration of bleaching events (Timmermann et al. 1999; Hoegh-Guldberg et al. 2007; Cai et al. 2014; Hughes et al. 2017). Climate change today is therefore regarded as the most significant threat to coral reefs worldwide (Veron et al. 2009; Hoegh-Guldberg et al. 2017).

A second major pressure on coral reefs is overfishing and fishing practices that damage reef habitat. Overfishing and poor fishing practices have led to the collapse of coral reef fisheries (Russ and Alcala 1989; Roberts 1995; Jennings and Polunin 1996), a change of fish and benthic community structure, and phase shifts in benthic communities, from coral domination to domination by fleshy macroalgae (Hughes 1994; Hughes et al. 2007; Ledlie et al. 2007;

Graham et al. 2015; Jouffray et al. 2015). In some instances these shifts to macroalgal dominated systems have become permanent, reducing the productivity of reefs and impacting on the livelihoods of people who rely on reef fish resources (Hughes 1994; Ledlie et al. 2007; Graham et al. 2015; Jouffray et al. 2015). The loss of key ecosystem functions, such as herbivory and predation, which regulate the dynamics on the coral reef ecosystem, in turn reduce the reefs' ability to tolerate and recover from other stressors such as coral bleaching events (Dulvy et al. 2004a; McClanahan et al. 2011; Bellwood et al. 2012). Furthermore, rampant coastal development, sedimentation, pollution among other local threats have also led to large-scale loss of seagrass beds, mangroves and coral reefs worldwide (Miller and Cruise 1995; Valiela et al. 2001; Pandolfi et al. 2003; Bellwood et al. 2004; Fabricius 2005; Orth et al. 2006, 2006; Carpenter et al. 2008).

The threats to tropical reef ecosystems are exacerbated by the combined effect of multiple stressors. For example, bleaching, acidification and diseases act synergistically to reduce coral reproduction, survival and larval settlement. Interaction with local stressors like sedimentation, overfishing and pollution heightens impacts on the reefs (Wilson et al. 2006; Ateweberhan et al. 2013). The effect of multiple simultaneous stressors synergistically break down the ecological components and processes that allow a coral reef ecosystem to recover from a disturbance (Hughes and Connell 1999; Wilson et al. 2006; Hoegh-Guldberg et al. 2007; Harborne et al. 2017). The significant losses of biodiversity, critical habitat, key ecological processes and valuable ecosystem services that coral reef ecosystems have suffered as a consequence of the multitude of widespread, repeated, prolonged and intensifying pressures highlights the urgent plight of coral reefs ecosystems (Bellwood et al. 2004, 2006; Orth et al. 2006; Hughes et al. 2018).

1.4. CONSERVATION OF CORAL REEF ECOSYSTEMS

Conservation efforts of coral reefs rely on a range of management strategies such as no-take marine protected areas (MPAs) (McClanahan et al. 2007b), fishing regulations (Cinner et al. 2009), trade mechanisms (e.g. Poh and Fanning 2012) and restorative techniques (White and Courtney 2004). These ongoing conservation efforts have had some localised success (e.g. Wells and Barzdo 1991; Alder 1996; Francis et al. 2002; Cunningham 2005; Christie and White 2007; Hilborn 2007; Rinkevich 2008). However, globally this ecosystem is in a critical state. Coral reefs are already undergoing radical change in their composition and further declines are predicted in biodiversity and in the area occupied as a result of anthropogenic climate change (Hoegh-Guldberg et al. 2007; Hughes et al. 2017, 2018).

Urgent and effective action is required to limit the impacts of climate change that are overpowering the conservation gains from other mitigation measures (Hoegh-Guldberg et al. 2007; Munday et al. 2008; Hughes et al. 2017, 2018). In addition to addressing climate change at an international scale through CO₂ emission reductions (Veron et al. 2009), further site-level management and protection mechanisms, which address the impacts of other pressures, such as poor fishing practices, are necessary to promote coral reef resilience (Hughes et al. 2010).

Marine Protected Areas (MPA) have become a popular means by which to protect ecosystems worldwide (De Santo 2013), and international agreements to protect a minimum of 10% of coastal and marine areas (UNEP 2010) have been met with a rapid increase in MPA estate (De Santo 2013; Singleton and Roberts 2014). Marine Protected Areas which prohibit the extraction of marine resources (no-take MPAs) have been shown to protect and restore habitats, reef fish populations and trophic interactions because they can remove many destructive practices and restrict or exclude extractive uses from such areas (Graham et al. 2003; Roberts et al. 2005; MacNeil et al. 2015). Age, size, isolation and enforcement have been shown to be key characteristics of effective MPAs (Edgar et al. 2014). While large, remote MPAs are more effective at protecting marine ecosystems than small MPAs near to high population centres, there is still the need for these types of MPAs in order to achieve ecologically coherent protected area networks (Roberts et al. 2001b; De Santo 2013; Singleton and Roberts 2014). More no-take MPA estate is required to meet international conservation targets, such as the Convention of Biological Diversity (CBD) and Aichi Target 11 which state that a minimum of 10 % of coastal and marine areas should be protected by 2020 to halt the rapid declines in biodiversity.

Fishing regulation is an important mechanism that can alleviate pressure on reef fish, playing an important role in maintaining coral reef resilience, through the actions of consumers such as large predators, herbivores, and scraping corallivores (Graham et al. 2003; Ledlie et al. 2007; MacNeil et al. 2015). While both MPAs and fishing regulations can be effective to manage coral reef fisheries (Cinner et al. 2009; Edgar et al. 2014), they are fraught with compliance challenges (e.g. Varkey et al. 2010), and do not always result in successful outcomes (Jameson et al. 2002; Cowx and Aya 2011).

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has been shown to be an effective instrument to complement other mechanisms to regulate the damage caused by the trade in some fish and coral species (Bruckner 2001; Vincent et al. 2014). Species listed in CITES and other species of conservation concern such as those in the International Union for Conservation of Nature's (IUCN) Red List of

Species are however hampered by a lack of data, leaving many key species unassessed (Bruckner 2001; Vincent et al. 2014).

Innovative technology is rapidly advancing coral reef restoration techniques, which are gaining traction as viable future conservation tools (Williams et al. 2018b). Effective conservation and options for the future management of coral reefs require a thorough understanding of the species, habitats and processes that comprise this ecosystem (Robinson 2006).

1.5. CORAL REEF RESEARCH

A fundamental starting point for inquiries into coral reef ecology is understanding the underlying benthic habitat composition (Mellin et al. 2009). Long-term monitoring of the benthic habitat composition provides reference points from which to detect change over time in relation to environmental or anthropogenic drivers (Hussain et al. 2013; Iovan et al. 2015). The spatial distribution of various benthic habitats provides a baseline to examine species associations with habitat. Characterising the benthic habitats and determining the species composition of species of fish assemblages that associate with specific habitats allows the identification of critical habitats for threatened or endangered species, juvenile life stages or spawning aggregations (e.g. Koenig et al. 2000; Nagelkerken et al. 2000). Furthermore, the benthic habitat may be defined on multiple scales of organisation, with fine-scale benthic habitat occurring within broader scales of benthic habitat (e.g. Pittman and Brown 2011; Phinn et al. 2012; Sekund and Pittman 2017). Associations of reef fish assemblages with benthic habitats in coral reef ecosystems may vary, depending on the scale of habitat considered (Green et al. 2015). The limited knowledge of reef fish assemblage associations with multiple scales of benthic habitats (Mellin et al. 2009) therefore requires further investigation.

The reef fish assemblage structure itself is a key driver and indicator of reef health as the fish assemblage can directly alter the reef through processes like herbivory, or indirectly through predator-mediated changes in the trophic structure, which in turn affect the benthic composition (Hughes et al. 2007; DeMartini et al. 2008; Sandin et al. 2008; Graham et al. 2015). Detailed knowledge of the reef fish assemblage structure can therefore be used to provide information on important ecosystem processes such as predation and herbivory, which maintain coral reef dynamics (McClanahan et al. 2011). Knowledge of the integrity of these ecosystem components and processes informs conservation goals and management

practices, such as fisheries and SCUBA diving in marine protected areas (Floros 2010; Bernard 2012; De Vos et al. 2014; McClanahan et al. 2015).

Researching the environmental effects on the relationships between benthic habitat and reef fish assemblages is important as it may explain the variability observed in the associations between the fish and habitat in different locations or under differing conditions (e.g. Friedlander and Parrish 1998; Friedlander et al. 2003). Understanding the effects of the environmental parameters on the relationship between reef fish and benthic habitat informs the appropriate management actions and interventions required. For example, the relationships between CO₂, sea surface temperature and coral bleaching established a critical link between coral reef ecosystems and the threats of climate change (Jokiel and Coles 1977; Brown 1997; Hoegh-Guldberg et al. 2007). Establishing the effect of a loss of hard-coral cover and three-dimensional structure as a consequence of coral mortality gave important insights into indirect and time-lagged effects of climate change on the reef fish assemblage (Pratchett et al. 2006; Wilson et al. 2006; Graham et al. 2007). The important conclusions that came about from coral-reef-climate-change studies have contributed to high-level political decisions, such as to limit CO₂ emissions to restrict mean global temperature increase to 1.5 °C (Veron et al. 2009; Mumby et al. 2011; Frieler et al. 2013; Schleussner et al. 2016; United Nations 2016). Furthermore, understanding the important ecological functions of an intact reef fish assemblage in enhancing the resilience of coral reefs to climate change has helped to establish tangible conservation targets, which maintains this critical ecosystem dynamic (Hughes 1994; Hughes et al. 2007; Myers et al. 2007a; Steneck 2012; Ferretti et al. 2013; Jouffray et al. 2015; Graham et al. 2015).

1.6. ENVIRONMENTAL DRIVERS IN CORAL REEF ECOSYSTEMS

Coral reefs are heterogeneous ecosystems, influenced by numerous environmental and anthropogenic variables that operate on multiple scales (Sheppard 1982; Friedlander and Parrish 1998; Friedlander et al. 2003; Gratwicke and Speight 2005; Eidens et al. 2015; Sekund and Pittman 2017). Broad-scale environmental variables, like the amount of reef area, and latitude and longitude, explain the distribution of coral and reef fish biodiversity on a global scale (Bellwood and Hughes 2001; Stuart-Smith et al. 2013). At the scale of an atoll or an island, other environmental variables control and modify the benthic habitat composition, including wave exposure, depth, sea surface temperature, salinity, and sediment among others (Done 1982; Sheppard 1982; Stoddart 1984; Brown 1997; Hoegh-Guldberg 1999; Dadhich et al. 2011; Chollett and Mumby 2012; Gove et al. 2015; Williams et

al. 2018a). Environmental drivers also act on the benthic invertebrate and fish community across a range of spatial scales, from geomorphic reef zones to broad-scale benthic habitat categories, like hard coral or seagrass, to fine-scale benthic cover, such as coral colonies (Sekund and Pittman 2017; Roche et al. 2018). The quest to understand the effect of environmental drivers on reef ecosystem structure over a range of scales is an ongoing challenge in the field of marine ecology (e.g. Done 1992; Bellwood and Hughes 2001; Anderson and Millar 2004; Sekund and Pittman 2017 to name but a few). Disentangling the influence of the individual abiotic variables on benthic habitat structure and the effect of physical and biological variables on the fish community structure over multiple scales is the central theme of this thesis.

1.7. KNOWLEDGE GAPS

The associations between reef fish and the benthic habitat is a fundamental research challenge at coral reefs. Previous research has identified depth, wave energy and cyclical environmental variables such as tide and time of day as critical environmental drivers which can alter benthic habitat and reef fish communities (e.g. Friedlander and Parrish 1998; Bellwood and Hughes 2001; Friedlander et al. 2003).

Depth is a major environmental driver of composition and structure of benthic community and reef fish assemblage composition (Drew 1977; Bak and Nieuwland 1995; Campbell et al. 2007; Fox and Bellwood 2007; Hoey et al. 2007; Brokovich et al. 2008; Zintzen et al. 2012; Williams et al. 2013; Fricke et al. 2014; Heyns-Veale et al. 2016; Asher et al. 2017). It is therefore crucial to sample across a range of depths to obtain a representative sample of the benthic and reef fish communities. The majority of studies on coral reefs are restricted to the lagoon reef and forereef slopes in less than 30 m depth, leaving deeper habitat adjacent and beyond the forereef slope understudied (Fitzpatrick et al. 2012; Whitmarsh et al. 2017). There is therefore a need for data on the reef fish assemblages in these deeper habitats and to determine how their habitat associations change under varying environmental conditions.

Wave energy is another key driver of the distribution of the benthic invertebrate and fish communities, as certain species are better adapted to tolerate high wave action, while others prefer sheltered conditions (Friedlander et al. 2003; Ponce de León and Guedes Soares 2005; Harborne et al. 2006; Kench et al. 2006). The wave energy from cyclones or hurricanes has been shown to have a destructive and long-lasting effect on the benthic habitat (Dollar 1982; Beeden et al. 2015; Wolff et al. 2016). The physical properties of wave energy on reefs and the effect of wave energy on the geomorphology of islands has been

well studied (Bustamante and Branch 1996, Lowe et al. 2005; Kench and Brander 2006; Kench et al. 2006, 2017; Monismith et al. 2013, 2015). Wave energy has been identified as an important variable to explain the distribution of benthic habitat in coral reef ecosystems, yet it has had limited use in predictive studies (Ballantine 1961, Graus and Macintyre 1989; Hamylton et al. 2012b; Chollett and Mumby 2012; Williams et al. 2013; Rattray et al. 2015). Other oceanographic processes like deep-water internal waves and topographically driven upwelling are important biophysical drivers that deliver cool particle-rich waters to coral reefs (Williams et al. 2018a; Riegl et al. 2019). Advances in wave modelling techniques, software and a greater understanding of different kinds of wave energy provide the opportunity to include this important environmental variable in predictive modelling (Williams et al. 2018a). Despite many years of research, it remains a challenge to build on our ecological understanding of the effect of environmental drivers on the associations between benthic habitat and reef fish which varies greatly between different study sites (Mellin et al. 2009).

The cyclical change of tide affects the benthos and fish assemblages by flooding the shallow lagoon reef flats making rich feeding grounds available to fish and other marine animals that temporarily exploit the habitats within the lagoon reef (Gibson 2003; Krumme et al. 2008; Krumme 2009). Flooding of the shallow lagoon during high tide connects mangroves, seagrass beds and coral reef habitat, and facilitates the transport of larvae, eggs, seeds, spores and fish among them (Nagelkerken et al. 2002; Gibson 2003; Mumby 2006; Krumme 2009). Strongly coupled with a change in tide is the cyclical change in the time of day (diel cycle), especially when the two coincide (Hobson 1973; Krumme 2009; Krumme et al. 2015; Kruse et al. 2016). Fish behaviour changes with the time of day from resting to feeding, and the movement of fish connects different habitats during the transition (Helfman 1986; Pitcher and Turner 1986). Tide thereby changes the structure of fish assemblages, as fish move between benthic habitat for feeding or shelter at different times of the tide. Despite the widespread and known effects of tide and time of day on the fish assemblages, it is not often included as a covariate in fish surveys, and the need for standardisation according to tide and time of day requires further investigation.

Reef-fish home ranges and therefore the scale of the habitat that fish use may be confined to a few centimetres, for small highly resident species, to several kilometres, for larger species that roam further in search of food (Meyer et al. 2007a; Green et al. 2015). It is important to use the appropriate scale when making inferences about the effect of the benthic habitat on fish assemblages, as it has implications for conservation and site management strategies (Pittman and Brown 2011; Sekund and Pittman 2017). Furthermore, it is important to classify the habitat at the appropriate level to match the scale which is being

investigated. Progress in this field in recent years has started building an understanding of how multiscale habitats influence patterns of diversity, species richness, and patterns for groups of specific species, but only limited work has been done on assessing reef fish assemblage structure across multiscale habitats (MacNeil et al. 2009; Mellin et al. 2009; Monk et al. 2011; Pittman and Brown 2011; Phinn et al. 2012; Nash et al. 2013).

1.8. ECOLOGICAL REFERENCE POINTS FROM BASELINE CONDITIONS

It is difficult to build an understanding of an ecosystem once key functions have been lost to the various pressures that act on it (DeMartini et al. 2008; Sandin et al. 2008; Friedlander et al. 2010; Sheppard et al. 2012). Government and site managers need ecological reference points to set tangible targets for conservation (Pauly 1995; McClanahan et al. 2011). The intact natural state of the environment, known as the baseline condition, represents an important ecological reference point upon which to assess species diversity, species distribution and ecological functioning (Green et al. 1996; Ward et al. 1999; Bellwood and Hughes 2001; Dankers et al. 2001; Costello 2009; Wabnitz et al. 2010; Phinn et al. 2012; Nagendra et al. 2013). In the absence of knowledge of the baseline condition, site managers often use the state of the ecosystem at the start of their careers as ecological reference points, which ignores the ecological deterioration which occurred prior to their careers (Pauly 1995). The continued regression in our understanding of the baseline condition is known as the shifting baseline syndrome (Pauly 1995; Knowlton and Jackson 2008). A shifting baseline may therefore lead to misguided conservation objectives and ineffective conservation strategies which are unlikely to change the course of the systematic deterioration of an ecosystem. Ecological reference points obtained from pristine sites are therefore critical to inform site management as it provides important information on ecosystem components and functions which have already been lost from degraded reefs. Anthropogenic impacts have already impacted reefs worldwide and there is limited information about baseline conditions for most coral reefs (Halpern et al. 2008; Knowlton and Jackson 2008). The escalation of the threats to coral reefs sets urgency to obtaining ecological information to inform such reference points of the baseline condition before further deterioration occurs (Pauly 1995; Knowlton and Jackson 2008).

There are few suitable places left where baseline information can be obtained on benthic habitat and reef fish assemblages, given the widespread and prevalent damage of stressors like global climate change, pollution and over-fishing (Dayton et al. 1995; Jackson et al. 2001; Pitcher 2001; Harborne et al. 2017; Hughes et al. 2018). Fisheries have impacted

heavily on the world's fish composition, especially through the loss of ecosystem engineers (Coleman et al. 1996) and top predators and their associated functional roles (Russ and Alcala 2004; Myers et al. 2007b; Heithaus et al. 2008; D'agata et al. 2016). Remote, isolated and protected areas where no or very low fishing occurs have been shown to have a high abundance and biomass of top predators (Friedlander and DeMartini 2002; McClanahan et al. 2007b; Sandin et al. 2008; DeMartini et al. 2008; Friedlander et al. 2010; D'agata et al. 2016; Graham et al. 2017). In the absence of reliable historical baseline data, large, isolated, remote islands, that have been protected for a long time, may provide the best chance to obtain ecological reference points which represent baselines prior to the effects of deleterious anthropogenic impacts especially in the highly populated tropical latitudes (Pauly 1995; Knowlton and Jackson 2008; Papworth et al. 2009; Sheppard et al. 2012; Edgar et al. 2014).

A number of ecological reference points have been developed as indicator metrics that reflect change in coral-reef composition and functioning (McClanahan et al. 2011). One key indicator is reef-fish biomass, which has been shown to predict the presence of important ecosystem processes like herbivory and predation. When reef fish biomass falls below 1130 kg/ha, several changes are observed in coral reef ecology, such as an increase in the variance of macroalgal cover and an increase in the ratio of macroalgae to hard-coral cover (McClanahan et al. 2011). When reef-fish biomass fell below 640 kg/ha, predation rates on urchins dropped. When fish biomass fell below 300 kg/ha, a whole suite of indicator metrics changed, such as a decline of species richness, a decline in the proportion of herbivorous fish in the assemblage, and a reduction in the cover of calcifying benthic organisms and hard corals (McClanahan et al. 2011). These indicator fish-biomass values are well below what has been measured at baseline sites like the Chagos, Kingman Atoll and Palmyra atoll (e.g. McClanahan et al. 2007b; Sandin et al. 2008; Friedlander et al. 2010; Graham et al. 2017). Fish biomass has been shown to be significantly greater at large, remote MPAs (wilderness sites) than small MPAs near areas with large human populations (McClanahan et al. 2011; Graham and McClanahan 2013; Edgar et al. 2014). Whilst many small, populated MPAs may still support some of the indicator metrics, they often lack the unique benthic communities and intact ecosystem processes which are present at wilderness sites (Graham and McClanahan 2013). Whilst reefs can recover to a point where fish biomass achieve such pre-exploitation levels and hard-coral cover can increase to former levels (e.g. McClanahan et al. 2007b), it is unknown whether the coral reef's community structure and species compositions could recover to former pristine levels (but see Steneck et al. 2019). Therefore the loss of these unique benthic communities and intact ecosystem processes from degraded or even small populated marine protected areas are likely to be irreversible

(Graham and McClanahan 2013). However, what is represented in terms of pristine levels of abundance, biomass, species richness and ecosystem functions have been shown to vary considerably between remote wilderness sites (McClanahan et al. 2015). While differences have been attributed to variation in abundance of large vagile predators, the causes of variation between pristine sites is still poorly understood (McCauley et al. 2012). Therefore, a need for data from additional remote wilderness sites is needed to obtain an understanding of regionally relevant conservation targets.

1.9. ALDABRA ATOLL AS AN ECOLOGICAL REFERENCE SITE

Aldabra is a large (34 by 14 km), remote raised coral atoll which is geographically isolated from populated landmasses in the Western Indian Ocean (WIO). Aldabra Atoll consists of multiple islands, separated by a large (155 km²) lagoon which is connected to the ocean via channels along the west and northern side of the atoll. The four main islands of Aldabra include Picard, Grand Terre, Malabar and Polymnie (Figure 1.1). Aldabra is 1115 km from Mahé (the Seychelles capital island), 630 km east of the African coastline, and 420 km northwest of Madagascar (Figure 1.1). Its nearest neighbours are the southern Seychelles' islands including Assumption (27 km), Cosmoledo (110 km), and Astove (150 km). The southern Seychelles islands are all geographically isolated and have low human populations, but only Aldabra has been officially protected since 1981 (Stoddart 1968a; Seaton 1991).

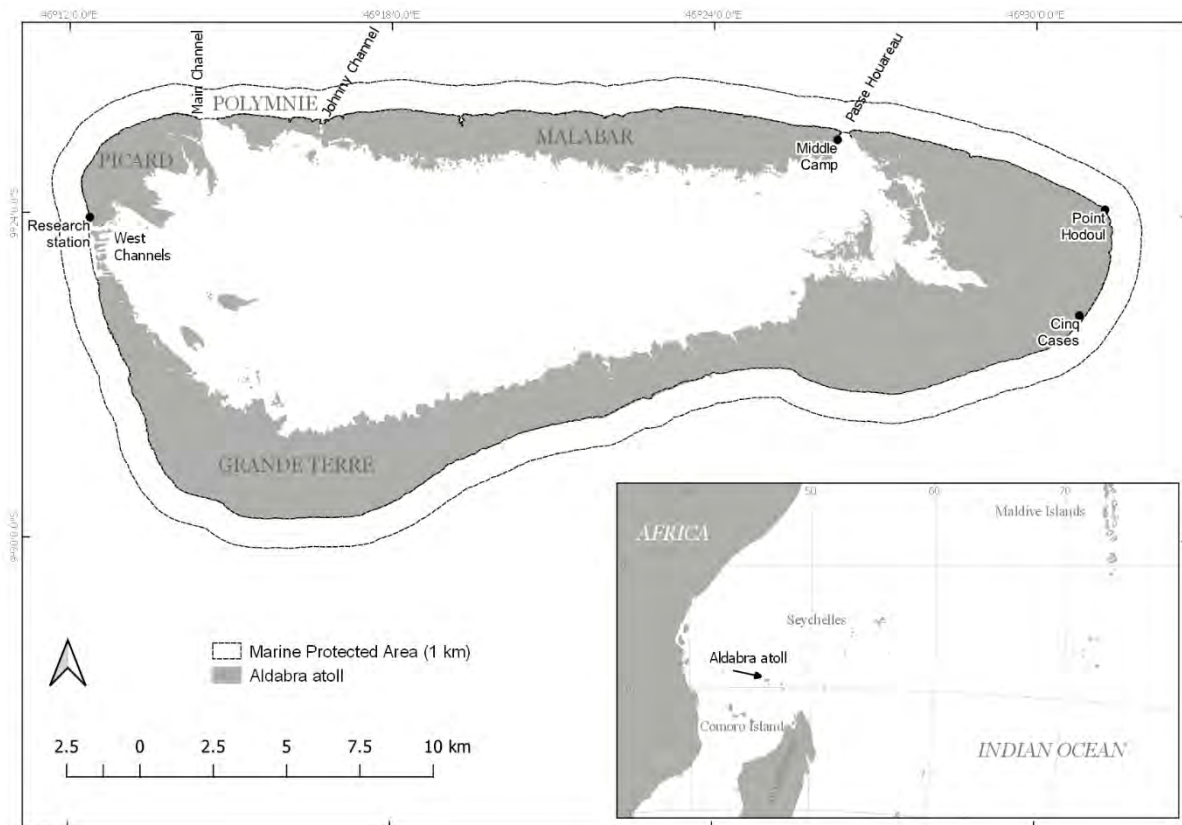


Figure 1.1. Aldabra Atoll is comprised of islands encircling a large lagoon (the four main islands are labelled). The Research Station is on Picard Island. Middle Camp and Cinq Cases are two remote satellite camps used for fieldwork. Exposure to breaking wave energy is greatest between Point Hodoul and Cinq Cases. The Channels that connect the sea to the lagoon are indicated in the map. Aldabra is in the Western Indian Ocean (WIO), 1115 km from Mahé and 420 km north of Madagascar.

Aldabra's geographical isolation, distance from trade routes and lack of freshwater has meant that people only ever settled temporarily (Stoddart 1971). Unlike Aldabra's neighbouring islands, which were mined for guano, Aldabra was historically only mildly exploited during seasonal occupation for harvesting of giant land tortoises, timber, turtles, fish and very limited growing of crops such as maize and sisal (Stoddart 1968a, 1971). In 1965 Aldabra was part of the British Indian Ocean Territory and proposed for the development of a strategic military base, to be shared with the United States of America (Stoddart 1968b). The intervention of the Royal Society of London, representing a number of conservation and scientific organisations, put forward proposals for the conservation of Aldabra for scientific research as the last undisturbed raised limestone island in the Indian Ocean (Stoddart 1968b). In November 1967, plans for the development of a military base were abandoned during the economic crisis which allowed the Royal Society of London to set up a research station on Aldabra Atoll (Stoddart 1968b, 1971). The military base was

subsequently built on Diego Garcia in the Chagos Archipelago (Lunn 2018). After the Royal Society's campaign, the Seychelles Islands Foundation (SIF) took over the management of Aldabra in 1979 under presidential decree and the atoll became a Special Protected Area (the highest conservation status in the Seychelles equivalent to IUCN 1a or 1b) (Seaton 1991). Aldabra's terrestrial and marine protected area has been officially protected since 1981 when declared a UNESCO World Heritage Site (WHS) as an outstanding example of a natural coral atoll. Aldabra's no-take MPA extends from the mean high-water mark to one km offshore (Aldabra Management Plan 2016). (When referring to Aldabra's MPA, no-take MPA is implied hereafter). Aldabra qualified as a WHS by satisfying several geomorphic and natural criteria, within which the site was described as having a pristine reef system unaffected by anthropogenic disturbance (<https://whc.unesco.org/en/list/185/>). Aldabra's coral reefs are known for high levels of fish species richness, with an abundance of herbivores and top predators (Potts 1980; Stevens 1984) and have an intact invertebrate community (Callow et al. 2001; Downing et al. 2005a). Aldabra has undisturbed seagrass beds, large populations of green and hawksbill turtles, migratory populations of marine mammals like humpback whales, and is the only location in the Seychelles with a breeding population of dugongs (Hermans and Pistorius 2008a; Mortimer et al. 2011; Hamylton et al. 2012a). The atoll also has expansive mangroves that are vital nursery ground for fish (Constance 2017).

Today, the only harvesting at Aldabra is carried out by the site management authority, SIF, which removes fish from the reef using regulated handline and troll fishing to supply protein to the approximately 15 – 20 staff within a spatially restricted area (Pistorius and Taylor 2009). Aldabra's long history of protection and geographic isolation has left its reef ecosystem largely intact and remote from direct anthropogenic disturbances (Stoddart 1971; Pistorius and Taylor 2009). Aldabra therefore offers the opportunity to assess the benthic invertebrates and reef fish assemblage to obtain valuable insight into the coral reef communities at a near-pristine shallow tropical marine ecosystem (Friedlander et al. 2015a). Aldabra also offers the opportunity to study the benthic habitat and reef fish assemblages from the whole forereef system, which has a perimeter of 85 kilometres (Friedlander et al. 2015a). Furthermore, Aldabra provides the opportunity to assess the effects of key environmental drivers on the benthic reef and fish community as it has a marked gradient in depth (0 – 50 m), a wide range of wave exposure conditions and a substantial tidal range (Stoddart et al. 1971; Pugh 1979). Aldabra's varied environmental conditions and together with the intact reef ecosystem makes it an important ecological reference point to study the effects of environmental drivers on the benthic habitat and fish assemblage in the near

absence of anthropogenic impacts (Stoddart 1968a; Downing et al. 2005b; Stobart et al. 2005; Edgar et al. 2014).

Aldabra, like others reefs in the Indian Ocean, did not escape the mass mortality of corals inflicted by the 1998 El Nino, and recently again in 2015/2016 (Cerutti et al. Submitted; Spencer et al. 2000; Sheppard and Obura 2005; Stobart et al. 2005; Normile 2016; Cerutti 2017). Coral reef surveys at Aldabra following the 1998 bleaching reported a decline between 20 – 40 % hard-coral cover, varying with depth, then a slow recovery over the following 7 years (Teleki et al. 1999; Buckley et al. 2005; Stobart et al. 2005). The reef fish assemblage did not significantly decline following the 1998 bleaching event (Downing et al. 2005b; Stobart et al. 2005). The recent global mass-bleaching event and predictions of more frequent mass-bleaching events in future sets urgency to obtain a detailed record of the baseline conditions of benthic and reef fish community from this important reference site for the WIO (Cerutti et al. Submitted; Cerutti 2017). The research presented in this study represents the coral reef ecosystem at Aldabra following approximately 14 years of recovery after the 1998 mass-bleaching event and predates the most recent mass-bleaching event in 2015/2016.

1.10. KNOWLEDGE GAPS OF ALDABRA'S CORAL REEFS

Early surveys of subtidal reefs carried out during the Royal Society's campaign on Aldabra Atoll included descriptions of the reef (Stoddart 1968b, 1984; Stoddart et al. 1971), and photographic surveys of small sections of forereef slope (Bellamy et al. 1969; Barnes et al. 1970; Drew 1977). Barnes et al (1971) and Drew et al (1977) described six benthic zones along the forereef slope at Aldabra Atoll, and some of the physical environmental factors, including depth and wave exposure, thought to control the benthic zoning. A number of intertidal studies were carried out describing parts of the intertidal lagoon reef habitat and the invertebrates that utilise this habitat (Taylor 1971). Early studies of the fish assemblage at Aldabra during this period included deep-sea fishing between 100 and 300 m, a number of studies on fish behaviour, and studies of the life-histories of the sharks at Aldabra (Potts 1970, 1973, 1980, 1981; Forster 1984; Stevens 1984).

Following the departure of the Royal Society in 1979, no published benthic surveys were carried out at Aldabra until 1998 when the "Shoals of Capricorn", a science research, training and education programme run in Mauritius and Seychelles by the Royal Society and Royal Geographical Society, surveyed Aldabra's reefs (Spencer et al. 2000). However, these

surveys of Aldabra's reefs were limited and no published literature on the forereef slopes could be found. In subsequent years, marine research at Aldabra was largely focussed on the change in benthic cover and the reef fish assemblage following the 1998 mass-bleaching event (Stobart et al. 2001, 2005; Engelhardt et al. 2002; Downing et al. 2005a; Sheppard and Obura 2005). In 2012 the site management authority, SIF, established a renewed marine research programme to monitor benthic invertebrate and reef fish communities at Aldabra Atoll studying twelve transects to record the changes to the benthic invertebrates and fish community over time (Haupt et al. 2013, 2015a). Subsequently, National Geographic's Pristine Seas expedition carried out a benthic and reef fish survey to assess the biodiversity status of the southern Seychelles Islands (Friedlander et al. 2015a). These surveys were limited to 10 and 20 m depth, and in similar localities to the surveys following the 1998 bleaching. All previous SCUBA-based benthic and fish surveys at Aldabra were limited in their spatial and depth coverage owing to the large size of the atoll and limitations of using SCUBA as a survey method. In addition, very few studies have been conducted in the east of the atoll owing to rough weather conditions experienced in the windward side of the coast (e.g. Forster 1984). The past SCUBA based research therefore collected incomplete data on benthic habitat and reef fish assemblages, which may not be representative for large sections and depth ranges of Aldabra's reefs.

In addition to the SCUBA-based methods, a number of recent studies have made use of fishing methods to study trends of fish species caught in the subsistence fishery and assess demographics of groupers at Aldabra (Grandcourt 2005; Pistorius and Taylor 2009). Fisheries based studies at Aldabra were limited to species targeted by the SIF-subsistence fishery, and consequently, there is no information about non-targeted species within this dataset. The limited spatial and species coverage by SCUBA and fisheries surveys means that there are fundamental knowledge gaps about reef fish assemblage, which limit effective management and protection at Aldabra (Aldabra Management Plan 2016). As such, there is a need to conduct a comprehensive survey of benthic habitat and reef fish assemblages at Aldabra Atoll's coral reef ecosystem.

Recently, remotely sensed imagery has been employed to map terrestrial vegetation, inner atoll lagoon habitat, and mangroves, and at a coarse scale the geomorphic reef zones of the seaward reef at Aldabra Atoll (Andréfouët et al. 2009; Hamylton et al. 2012b; Walton 2015; Constance 2017). The geomorphic reef zones of the Aldabra forereef were mapped using coarse-scale Landsat (30 m resolution) imagery and excluded information on benthic cover information (Andréfouët et al. 2009). Subsequently, high-resolution Worldview imagery (4 m²) was used to assess the use of remotely sensed imagery to detect change of benthic

habitat coverage but the study was restricted to the reefs of Picard Island only at Aldabra (Andréfouët 2012). Neither of these two studies of the seaward reef implemented ground truthing data and both only provided benthic habitat data on a relatively coarse scale. There is still a fundamental gap to determine and map the benthic habitat of the Atoll's seaward reefs.

The use of remotely sensed imagery to map benthic habitat is an efficient means to obtain spatially comprehensive benthic habitat data, which has had a wide application from mapping mangroves, seagrass beds to coral reefs in shallow tropical marine environments (Green et al. 1996; Green and Edwards 2000; Mumby and Edwards 2002). Using remote sensing is more cost-efficient than obtaining comprehensive data using traditional methods, such as SCUBA-based benthic surveys, which cover only a small area of the reef (Green and Edwards 2000). However, such traditional methods are still used to obtain ground truthing data to train and validate habitat maps derived from remotely sensed imagery, but the total reliance on these methods have been greatly reduced. Furthermore, remotely sensed imagery is readily scalable, which affords the ability to derive benthic habitat maps at multiple scales, which in turn gives the opportunity to choose appropriate scales to assess fish-habitat use (Mellin et al. 2009; Phinn et al. 2012).

Different to traditional fishery-based assessment methods, like long-lining or trawling, Baited Remote Underwater Video systems (BRUVs) are a non-extractive method causing minimal damage to habitat and is, therefore, suitable to use in MPAs (Willis and Babcock 2000; Cappo et al. 2004; Brooks et al. 2011). SCUBA-based studies on coral reefs are often limited to depths between 5 m and 30 m (Watson 2005; Watson et al. 2005a; Harvey et al. 2012b), while BRUVs are able to sample a much wider depth range, from 0.5 m to over 1000 m (Cappo et al. 2004). The ability to deploy multiple BRUVs simultaneously allows for efficient sampling across a depth range (Bernard 2012). Baited Remote Underwater Video systems (BRUVs) also avoids a species detection bias which affects Underwater Visual Census (UVC) methods where the presence of a SCUBA diver deters large mobile species like sharks (Watson and Harvey 2007; MacNeil et al. 2008; Langlois et al. 2010; Bernard et al. 2013). Baited Remote Underwater Video systems (BRUVs) have been shown to outperform fishing as a survey method to assess fish assemblages because they have lower variability in the data and include data on non-targeted species (Cappo et al. 2004; Brooks et al. 2011; Bernard 2012).

It is important to understand biases and the appropriateness of a sampling method to assess the fish assemblage to ensure accurate interpretation of the data, as the use of different methods can lead to different results (Bijoux et al. 2013). The different survey methods have

their own biases and strengths, where some, like BRUVs, are well suited to observe mobile predatory species and SCUBA is more effective at observing cryptic fish species (Watson et al. 2005b). Consequently, the use of multiple methods is necessary to obtain a holistic sample of the reef fish community in a diverse tropical reef ecosystem. The use of bait with remote underwater video systems (BRUVs), has been advocated for sampling reef fish assemblages over unbaited RUVs, given the greater precision obtained from more distinctive assemblages and greater detection probability of large carnivores in BRUVs (Watson 2005; Harvey et al. 2007; Bernard and Götz 2012). In areas with high levels of predator abundances, as is expected from ecological reference sites like Aldabra, the presence of bait may alter the observed fish assemblage as has been observed in previous studies (e.g. Harvey et al. 2007; Bernard and Götz 2012).

The general shortage of information on scales of habitat and the association of fish to a range of habitat scales requires a comprehensive survey of the reef habitats and fish communities to improve this knowledge gap of coral reef ecosystem dynamics. A second core motivation was to better understand the spatial distribution of reef biota at various scales and in relation to various environmental drivers at an ecological reference. The knowledge obtained from an ecological reference site provides the opportunity to understand the effects of environmental variables on the benthic reef invertebrates and fish without confusing their effects with the influences from local human stressors on the ecosystem.

To ensure effective management, the SIF requires a spatially comprehensive and detailed understanding of benthic habitat and reef fish assemblage structure at Aldabra. Furthermore, baseline data on the benthic composition and reef fish assemblage structure are required to inform the MPA's marine monitoring programme.

1.11. AIMS, HYPOTHESES AND OBJECTIVES

The aim of this research is to establish the associations between the benthic habitats and reef fish assemblages and determine how environmental drivers influence reef ecosystem structure at a pristine tropical atoll. The ecological reference points obtained from establishing these associations at a large, remote, isolated and protected tropical atoll in the WIO can provide direction to setting regional and local conservation goals and inform marine protected area management (McClanahan et al. 2011, 2015; MacNeil et al. 2015).

The hypotheses that this research aimed to address were:

H. 1.1.) Environmental drivers such as depth and exposure to wave energy determines the spatial distribution of benthic habitats at a coral reef ecosystem.

H. 1.2.) The reef fish assemblage structure is explained by multiple scales of habitat and modified by the effects of environmental drivers such as depth, wave energy and cyclical temporal drivers such as time and tides.

H. 1.3.) The reef fish assemblage at Aldabra Atoll represents a pristine reef fish assemblage, comprising high levels of herbivores and predators.

The following five primary objectives were set to address the three hypotheses in the thesis, all directed at Aldabra's seaward reefs down to 50 m:

Obj. 1.1.) The first objective was to characterise the benthic habitat and map its spatial distributions, using remotely sensed imagery and ground truthing data.

Obj.1.2.) The second objective was to assess the influence of depth and exposure to wave energy on the distribution of benthic habitats.

Obj.1.3.) The third objective was to identify a suitable standardised method to survey the reef fish diversity and assemblage structure by comparing BRUVs and RUVs.

Obj.1.4.) The fourth objective was to determine the effect of tide and time of day on the reef fish assemblage, using BRUVs and RUVS on spring tides.

Obj.1.5.) The fifth objective was to establish the association between reef fish assemblage structure and benthic habitats, and to test how fish size influences the scale of habitat at which the associations are most apparent.

1.12. THESIS OVERVIEW

This thesis provides critical information about the distribution of benthic habitat and quantifies fish inside and outside of the existing MPA at Aldabra and serves as an ecological reference point upon which trends observed at Aldabra in the future can be assessed.

1.12.1 Chapter 1: General Introduction

The General Introduction (Chapter 1) aims to provide the context around the value and importance of tropical reef ecosystems and the multiple severe pressures impacting these systems. Chapter 1 describes Aldabra as a modern-day pristine site that serves as a natural

laboratory from which inferences can be drawn to guide our understanding of reef ecology and highlights the plight of more degraded tropical reefs in the WIO. The rationale behind the research questions are provided and the higher-level hypotheses and objectives are set out for the thesis (Figure 1.2).

1.12.2 Chapter 2: Characterising and mapping the benthic habitat of Aldabra's Seaward reefs at multiple scales using remotely sensed satellite imagery

In Chapter 2 the benthic habitat is characterised and mapped at three scales, consisting of geomorphic reef zones, and the broad and fine-scale benthic habitat categories of the entire seaward reef system around of Aldabra to a depth of 50m. Four categories of geomorphic reef zones, such as the reef flats and forereef slope, were defined and mapped by tracing visible outlines on a satellite image. The broad-scale benthic habitat categories were defined from major benthic habitat types, such as hard coral, seagrass, epilithic algal matrix, soft coral, etc. Fine-scale benthic habitat categories were defined from categorising minor benthic cover categories to the finest level recognisable for benthos, from video imagery. This included species-level taxa such as *Physogyra lichtensteini*, genus level, such as *Rhytisma* spp, and substratum and biota combinations such as epilithic algal matrix on rubble. The classification of benthic habitat categories and mapping of the habitat facilitated the study of the relationship between fish assemblage structure and benthic habitat. There was sufficient confidence in the accuracies of the benthic habitat maps to allow the maps to be used to assess relationships between benthic habitat and fish assemblages in the following chapters (Figure 1.2).

1.12.3 Chapter 3: The effect of depth and wave energy on the probability of occurrence of six benthic habitat categories

This Chapter establishes the fundamental effect of two of the key environmental drivers on the character and spatial distribution of benthic habitat around Aldabra. A wave model was developed using linear wave theory for a fetch with an area of 600 km² around Aldabra informed by wind data collected at the atoll. The probability of occurrence of six broad-scale benthic habitat categories (which were mapped in Chapter 2) was assessed against gradients of depth and wave energy using Generalised Additive Models (GAMs).

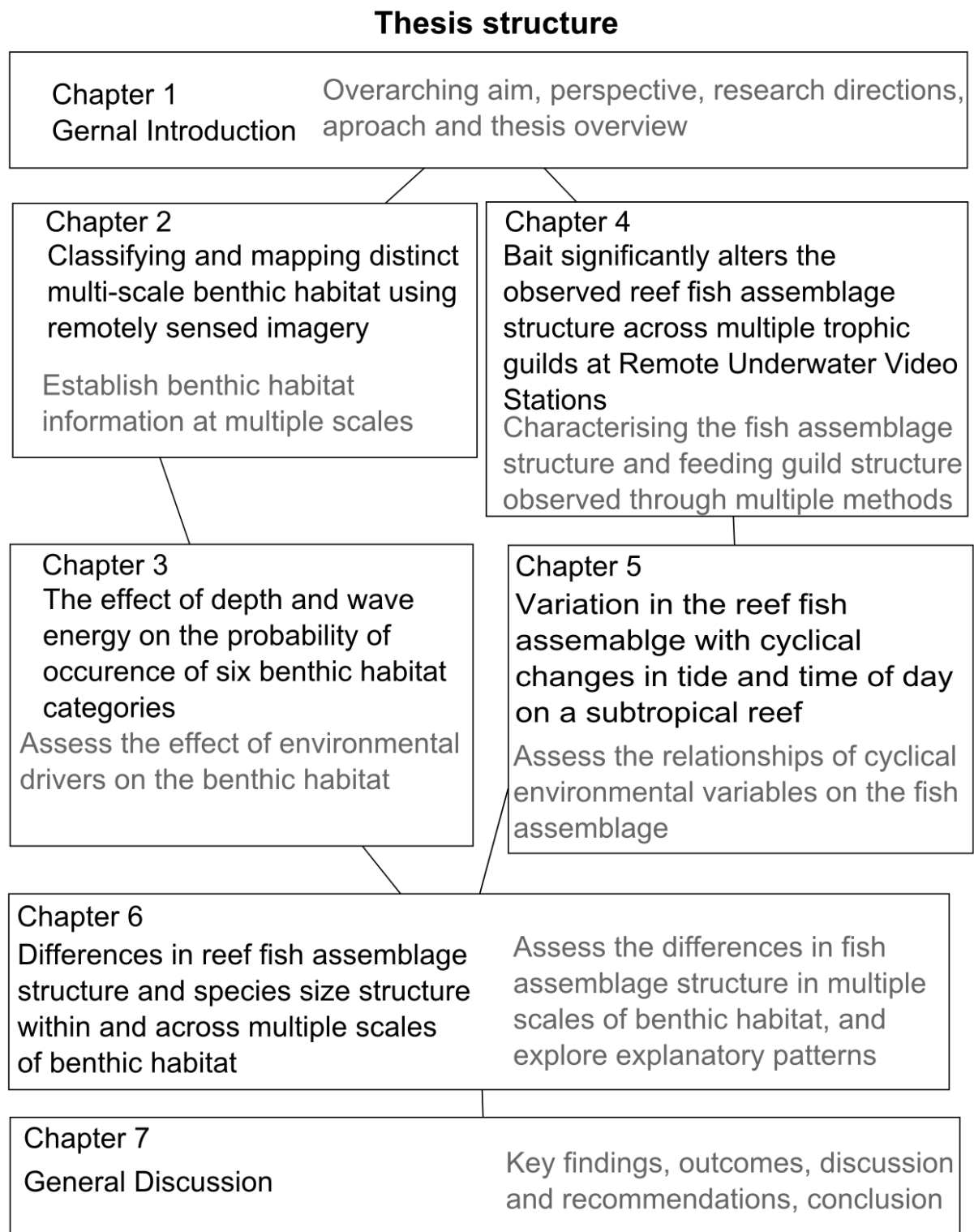


Figure 1.2. Flow diagram showing an overview of the eight chapters and how they fit together to bring the topics covered in the thesis together.

1.12.4 Chapter 4: Bait significantly alters the observed coral reef fish assemblage structure across multiple trophic guilds at Remote Underwater Video Stations.

The differences between the observed reef fish diversity and assemblage structure recorded using two methods, namely BRUVs and RUVs, were established for the overall assemblage structure and within multiple trophic guilds using multivariate and univariate statistics. The results from this chapter quantifies the fish assemblage structure and informs the choice of sampling method used to assess fish assemblage structure for the remainder of the thesis.

1.12.5 Chapter 5: Variation in the reef fish assemblage with cyclical change in tide and time of day on a subtidal tropical reef

Chapter 5 investigates the effects of tide and time of day on the fish assemblage structure in four geomorphic reef zones. Reef fish assemblages were recorded using BRUVs and RUVs during spring tides in the morning, midday and evening in a variety of habitats between 0 and 55 m on the west coast of Aldabra Atoll's seaward reefs. The results from this chapter quantify the differences between the reef fish assemblages during different tides and times of day.

1.12.6 Chapter 6: Differences in reef fish assemblage structure and species size structure within and across multiple scales of benthic habitat

In Chapter 6 the fish assemblage structure is compared between multiple scales of habitat, using the mapped habitats from Chapter 2. Baited underwater Video systems (BRUVs) and unbaited RUVs data from the forereef of Aldabra were analysed to determine the differences between reef fish assemblages associated with the different benthic habitats. Fish body size was investigated as a driver of differences between fish assemblage composition across multiple scales of habitat.

1.12.7 Chapter 7: General Discussion

The General Discussion addresses the high-level objectives from the General Introduction and draws the findings of the thesis together. The implications of the results from the thesis are discussed in a broader geographic and conceptual context, showing the value of remote, isolated protected reefs systems as ecological reference points in the Western Indian Ocean.

Chapter 2. Characterising and mapping the benthic habitat of Aldabra's Seaward reefs at multiple scales using remotely sensed satellite imagery.



The Aldabra seaward reef showing a variety of benthic habitat along the lagoon and forereef. Photo: ZilAir 2013

2.1. ABSTRACT

The aim of this chapter is to gain an understanding of the benthic habitat types which characterise Aldabra's seaward reefs and map their geographic distribution. A benthic habitat map was required to assess reef fish associations with habitats at Aldabra and to inform marine spatial planning being undertaken in the Seychelles. The objective of this study was to characterise and map the benthic habitats at multiple scales between 0 and 50 m depth at Aldabra, using a supervised maximum likelihood habitat classification of remotely sensed imagery and ground truthing data. The ground truthing data was obtained from 20 still frames taken from each of the randomly stratified and systematic 361 drop-camera and walked video transects collected on Aldabra's forereef and lagoon reef flats. Points (20 for drop-camera and 4 for walked) were overlaid onto each image and the benthic type identified to the lowest taxonomic level possible. Hierarchical cluster analyses of the ground truthing data were used to assign samples to habitat categories, which were characterised based on relative abundance and frequency of benthic types in each cluster. GeoEye satellite imagery with a resolution of 4 m² consisting of four spectral bands (Red-Blue-Green-InfraRed) were atmospherically and water-depth corrected. Spectral signatures for habitat categories were trained on 80% of the ground truthing data and the remainder used for accuracy assessment. The habitat maps were developed at three hierarchical scales, which differed in their coarseness of the habitat classification, namely: geomorphic zones, broad-scale habitats and fine-scale habitats. Four categories of geomorphic reef zones, namely the reef flats (19.2 km²), top of the forereef slope (7.8 km²), deep forereef slope (11.6 km²), and reef platform (14.3 km²) were manually delineated following the visual outlines of reef zones from satellite imagery. The broad-scale habitats, namely, (1) Epilithic algal matrix, 2) Hard and soft coral, 3) Rubble, 4) Macroalgae, 5) Seagrass and 6) Sand were characterised and mapped using a supervised classification and ground truthing data. Similarly, twelve fine-scale benthic habitats were characterised and mapped, for example, Hard coral including massive and submassive forms (11 %), (1 %) *Millepora* and (2 %) *Rhytisma*. Broad-scale habitat maps had an overall producer accuracy of 54 % and 29 % at the fine-scale habitats. This study presents the first classification and maps of benthic habitats on the seaward reefs at Aldabra Atoll. The forereef slopes were dominated by hard coral and very low macroalgal cover, an indication of a productive and resilient reef. The spatial distribution and characteristic habitat types serve as an ecological reference point to compare to other reefs in Western Indian Ocean (WIO) and to Aldabra itself in future. The benthic habitat maps were subsequently used to motivate the expansion of Aldabra Atoll's Marine Protected Area (MPA).

2.2. INTRODUCTION

The overarching aim of this chapter was to gain an understanding of the types of benthic habitat and their spatial distribution at Aldabra Atoll's seaward reef. Classifying the marine environment into characteristic thematic habitats and then mapping the spatial configuration thereof provides a reference point of the spatial distribution of various benthic habitat categories at a point in time. Categorical habitat maps are often used to ensure representative sets of habitat categories are protected in systematic conservation planning and are therefore essential for site management (Margules and Pressey 2000; Stevens 2002; Villa et al. 2002; Great Barrier Reef Marine Park Authority 2003; Nagendra et al. 2013). Remote sensing is a powerful tool used to map the benthic habitat in tropical marine environments in relatively shallow waters (0 – 20m) and is increasingly being used to assess and map impacts to these environments, such as coral bleaching (Andréfouët et al. 2002, 2003; Mumby and Edwards 2002; Kerr and Ostrovsky 2003; Klaus and Turner 2004; Hamylton 2011; Hamylton et al. 2012b; Barnes et al. 2015; Iovan et al. 2015). Furthermore, benthic habitat maps are a valuable starting point to ecological studies of the associations between benthic reef and fish communities (e.g. Friedlander and Parrish 1998; Friedlander et al. 2003; Harvey et al. 2007).

The degradation of benthic habitat is therefore likely to have an impact on the reef fish community. Coral reefs in the Western Indian Ocean (WIO), suffered significant mortality following the 1998 mass-bleaching event (Goreau et al. 2000; Spencer et al. 2000; Turner et al. 2000b; Graham et al. 2006). Reefs in the Granitics (the inner islands are comprised of granite as opposed to limestone) of the Seychelles suffered 90 % coral mortality, and some reefs underwent a phase shift from coral to macroalgal-dominated communities (Turner et al. 2000b; Graham et al. 2006, 2013, 2015). Aldabra Atoll suffered up to 41 % coral bleaching and mortality (Spencer et al. 2000; Sheppard and Obura 2005; Stobart et al. 2005). A slow recovery of hard coral was reported from nine transects on the seaward reefs of Aldabra in 10 and 20 m water depth over seven years following the mass bleaching, with no evidence of a phase shift to macroalgal-dominated communities (Stobart et al. 2005). The composition of the benthic habitat at Aldabra changed during the recovery phase due to colonisation dynamics favouring certain benthic species over others and weakened immune response to coral disease outbreaks could have caused further changes (Loya et al. 2001; Stobart et al. 2005; Bruno et al. 2007). There is therefore a need to quantify the post-1998 bleaching benthic community. The surveys in which coral recovery was monitored reported benthic change at a very fine scale, and there were no sites on the most exposed east side of the

atoll. It remains unclear what the distribution and status of the benthic habitat at Aldabra were after 15 years of recovery.

Following the 1998 mass-bleaching event, no significant changes in the fish community were reported after seven years of recovery at the reef (Downing et al. 2005a). However, the association of reef fish with benthic habitats can exist at different scales of habitat for different species owing to differences in home range and niche requirements and it is therefore important to assess fish within the appropriate scale (Andréfouët et al. 2002; Mellin et al. 2009; Sekund and Pittman 2017). Knowledge of the spatial distribution of characteristic microhabitats, fine-scale habitats, broad-scale habitats or geomorphic zones (habitat at multiple scales hereafter for simplicity) is therefore essential to inform the associations between reef fish and habitat (Mellin et al. 2009). Microhabitats may be considered an individual coral head, or a single species of coral within which niche specialists such as certain damselfish (Pomacentridae) species live (Ormond et al. 1996). Fine-scale benthic habitat consists of a uniform substrate and unique combination of benthic organisms (benthos) occurring at the spatial scales of 10 – 100 m. Fine-scale benthic habitats may be considered as habitats where sufficient information is available on the benthos to characterise biotopes (e.g. Klaus and Turner 2004). Broad-scale benthic habitats include fundamentally different habitat categories, such as seagrass, beds, coral reefs or sandy terraces, and typically occur at greater spatial scales than fine-scale habitats (e.g. Sekund and Pittman 2017). Geomorphic reef zones include the distinct zonation, often with depth, of geomorphological features at the scale of the seascape (Blanchon 2011).

Geomorphologic zones at tropical atolls typically include a lagoon reef, forereef slope and the reef platform, within which subzones may be recognised, such as a back reef and reef flats within the lagoon reef (Blanchon 2011). The high spatial resolution at which remotely sensed imagery is collected by satellites lends itself to mapping habitat at differing levels of thematic detail as it may be able to detect a range of habitat scales, from fine-scale habitat to geomorphic reef zone habitats (Phinn et al. 2012).

There have been several previous studies that have mapped terrestrial (e.g. Walton 2015), mangrove (e.g. Constance 2017) or marine habitat at Aldabra Atoll (e.g. Andréfouët 2012) or studied the benthic composition of the forereef slope (e.g. Barnes et al. 1970; Sheppard and Obura 2005; Stobart et al. 2005), but none of these studies has attempted to characterise and map the spatial configuration of the benthic habitat of the seaward reefs at Aldabra. Barnes et al. (1971) provided the first benthic zoning study of the forereef slope, in which six zones were described according to the dominant groups of benthic cover, but this was limited to the fourteen transects sampled, and no attempt was made to map the spatial

configuration of the benthic zoning. Subsequent studies of the reefs at Aldabra Atoll focussed on quantifying the change of benthic community composition at a fine scale following the 1998 bleaching event, and determining the ecosystem health in the Southern Seychelles islands. (Barnes et al. 1971; Drew 1977; Sheppard and Obura 2005; Stobart et al. 2005; Friedlander et al. 2015b). In 2009 the physical extent of the Aldabra forereef was mapped using satellite imagery with a low spatial resolution (Landsat 30 m) during the Millennium Coral Reef Mapping Project (Andréfouët et al. 2009), but this did not include any detail on benthic habitat. Subsequently, the forereefs of Picard Island at Aldabra were mapped to showcase the use of remotely sensed imagery and image processing techniques to detect habitat change, but this study was confined to a small area on west coast of Aldabra, and only included a limited amount of detail on the benthic habitat (Andréfouët 2012). Neither of these two studies included ground truthing data to validate the resulting maps (Andréfouët et al. 2009; Andréfouët 2012). In another study, Aldabra's inner lagoon habitats were mapped by Cambridge Coastal Research Unit (CCRU) in 2009-2012, but this project did not include the seaward reefs (Hamylton et al. 2012b). There is currently no benthic classification system or comprehensive benthic habitat map of Aldabra Atoll's seaward reefs.

The aim of this study was to characterise and map benthic habitat at multiple scales for the entire seaward reef of Aldabra Atoll using a supervised classification of remotely sensed imagery to provide a reference point of the current status benthic habitat to guide future management decisions.

Four hypotheses were tested in this chapter:

H. 2.1) Aldabra supports a diverse variety of benthic habitats with multiple fine-scale categories of coral, seagrass, macroalgae and sand and rubble-filled terraces.

H. 2.2) Forereef slopes are dominated by hard-coral habitat categories, and only small areas of macroalgal habitat occur.

H. 2.3) Supervised image classification results in poorer accuracy in fine-scale benthic habitat maps compared to broad-scale maps.

The specific objectives of this chapter were:

Obj. 2.1) Derive a systematic classification from hierarchical cluster analysis of ground truthing data collected using towed underwater videos of Aldabra's seaward reefs around the entire atoll from the shore to 55 m depth.

Obj. 2.2) Map the multiple scales of benthic habitat cover at Aldabra Atoll between 0 and 55 m depth using a hand tracing and supervised habitat classification of GeoEye satellite imagery with four spectral bands and a spatial resolution of 4 m².

Obj. 2.3) Determine a standard level of correct habitat assignment using standard measures of the accuracy of supervised habitat maps from a subset of the ground truthing data.

2.3. METHODS

Remotely sensed imagery was processed to map the seaward benthic habitat at Aldabra Atoll at three tiers, namely, geomorphological zones, broad-scale benthic communities, and fine-scale benthic communities. All benthic habitat maps used the same remotely sensed imagery and image pre-processing techniques.

The process of creating a habitat map for the seaward reefs of Aldabra followed a series of steps outlined in the flowchart (Figure 2.1) below as recommended by Green and Edwards (2000).

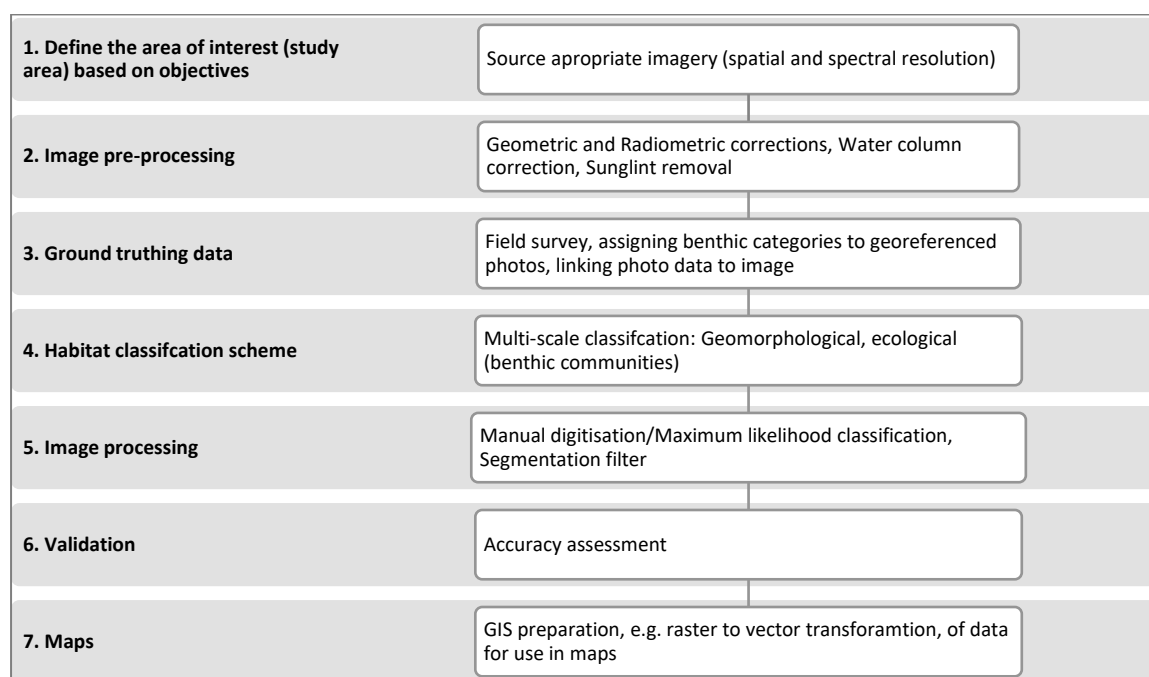


Figure 2.1. Steps followed to produce Aldabra reef habitat map. On the left of the flowchart is the step, and on the right is the detailed actions associated with each step.

2.3.1 Study area

Remotely sensed satellite imagery was processed to map the seaward reefs of Aldabra Atoll in the WIO (Figure 2.2). The area mapped started from the shore and extended at least 1.5 km beyond the visually estimated offshore extent of forereef slope on the seaward reef, to ensure that the entire seaward reef was included. The extent of the forereef slope was visually estimated as it could be seen from satellite imagery. The seaward reef included the lagoon reef, forereef slope and reef apron to approximately 50 m depth.

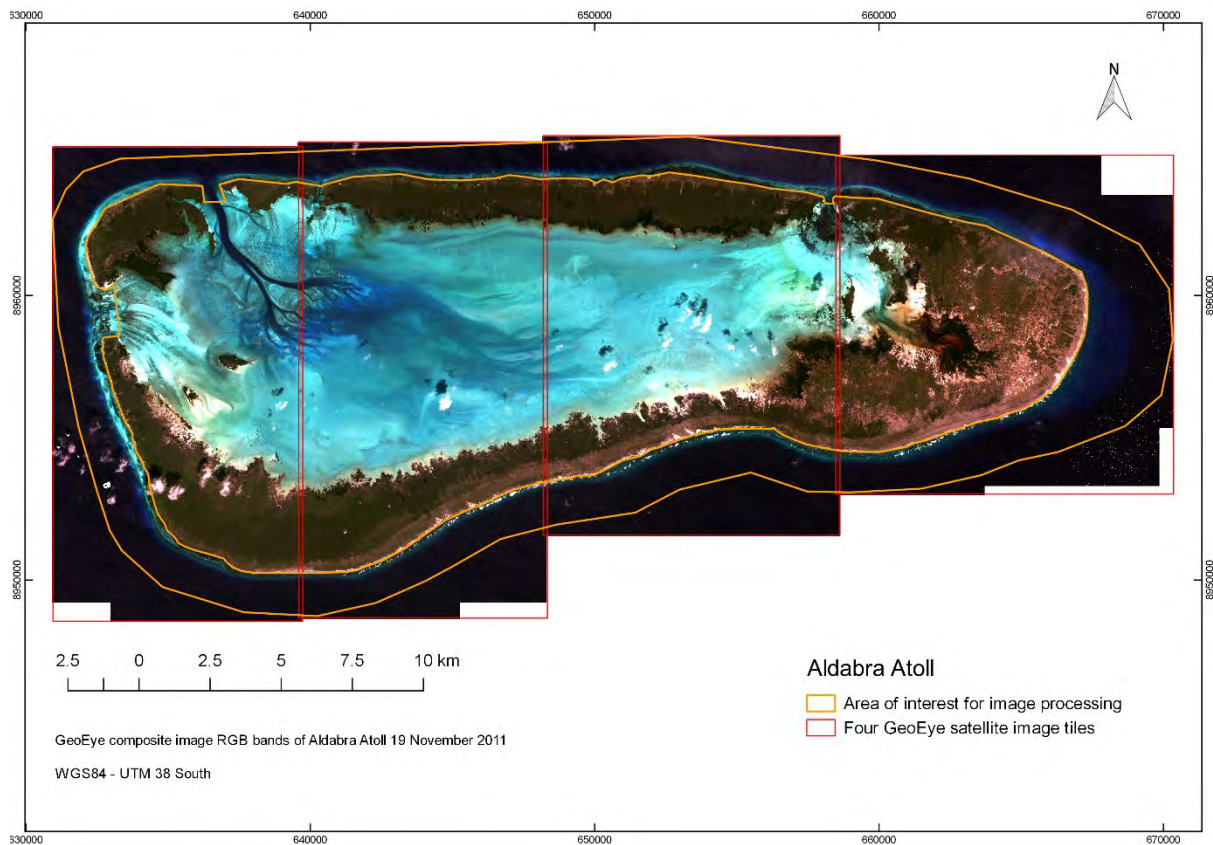


Figure 2.2. GeoEye satellite image (19 November 2011) showing Aldabra Atoll. The image consisted of four overlapping tiles, comprising four spectral bands, with low (< 2 %) levels of cloud cover and low levels of wave action.

2.3.2 Remotely sensed imagery

The GeoEye satellite imagery was received as a single time frame covering Aldabra Atoll on the 19 November 2011 as four tiles (Figure 2.2). The imagery consisted of multispectral bands including Blue, Green, Red and Near Infra-red (BGRN) and panchromatic, received in GeoTIFF file format at 11 bits per pixel with a 4 m² spatial resolution. The imagery was received as standard geometrically corrected imagery which had been projected to Universal Transverse Mercator, Southern hemisphere, zone 38, i.e. WGS 84, UTM 38 south, using cubic convolution interpolation. The GeoEye spectral range values are given below (Table 2.1).

GeoEye satellite imagery was used because a 4 m² spatial resolution is appropriate to map fine-scale benthic communities, and the image had good clarity and was nearly cloud-free (cloud cover 2 % over the area of interest) (Phinn et al. 2012; Nagendra et al. 2013). The low levels of wave action made it possible to assess the nearshore areas, which were masked in

comparable or higher spatial resolution imagery available at that time, e.g. World View2 and orthophoto imagery.

Table 2.1. Specifications of image band spectral range and other characteristics of the GeoEye satellite imagery

	GeoEye
<i>Bands</i>	4 Multispectral (RGBN)+Panchromatic
<i>Panchromatic</i>	450 - 800 nm
<i>Blue</i>	450 - 510 nm: 480 nm: 0.48 microns
<i>Green</i>	510 - 580 nm: 545 nm: 0.545 microns
<i>Red</i>	655 - 690 nm: 672.5 nm: 0.6725 microns
<i>Near Infra-Red</i>	780 - 920 nm: 850nm: 0.85 microns
<i>Sensor Resolution</i>	0.46
<i>Output resolution available</i>	1.86*1.86m at nadir
<i>Number of images of different dates</i>	Single source – 19 November 2011, received 4 tiles.
<i>Cloud cover</i>	<2 %
<i>Surface obstruction estimate</i>	<3 %
<i>Source Image ID</i>	2011111907112921603031604792
<i>Inspection results summary</i>	Good clear image, covers an area of interest, low levels of cloud cover and wave action.

2.3.3 Image pre-processing

Pixels outside of the area of interest were removed using a mask as these affect image classification procedures. A binary raster image of the area of interest (a mask) was multiplied with the imagery to exclude pixels outside of this area. Pixels outside the area of interest include the deep water beyond the shallow reef platform and the land and inner lagoon. The removal of unnecessary pixels reduces the range of pixel values and improves user ability to discern fine-scale differences between habitats resulting from cluster analysis. The GeoEye imagery was geometrically and then radiometrically corrected using Idrisi Selva (Eastman 2009), and QGIS (Quantum-GIS-Development-Team 2017), as detailed below.

2.3.3.1 Geometric corrections

The standard geometrically corrected GeoEye imagery required further geometric corrections, as the georegistration was incorrectly offset by 17.43 m east and 35.81 m north. (Determined from a comparison to the very high spatial accuracy orthophoto imagery (± 1 cm spatial error)).

Waypoints were taken for well-known and easily recognisable features, namely the camping huts at Cinq Cases, Dune De Mess and Dune Jean-Louis, Anse Mais, Malabar, Middle Camp, and the Research Station and used to inform georegistration of the imagery. The

original georegistration coordinates of the GeoEye imagery was changed by applying a uniform shift of 17.43 m west, and 35.82 m south which aligned the GeoEye imagery with the orthophoto imagery. This was preferred over rubber sheet transformation to preserve digital number (DN) values as accurately as possible, given that a uniform shift was sufficient to correct the image geometrically.

2.3.3.2 Radiometric corrections

Radiometric corrections applied to imagery included atmospheric correction, sunglint removal and water column correction. Atmospheric correction was applied prior to sunglint removal, followed by water column correction as recommended (Green and Edwards 2000).

2.3.3.2.1 Atmospheric correction

Atmospheric correction was applied to each of the four bands using the Cos(t) method in the atmospheric correction module (ATMOSC) in Idrisi (Chavez 1996). The Cos(t) method was used as the not all parameters required for full atmospheric correction could be determined, such as optical thickness and spectral diffuse sky-irradiance. Optical thickness varies as primarily a function of Rayleigh scattering, aerosols, moisture and ozone content for which there was insufficient data to implement the full atmospheric correction. The Cos(t) model incorporates all of the elements of the Dark Object Subtraction model, plus it estimates the effects of absorption by atmospheric gases and Rayleigh scattering without requiring additional parameters (Chavez 1996). Spectral diffuse sky-irradiance and downwelling spectral irradiance were assumed to be 0.0, while the atmospheric transmittance was estimated as the cosine of the solar zenith angle ($90^\circ - \text{solar elevation}$), as described for the method (Chavez 1996). Areas of deep water under cloud shadows were chosen (visually selected) as training areas for maximum light absorption. The Cos(t) module uses the training areas to estimate the atmospheric haze. The following parameters were applied to the atmospheric correction model (Table 2.2).

Table 2.2. GeoEye satellite image properties used within the Cos(t) atmospheric correction model.

Band	Blue	Green	Red	Near Infra-Red
<i>Date</i>	2011-11-19	2011-11-19	2011-11-19	2011-11-19
<i>Time (GMT)</i>	07.183	07.183	07.183	07.183
<i>Wavelengths (mid of band)</i>	0.480	0.545	0.6725	0.85
<i>Haze (DN)</i>	413	218	108	82
<i>Offset/Gain</i>	y	y	y	y
<i>Offset</i>	0.000	0.000	0.000	0.000
<i>Gain</i>	0.014865	0.017183	0.016194	0.009593
<i>Nominal Collection</i>	26.845	26.845	26.845	26.845
<i>Azimuth</i>				

<i>Sun Angle Elevation</i>	66.49794	66.49794	66.49794	66.49794

2.3.3.2.2 *Sunglint removal*

A regression-based method developed by Hedley et al (2005) was used to remove sunglint from the image bands. Sunglint is a water surface feature that confounds the benthic feature detection as a result of specular reflection of incident radiation (Hedley et al. 2005; Kay et al. 2009). The method regresses a sample of the near infra-red (NIR) band pixels against each of the remaining visible (red, green and blue (RGB)) bands (Hedley et al. 2005):

$$R'_i = R_i - b_i \times (R_{NIR} - Min_{NIR}) \quad (\text{Eqn. 2.1})$$

Low, medium and high reflectance values in the imagery were sampled over deep water (Figure 2.3) to inform the regression equation (Eqn.2.1). Near infra-red (NIR) pixels were assumed to have the 'ambient' NIR value (Min_{NIR}) in the absence of sunglint, which was sampled from deep water areas under cloud shadows where spectral reflection was lowest (yellow polygons on the image in Figure 2.3). Mean reflectance values for the three categories, high, medium and low, are presented in Table 2.3. Sunglint was removed from the imagery by multiplying the slope (b_i) of the regression with the difference between the reflectance of NIR (R_{NIR}) and ambient NIR (Min_{NIR}), and then subtracting it from each pixel's value for the respective bands in turn. Calculations were carried out using the REGRESS module in Idrisi. After sunglint removal, only the corrected three visible spectral bands, Red, Green and Blue (RGB), were used in further image processing.

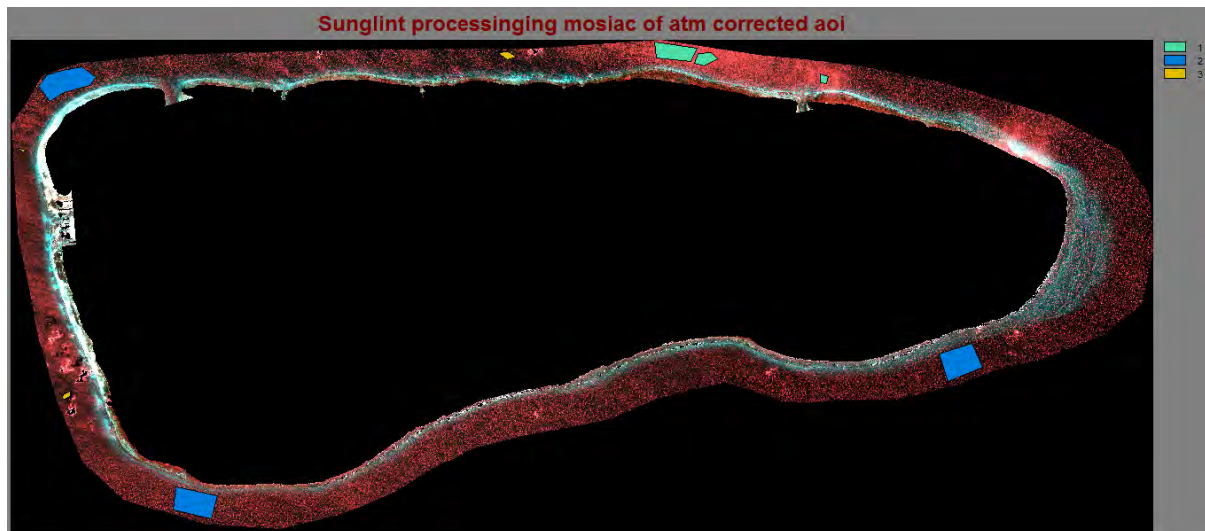


Figure 2.3. The groups pixels from three categories of visually detectable reflectance values (1 = high, 2 = medium, 3 = low) in the near infra-red band (NIR) from atmospherically corrected GeoEye imagery of the area of covering the seaward reefs around Aldabra Atoll.

Table 2.3. The mean reflectance values of blue, green, and red (BGR) and near infrared bands from areas with varying levels of reflectance values from atmospherically corrected GeoEye satellite imagery. The slope of the regression for the respective bands was determined for the difference between near Infra-Red and the spectral band, and ambient near Infra-Red values, at high medium and low reflectance values.

Level of sunglint	Blue	Green	Red
High (1)	0.016	0.04	0.03
Medium (2)	0.014	0.03	0.012
Low (3)	0.008	0.007	0.00171
Slope (b_i)	0.779707	0.949805	0.994230
Ambient NIR	0.006252	0.001893	0.001118

2.3.3.2.3 Water column correction

Water column correction was carried out to remove the effect of the same substrate absorbing and reflecting light at different levels as a result of being at different depths, which occurs as a result of the attenuation of light with depth (Lyzenga in Green and Edwards 2000). Depth soundings were taken at 117 points over homogeneous sand habitat using the sonar fitted to the boats during high tide and standardised to mean sea level.

Image values of all three bands were log-transformed, and then the variance of reflectance values within a single habitat type (sand) calculated. Variance values of the respective bands were used to calculate the attenuation coefficients for band pairs, using the formulae which minimize mean square deviation, as below.

$$a = \frac{\sigma_i - \sigma_j}{2\sigma_{ij}} \quad (\text{Eqn.2.2})$$

$$\frac{k_i}{k_j} = a + \sqrt{a^2 + 1} \quad (\text{Eqn.2.3})$$

Let σ be the variance, and k be the attenuation coefficient, and i and j denote the respective band pairs. The parameter values are provided below (Table 2.4). The result is a set of three images that are depth invariant or put in other words, spectrally corrected for differences in depth, which are carried forward in image analysis.

Table 2.4. Pixel variance of log-transformed band pairs used as parameters for water column correction.

	Blue / green (bands 1 / 2)	Green / red (bands 2 / 3)	Blue / red (bands 1 / 3)
σ	0.044	0.082	0.006
a	-0.332	-0.123	-0.340
$\frac{k_i}{k_j}$	0.722	0.885	0.716

2.3.4 Ground truthing data

The ground truthing data includes the a) sampling approach, b) data processing, and c) linking the field data to the maps.

2.3.4.1 Sampling approach

Field surveys were carried out between November 2012 and January 2013 to obtain ground-truthing data, which were used to train and validate benthic cover maps. Georeferenced video-transects were undertaken to collect benthic cover data that could be coupled with pixels on the satellite imagery once processed. For all field surveys, date, depth, geomorphic zone, including reef platform, forereef slope, lagoon reef, and video id number, site, time, tide and weather were recorded.

The field survey design used two different methods: Boat-based surveys were used for the forereef slope while surveys on foot in the lagoon reef were employed because access was limited for boats in the shallow lagoon due to low tide and waves through passes. While the video data analysis was similar in the two methods, videos were recorded using lighter equipment that was easier to carry in the lagoon than on the boat. The methods are outlined in a flow diagram below (Figure 2.4), showing how the process of ground truthing data collection and data consolidation. The detailed descriptions of the respective data collection methods for the forereef and the lagoon follow thereafter.

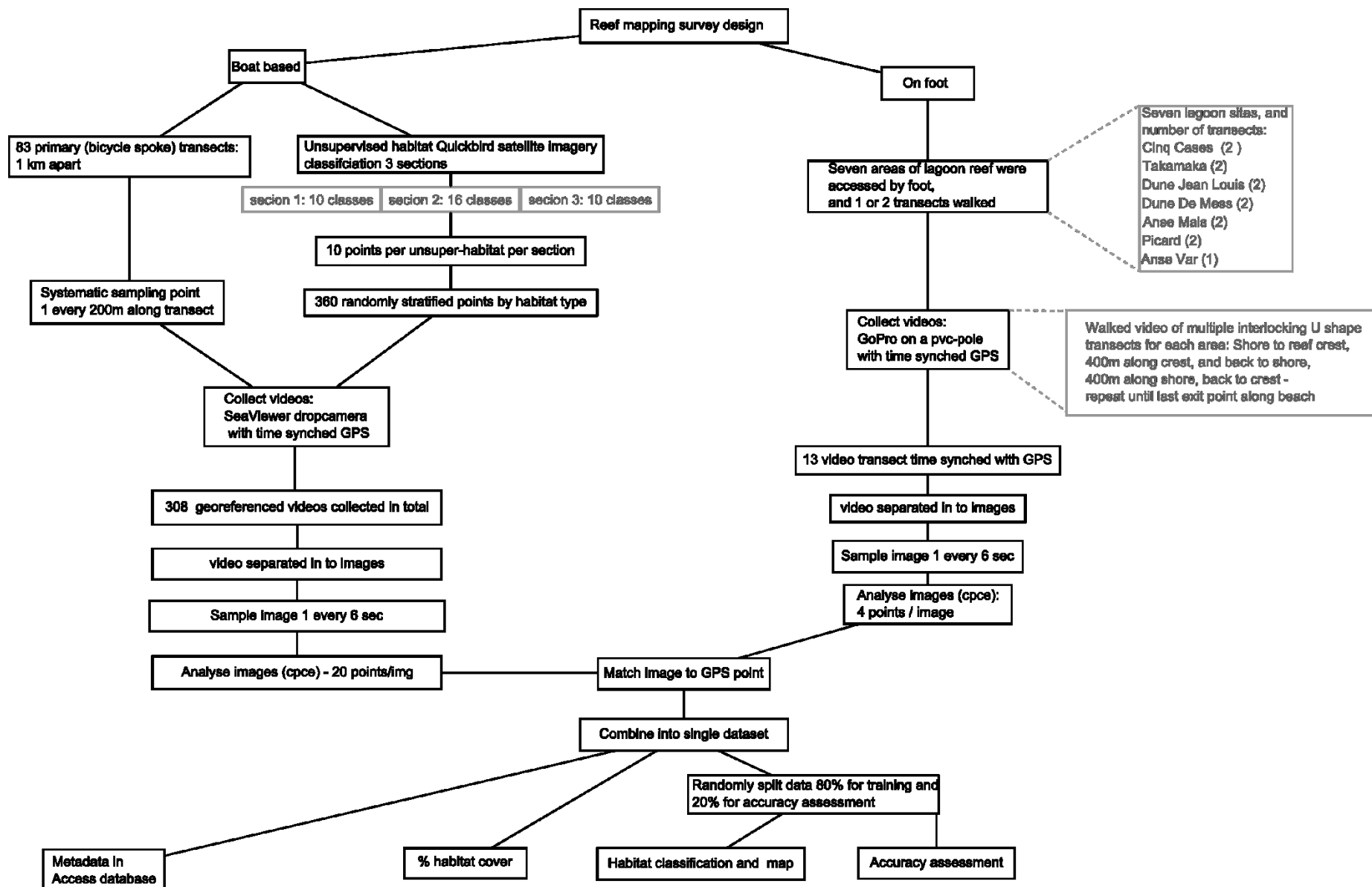


Figure 2.4. Flow diagram showing the steps followed to collect the field survey data used to create the habitat map for the Aldabra forereef and the outer lagoon reef.

2.3.4.1.1 Boat-based surveys

Boat-based surveys were conducted from SIF's boats, Bizou and Dugong, fitted with Garmin GPS 521s and depth finder (Figure 2.5). Boat-based surveys primarily included the forereef slope and reef platform (reef apron) and were surveyed using a SeaViewer DropCam at randomly stratified and systematically stratified sampling localities, described below. All video data were collected between November 2012 and January 2013.



Figure 2.5. SIF vessels, Dugong (left) and Bizou (right) used for marine reef mapping work at Aldabra Atoll 2012 – 2013.

2.3.4.1.1.1 Randomly stratified points within unsupervised habitat classification

Unsupervised classification of archived Quickbird satellite imagery of Aldabra was used to derive a preliminary estimate of the spectrally distinct pixels which were assigned to one of 36 habitat type categories (Table 2.5) and used to inform sampling design. The unsupervised habitat map was then used to select a randomly stratified set of sampling point localities (using Research tools module in QGIS), in which there were ten points per unsupervised habitat type categories. The randomly stratified sampling design yielded 360 points, see Figure 2.7.

2.3.4.1.1.2 Unsupervised classification

As the GeoEye imagery was not available prior to the ground-truthing surveys, Quickbird imagery, consisting of three images from different dates (2003 – 2004), was used to plan the survey. An unsupervised habitat classification routine was applied independently to each of these three satellite images, given that they were taken on different dates and had different atmospheric and reflectance properties. Each image was geometrically inspected, but no correction was required. Radiometric correction included only atmospheric correction, using the same method described for GeoEye imagery earlier. No water column correction was attempted, as no bathymetric data were available prior to the unsupervised classification.

The unsupervised classification used the ISOCLUST module in Idrisi, which is an iterative self-organising classifier similar to the better known ISODATA (Ball and Hall 1965 in Eastman 2009). The method draws on a maximum likelihood classification procedure, signature development for each cluster, and a clustering algorithm where the user defines the sought number of clusters. The number of clusters was varied for each set of images. The westernmost image covering Picard and West Grand Terre, and the easternmost image, covering east Grand Terre were assigned 10 clusters, each, while the central image covering Malabar and South Grand Terre were assigned 16 clusters given that the area in this image almost doubles that covered in the other two images. The resulting classification was visually evaluated based on clusters that appeared to correlate with habitat types of the true colour image. This unsupervised classification was used to assign the randomly stratified ground truthing points described above.

2.3.4.1.1.3 Systematic sampling points on primary transect lines

Aldabra was divided into 83 primary transects lines, which were set at 1 km apart, starting with T01 at the Main Channel, clockwise around the atoll to T83 on northern Picard (Figure 2.6). The primary transect lines were systematically separated by 1 km to ensure that data were collected all around the atoll, and the survey points at different depths perpendicular to the shore. A total of 498 survey sample points was planned for systematic surveys from six survey points positioned every 200 m along the 83 primary transects (Figure 2.7). In total 858 randomly stratified and transect points were planned for the SeaViewer DropCam survey.

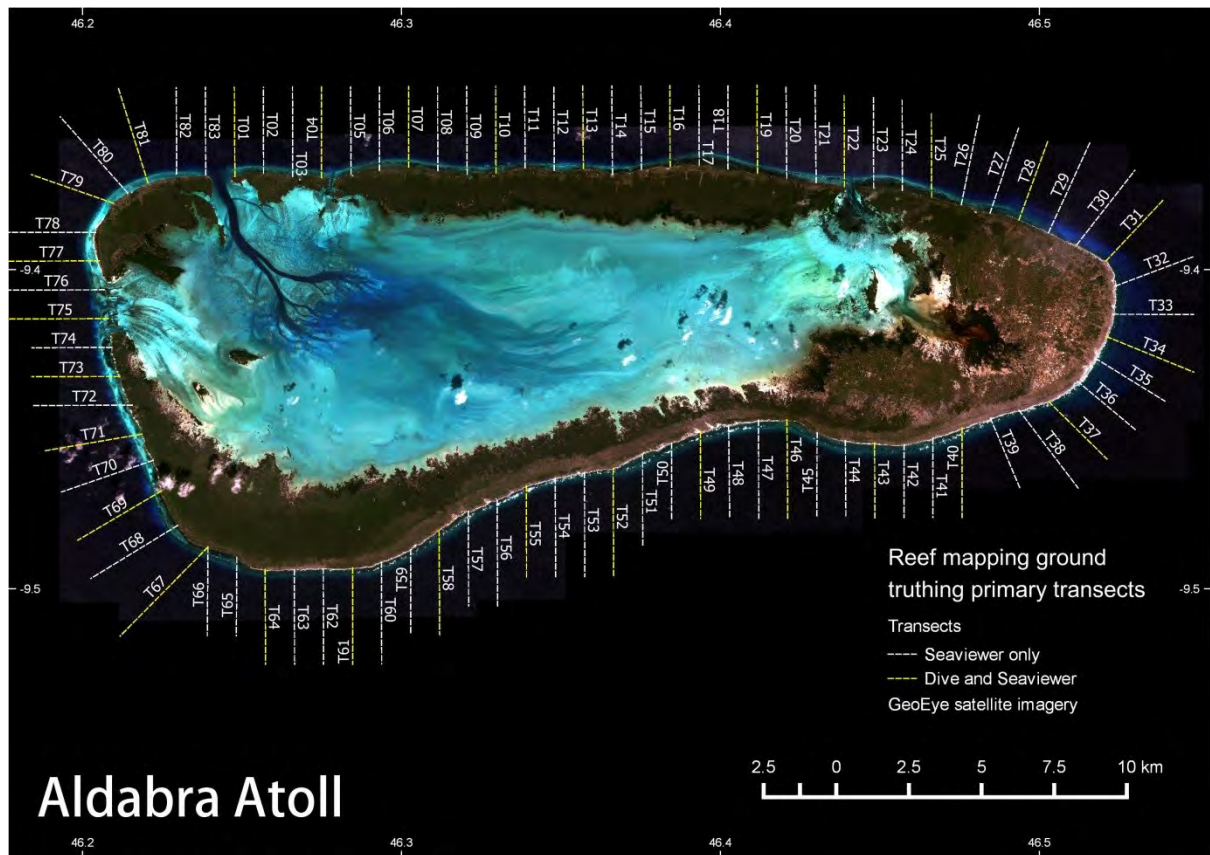


Figure 2.6. The 83 primary (bicycle spoke) transects on Aldabra Atoll used to collect ground truthing data on the forereef slope.

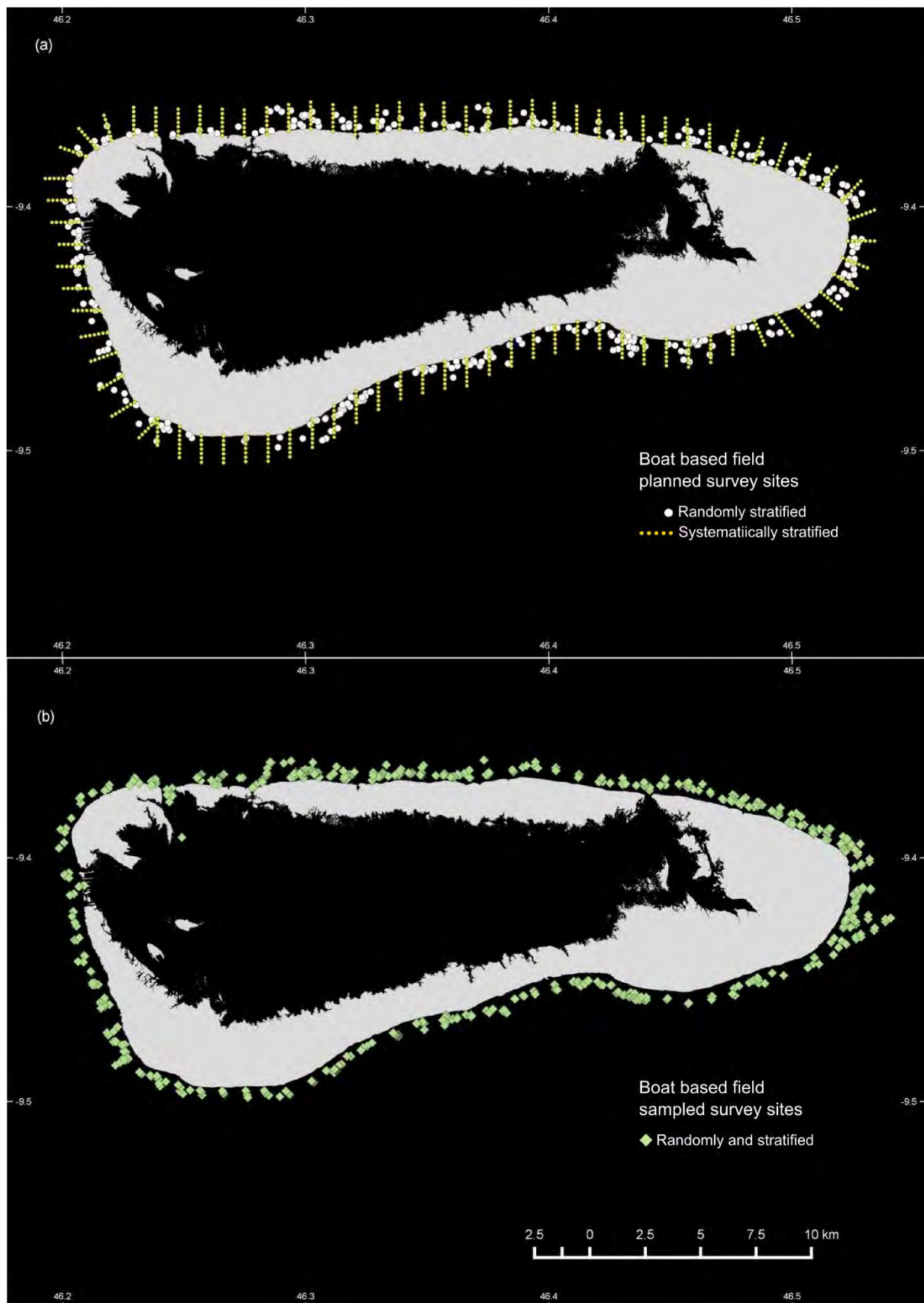


Figure 2.7. The boat-based spatial survey design consisting of (a) planned, 360 randomly stratified and 498 systematically stratified video sampling locality points and (b) the actual sites where video sampling occurred at seaward reefs of Aldabra Atoll between 0 and 60 m.

2.3.4.1.1.4 SeaViewer DropCam equipment and operation

An analogue SeaViewer DropCam 950 with 60 m of electric cable and a light with dimmer switch, running off a 7 AH 12 V battery, was used to record underwater videos of the benthic habitat on the reef at survey sites (Figure 2.8). The SeaViewer DropCam provided a fixed focus live video feed at 800 television lines with a resolution of 976 x 582 at 60 frames per second to a 7-inch LCD screen on the consul unit on the boat. A GPS, connected to the console, overlaid the locality coordinates onto the video which was stored on the memory card (Figure 2.12). An additional safety line (4 mm black braided hand line) was mounted by a cable tie to the camera to secure it in the event it should become snagged on the benthos (Figure 2.8). The camera was weighted with three large chain-links weighing 2.5 kg (attached to the secure line), and a fin attached to ensure directional stability in the water column during recordings. A light was regulated from the onboard consul unit to illuminate the substrate at a depth beyond 15 m.

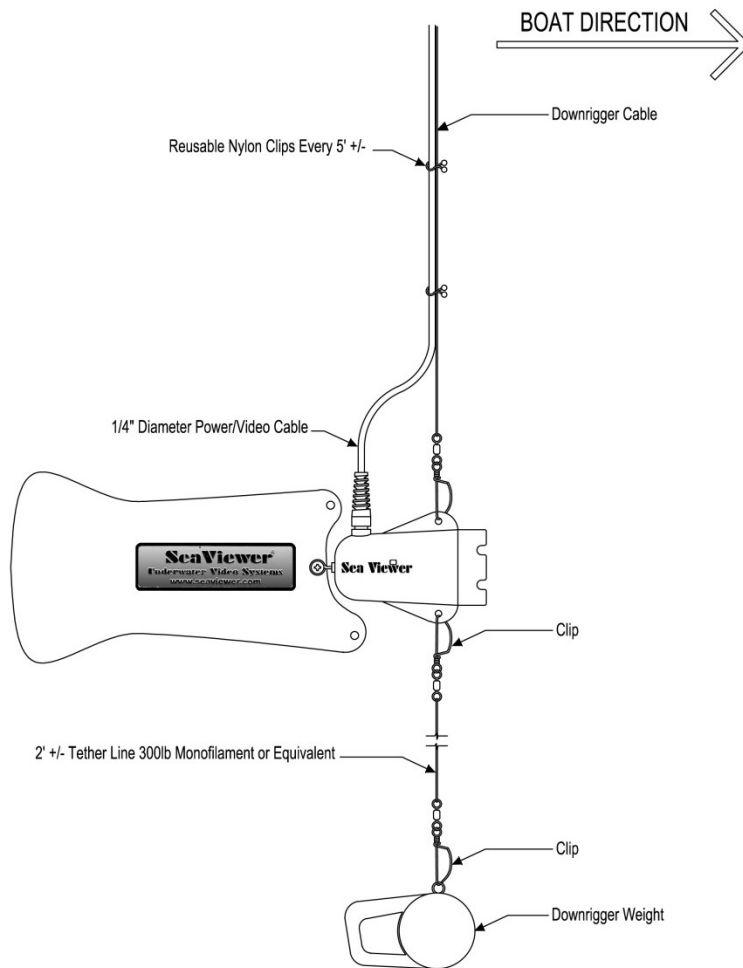


Figure 2.8. Figure from SeaViewer DropCam 950 showing the camera, directional fin, and weight attached to a secure line used to record underwater videos of the forereef at Aldabra (Illustration was taken from SeaViewer manual).

The weighted camera was lowered over the side of the boat at the forereef sampling localities. Each video deployment typically lasted 2 – 3 minutes per sample, during which the boat engine was switched off to avoid the cable being caught in the propellers, therefore each video was recorded while the boat was drifting freely. During each video, waypoints were taken using a handheld Garmin Etrex-h GPS when a change in habitat or geomorphological zone was noticed on screen from the live video feed, and the associated site descriptions and metadata were described onto a data sheet (Figure 2.9).



Figure 2.9. SeaViewer DropCam in action a) the camera with chain links as weight and directional fin, b) the boat-based consul unit with GPS and screen, c) data recording and underwater camera piloting

2.3.4.1.2 Surveys on foot

Surveys of the reef flats were carried out on foot by two teams, each equipped with a time-synced underwater camera and a Trimble Juno 3B GPS. Thirteen video survey transects were walked starting from the campsites around the atoll during daytime low tides. Each team walked a series of continuous interlinked L-shape transects, starting from the shore to the reef crest, and then parallel to the reef crest for 50 paces, and then back to the shore, and then 50 paces parallel to the shoreline. The lengths of each transect were necessarily different, given the varying distance between the shore and the reef crest. The distance walked parallel to the shore or reef crest was limited to 50 paces. The number of L-shaped transects was determined by access to the shore, which had to terminate at a beach with access back to remote satellite camps. The walk was carried out at a steady and consistent speed. The cameras were immersed in the shallow water approximately 10 cm above the substrate and steadily walked as described, thereby recording a relatively narrow strip along each transect.

Three underwater cameras, all GoPro Hero 3 high definition (1280 x 720) in an underwater housing, were set to record video at 11 megapixels at “Medium” field of view resulting in a video with an aspect ratio of (1.78:1) and a frame rate of 25 frames per second. The camera was mounted to a PVC pole, and the time synced GPS set to record a live GPS track taking a reading every second to allow a spatial match between images and position on the satellite imagery.

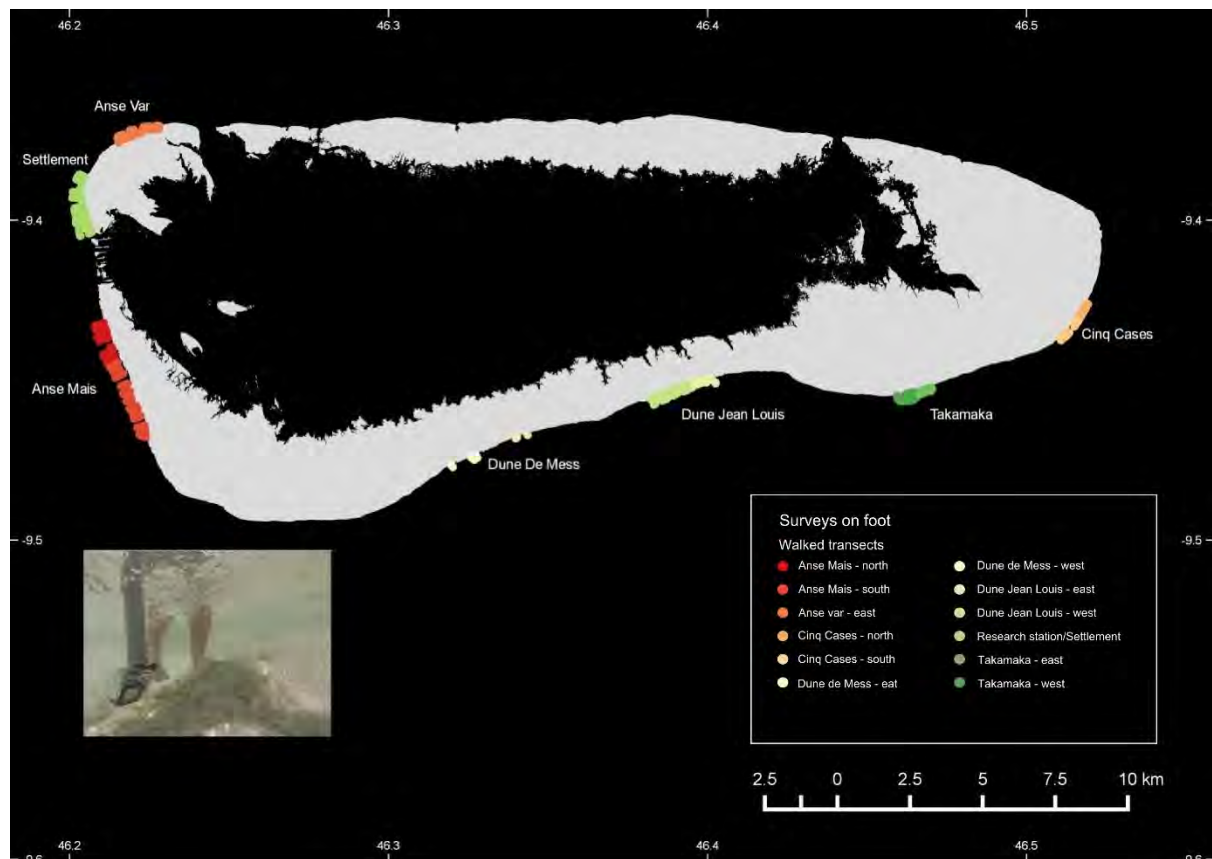


Figure 2.10. Map showing the ground truthing coverage obtained using mounted GoPro cameras and time synced GPSs during surveys on foot in shallow lagoon reef of Aldabra Atoll in a depth of 0 - 2 m. Inset shows an underwater view of the GoPro camera mounted on a PVC pole recording a video of the benthos.

2.3.4.2 Survey data processing

2.3.4.2.1 Spatial data – conversion from GPS points to homogenous polygon sections

Each set of GPS points, associated with a walked video transect, were connected to form GIS shapefile lines that were associated with each video, using the corresponding sampling site ID numbers. Videos and corresponding GIS shapefile lines were split into sections of homogenous habitat using the GPS points recorded during the survey (Figure 2.11) and confirmed by playing back videos and checking GPS points in relation to GPS points overlaid onto videos. Videos for which the GIS shapefile lines were shorter than 20 m were discarded. The GIS shapefile lines collected from a boat using SeaViewer Dropcam were converted to polygons by buffering the video lines with 5 m on either side and 1 m either side for walked surveys (GoPro camera), based on the estimated Field Of View (FOV). The polygons represent the area on the map for which ground truthing data could be matched to the pixel values in the satellite imagery.

2.3.4.2.2 Video to photographic conversion

The video samples were converted to editable AVI video formats using VideoPad (NCH software 2012) and then exported to Multiple JPEGs, maintaining the recorded resolution. The MJPEGs were subsampled at a rate of 6 frames per minute (i.e. every ten seconds) to avoid overlap in images, using free software, VirtualDub (Phaeron 2012). The resulting sets of frames were screened, and poor-quality images were removed from the data set prior to further processing. The 237 boat-based (SeaViewer DropCam) videos resulted in 247 video samples, once videos were split according to homogenous habitat, which were converted into a total of 4464 still frames. The 12 interlinked L-shaped shallow water videos collected on foot were split into 129 homogenous samples and then converted into 3313 images.

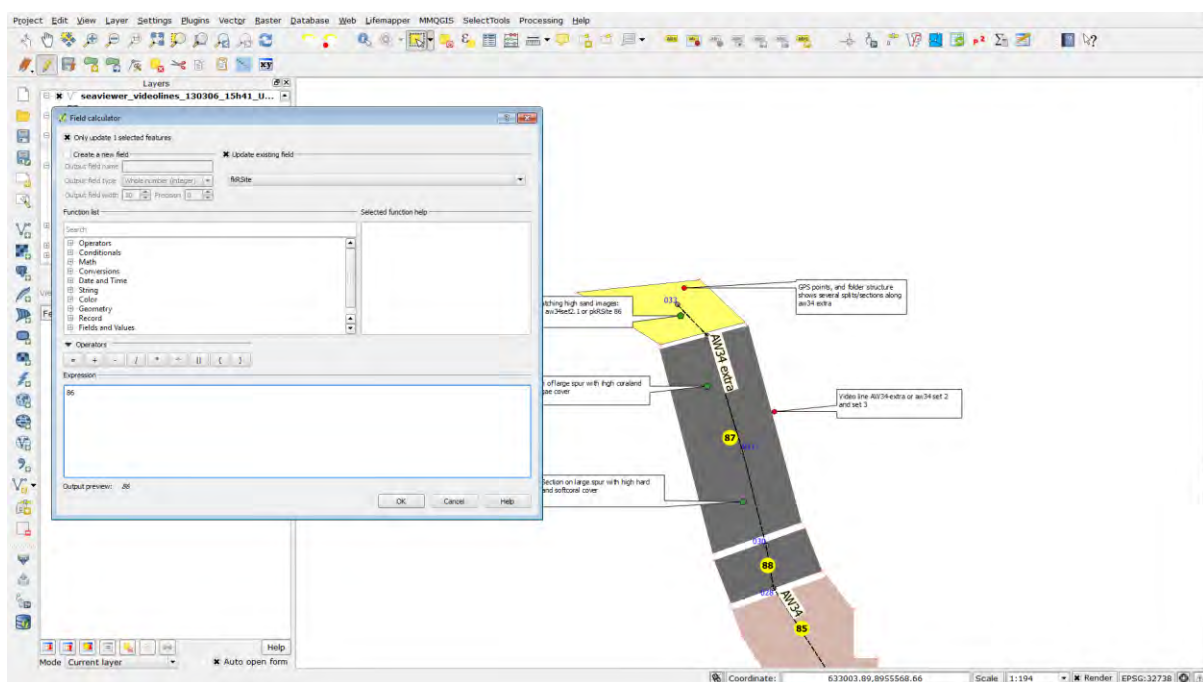


Figure 2.11. A video transect line being split into sections of homogeneous habitat using a GIS using the GPS points recorded during sampling, and a review of the video imagery.

2.3.4.2.3 Photographic analysis using CPCe

The benthic images were analysed per homogenous sample using CPCe (Coral Point Count with Excel Extensions), (Kohler and Gill 2006). At the start of processing each new sample, geomorphic zone, depth, date and time were completed as CPCe header data associated with each photo within a sample. Each photo within a sample was then processed. A border was manually drawn around the area that could be accurately identified for each image. Each image was then divided into 4 equal size rows, and five equal size columns, making 20 equal size blocks covering the entire image. The CPCe software then randomly places a point within each of these blocks, i.e. randomly stratified design (Figure 2.12). The random stratification ensures an even spread of the 20 points across the blocks and a random

position within each block. The number of CPCe points per image was determined using Jaccard self-similarity test described in the statistics section below. The CPCe software facilitates labelling these points using user-defined benthic cover types, e.g. “sand”, “rock”, “coral”, etc. The user-defined benthic habitat types followed a nested design, see Table 2.5, where minor benthic types were grouped within major benthic types. In total 102532 points on the 7777 images were labelled (annotated with minor and major benthic type labels) to provide the data to derive benthic community classifications. The benthic types were labelled at 20 points on each of the 4464 drop-camera still frames and four points on each of the 3313 walked transect images.

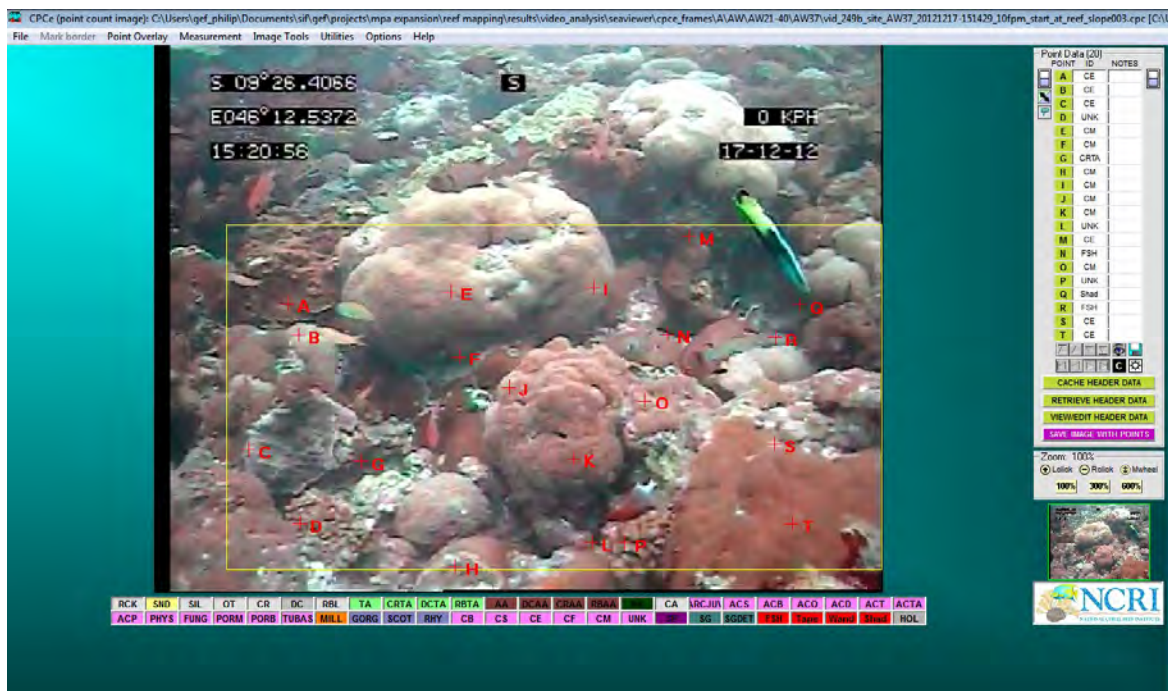


Figure 2.12. The software, Coral Point Counts with Excel Extensions (CPCe), used to quantify benthic photographs into data. Note the time and coordinates in the top left-hand corner.

2.3.4.2.4 Benthic cover types used in CPCe analysis

The benthic cover type refers to a specific benthic species, a group of species or substrate that was used during CPCe analysis to label the points that were overlaid onto each image. Benthic types were limited to a relatively basic level to ensure consistent identification as the resolution of the images obtained by the SeaViewer DropCam 950 was relatively low. In addition to the CPCe labelling, the substrate type was assigned to each point based on the benthic cover type is likely to associate with a specific substrate. All benthic-cover types that could reliably be identified during image analysis were included as “benthic types” (Table 2.5).

Table 2.5. Substrate and benthic habitat types used to label randomly stratified points which were overlaid onto video still frames.

	Substrate	Major benthic type	Minor benthic type
1	Sedimentary	Sand	Sand
2	Limestone	Limestone	Limestone
3	Rubble	Rubble	Rubble
4	Limestone	Coral	<i>Acropora</i> arborescent table
5	Limestone	Coral	<i>Acropora</i> corymbose
6	Limestone	Coral	<i>Acropora</i> digitate
7	Limestone	Coral	<i>Acropora</i> juvenile
8	Limestone	Coral	<i>Isopora palifera</i>
9	Limestone	Coral	<i>Acropora</i> short branching stag
10	Limestone	Coral	<i>Acropora</i> staghorn
11	Limestone	Coral	<i>Acropora</i> tabular
12	Limestone	Coral	Branching hard coral unidentified
13	Limestone	Coral	Encrusting hard coral unidentified
14	Limestone	Coral	Foliose hard coral unidentified
15	Limestone	Coral	<i>Fungia</i>
16	Limestone	Coral	Massive hard coral unidentified
17	Limestone	Coral	<i>Physogyra lichtensteini</i>
18	Limestone	Coral	<i>Porites</i> branching
19	Limestone	Coral	<i>Porites</i> massive
20	Limestone	Coral	Submassive hard coral unidentified
21	Limestone	Coral	<i>Tubastrea</i>
22	Limestone	Coral	Unknown coral
23	Limestone	Fire coral	<i>Millepora</i>
24	Limestone	Soft coral	<i>Gorgonia</i>
25	Limestone	Soft coral	Other soft corals
26	Limestone	Soft coral	<i>Rhytisma</i>
27	Limestone	Dead standing hard coral recent white	Dead standing hard coral recent white
28	Limestone	Fine turf	Fine turf algae
29	Limestone	Fine turf	Fine turf algae on dead rock
30	Limestone	Fine turf	Fine turf algae on dead coral
31	Rubble	Fine turf	Fine turf algae on rubble
32	Limestone	Coralline algae	Coralline algae
33	Limestone	Algal assemblage	Algal assemblage
34	Limestone	Algal assemblage	Algal assemblage on dead coral
35	Limestone	Algal assemblage	Algal assemblage on dead standing
36	Rubble	Algal assemblage	Algal assemblage on rubble
37	Limestone	<i>Halimeda</i>	<i>Halimeda</i>
38	Sedimentary	Seagrass	Seagrass
39	Sedimentary	Detritus	Seagrass detritus
40	Limestone	Sponge	Sponge
41	Limestone	Other zoo	Other zoo
42	Fish	Tape wand shadow	Fish
43	Shad	Tape wand shadow	Shadow
44	Tape	Tape wand shadow	Tape
45	Wand	Tape wand shadow	Wand

The benthic type “Other zoo” included Ascidians, Cyanophytes, Hydrozoans, *Palythoa* sp., *Protopalythoa* sp., and *Zoanthus* sp., which were lumped together because they were present in low abundance and difficult to distinguish from the low-resolution SeaViewer videos. Points overlaid onto the image for which the benthic type was obscured or could not be identified were assigned to one of the tape, wand, shadow or fish. These points were removed prior to analysis. Autocorrelation between images was avoided by leaving a time interval of ten seconds between still frames taken from the survey videos. During the time interval of 10 seconds, it was assumed that the camera drifting with the boat in the current did not capture the same piece of reef in the consecutive still frames.

2.3.4.2.5 The number of points per ground truthing image

Twenty points were labelled according to major and minor benthic cover type to analyse each SeaViewer image, and four points were used for GoPro image analysis. The minimum number of points per image that was required to represent benthic cover per transect were determined using a self-similarity test in which Jaccard similarity was regressed against the number of sampling points per image. Similarity and dissimilarity distances indicate how similar (or different) samples are from one another (Chao et al. 2005). A subsample of 20 consecutive images (frames) from 15 randomly selected videos on the forereef slope from five depth categories, were submitted to the self-similarity test (three per depth category). Thirty points were projected onto each image, and the minor and major benthic cover types labelled in CPCe (see below). Jaccard similarity was calculated for each image from the labelled benthic cover points and compared to 10 permutations of the data labels across the entire video transect. Self-similarity tests started off using 30 points per image and were randomly resampled down to 1 point per image, systematically removing 1 point at a time. Binomial generalised linear models were fitted to the data in the GGLOT2 package (Wickham 2009) showing the decline in Jaccard similarity with a decrease in the number of points labelled per image. Based on initial findings 20 points achieved > 92.5 % accuracy in broad-scale and fine-scale habitat categories (Figure 2.13).

The tests were repeated for GoPro video transects, using a subset of 10 L-shaped video transects taken from the shore to the reef crest, from which 20 consecutive images were labelled with 25 points. Only four points per image were required for photos from GoPro videos of the reef flats to achieve 90 % accuracy for broad-scale and fine-scale benthic categories. Far fewer points were required for GoPro images because the camera was close to the substrate (i.e. a small area was sampled), and the fewer categories of habitat type occurred on the reef flats.

The difference in the number of points projected onto the SeaViewer and GoPro images was a decision based on the greater area sampled by the SeaViewer camera in a potentially more complex environment.

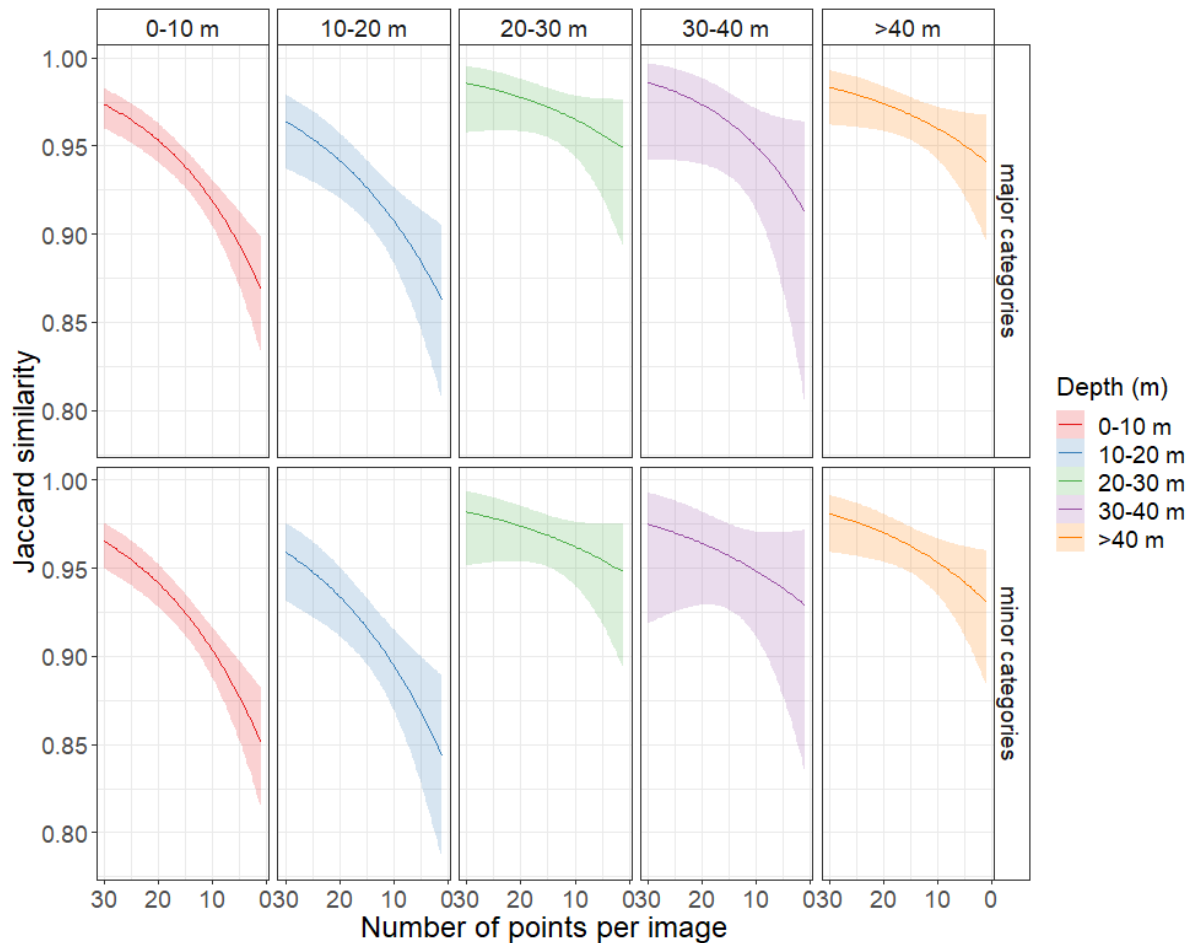


Figure 2.13. Generalised linear models of Jaccard similarity of percentage cover estimated for major and minor benthic types from SeaViewer images, showing the number of CPCe points per image on the X-axis, and Jaccard similarity on the Y-axis.

2.3.4.2.6 Assembling benthic community data matrices

Once all images were analysed (benthic types labelled), the CPCe data from the SeaViewer and GoPro data sets were then consolidated into two independent data frames, one containing the percentage coverage per major benthic type for each site, and the other containing the percentage coverage per minor benthic type for each site.

2.3.4.2.7 Post hoc benthic type aggregation consolidation

A few benthic cover types were not easy to distinguish from each other during CPCe analysis. These benthic cover types were identified and consolidated into new benthic types by adding their percentage cover values to derive a new totals value for the consolidated benthic types to reduce inaccuracy in the data (Table 2.6).

Table 2.6. Ten of the minor benthic cover types (Table 2.5) were consolidated into three types to limit effects of misidentification and inconsistency in labelling.

Consolidated benthic type	Original type - 1	Original type - 2	Original type - 3	Original type - 4
Rubble	rubble	fine turf algae on rubble	algal assemblage on rubble	
Epilithic algal matrix	coralline algae	fine turf algae	fine turf algae on dead rock	fine turf algae on dead coral
Fleshy algal reef	algal assemblage	algal assemblage on dead coral	algal assemblage on dead standing	

2.3.5 Statistical analysis

2.3.5.1 Classification of benthic communities

The two data sets, percentage major and minor benthic cover per site, were treated separately in the analysis described below. The same methods were used on both data sets and therefore it is referred to as only as the benthic cover data when referring to the two respective data sets. All analyses were carried out using a number of packages in R statistical environment, versions 3.1 – 3.4 (R Core Team 2016). Packages and functions used in R are referred to using capital letters in the description below.

The benthic cover data were arcsine transformed to reduce the effect of highly abundant groups throughout the data, as recommended for percentage counts in reef mapping routines (Green and Edwards 2000).

Resemblance matrices (dissimilarity distance) of the transformed benthic cover data were calculated using Bray-Curtis dissimilarity distance (Bray and Curtis 1957) using VEGAN (Oksanen et al. 2016). The resemblance matrix data were submitted to an agglomerative hierarchical cluster analysis. Samples were linked to one another to using the flexible beta method to derive the hierarchical cluster analysis tree using AGNES and CLUSTER packages (Maechler et al. 2016). Flexible beta was used as it provides flexibility in determining tree fusion points (Lance and Williams 1966; Green and Edwards 2000). Parameters for flexible beta were set as follows: Alpha 1 = 0.625, alpha 2 = 0.625, beta = - 0.25, and gamma = 0, giving an intermediate fusion level result as recommended for studying biological cover (Legendre and Legendre 2012).

The classification tree was “cut” into the six and twelve clusters (or categories) for broad-scale and fine-scale benthic categories respectively, using CUTTREE in the STATS package (R Core Team 2016).

The number of clusters used for broad-scale and fine-scale benthic habitat categories was determined using a stepwise process: The classification tree was resampled, and each time the tree was cut into a different number of clusters. Clustering results were then evaluated for 1) number of samples (sites) per cluster, 2) fusion plot of node heights and 3) a silhouette width plot, and 4) unresolved clustering and biological redundancy of clustering, to determine the number of clusters. No trees with fewer than ten members (samples) per cluster (habitat category) were accepted. Fusion plots and silhouette plots indicate the amount of dissimilarity explained by the incremental addition of more clusters to the tree. The plots were visually examined and six to eighteen clusters to examine the number of clusters which explained the greatest amount of dissimilarity per cluster for the two respective data sets.

Clustering results were then evaluated by considering the characteristic benthic cover types that comprised each benthic habitat category to assess redundancy or unresolved biological clustering. Biological redundancy was defined as the point where additional information on the composition of habitat categories supplied by splitting the tree into more clusters became repetitive of information already contained in other clusters.

Six and twelve clusters (benthic categories) were determined as satisfying the criteria for the broad and fine-scale benthic classifications.

2.3.6 Characterising benthic habitats

The six broad-scale and twelve fine-scale benthic habitat categories were characterised using indicator values which quantify the distinctiveness of each benthic habitat category. The indicator values represent the relative contribution of each benthic cover type to the distinctiveness of each category based on its abundance and frequency of occurrence within a benthic habitat category while taking its contribution to the other benthic categories into account. Indicator values were calculated using the INDVAL (indicator value) function in the LABDSV package (Roberts 2016). The benthic types with the greatest INDVAL scores were used in the naming of habitat category, and the mean percentage per broadscale habitat category following the category name. For fine-scale habitat categories in the percentage contribution of each of the hard-coral genera, species or growth form was presented with respect to the total hard coral cover. For example, 'Hard coral (19 %) consisting of massive and submassive forms (11 %), (1 %) *Millepora* and (2 %) *Rhytisma*' means that the category consisted of 19 % hard-coral, of which 11 % was submassive forms, and as second broader category 1 % *Millepora* and 2 % *Rhytisma*. Submassive forms therefore only contributed 2.1 % to the overall habitat category.

Capital letters were used to denote benthic community categories, to distinguish it from the benthic cover types (Table 2.5) used during CPCe labelling to avoid confusion between the two. Major and minor are used to refer to benthic cover types, and broad and fine-scale are used to refer to benthic habitat categories.

In addition to the benthic cover, the geomorphic reef zones were characterised. The seaward reef was divided into four prevalent geomorphic reef zones, including the lagoon reef, the forereef slope, and the reef apron (reef platform), and the topography, aspect and slope qualitatively described.

2.3.7 Image processing

Image processing was carried out at three thematic scales, including the geomorphic reef zone, broad-scale and minor benthic habitat maps were developed in GIS and image processing software as described below.

2.3.7.1 Geomorphological zone map

A map of the geomorphologic zones was manually digitised in QGIS shapefiles following the outlines of the four geomorphic zones, including lagoon reef, shallow forereef slope, deep forereef slope and reef apron, from the atmospherically corrected satellite imagery (described in earlier). Field data, including videos and photos (described earlier) were used to assist the delineation of geomorphic boundaries.

2.3.7.2 Benthic community maps

The ground truthing video polygons (See the section: Survey data processing) were associated with the benthic habitat categories to train statistical models in order to develop spectral signatures for the six broad-scale and twelve fine-scale benthic categories, respectively, which were used to inform supervised maximum likelihood image classification.

2.3.7.2.1 Splitting the data into training and testing sets

A random selection of 80 % of the ground truthing video polygons, stratified according to benthic habitat categories, were used to derive spectral signatures and train the supervised classification. The benthic categories of the remaining 20 % of pixels were used to validate the model.

2.3.7.2.2 Spectral signature development

The training set of video polygons (training polygons) were converted from shapefiles to raster format that matched the scale and extent of the pre-processed imagery. These training rasters were used to develop spectral signatures for each habitat class using the MAKESIG module in Idrisi. The MAKESIG module associates the corrected imagery pixel

values at the training sites and calculates the signature values, namely, minimum, maximum, mean, and variance of each benthic category. The signature files were subsequently used in the maximum likelihood classification.

2.3.7.2.3 *Maximum likelihood classification*

Maximum likelihood was used to classify thematic benthic habitat from the three bands of pre-processed satellite image pixels according to the spectral signatures developed from training data. The maximum likelihood classification was based on the probability density function which was obtained from the spectral signatures of the respective benthic cover categories. The algorithm assigns pixels to the most likely class associated with each pixel, based on a comparison of the posterior probability that it belongs to each of the signatures being considered. It was assumed that there was an equal a priori probability that a pixel belonged to any of the categories, and image processing was carried out using the MAXLIKE routine in Idrisi.

2.3.8 **Accuracy assessment of habitat map**

The validation of the map was done through an accuracy assessment, which measured the agreement between the reef map produced from training data (80 %) against an unused set of 20 % of the data. The producer (error of commission) and the user (error of omission) accuracies were cross-tabulated in an error (confusion) matrix, using the maximum likelihood produced habitat maps. Producer error is therefore when incorrectly assigning a category to a pixel that has another value, while user error is when a category is left out from the pixel being assessed (Green and Edwards 2000). Only pixels that occur within the lagoon reef, forereef slope, and reef platform for which ground truthing training data were collected (i.e. not deep water or masked pixels) were included in the accuracy assessment to avoid inaccurate estimations of accuracy.

The Kappa Index of Agreement (KIA) was calculated as a second measure showing the proportionate reduction in error generated by a classification process compared with the error of a completely random classification (Rosenfield and Fitzpatrick-Lins 1986). Results are presented for the KIA overall accuracy and accuracy per classified category. The KIA has been heavily criticised for confusing location and quantity in the assessment of thematic habitat maps, which may lead to inaccurate results (Pontius and Millones 2011; Olofsson et al. 2014), and therefore a third measure of accuracy was included.

This third measure, the Tau coefficient (T), indicates the percentage of correctly assigned pixels compared to a random assignment of pixels (Green et al. 2004). Tau coefficients (T),

indicate the percentage of correctly assigned pixels compared to a random assignment of pixels (Green et al., 2004), and are therefore more readily interoperable than Kappa statistics. Tau measures excluded pixels values that were incorrectly classified as deep water, to avoid having to include correctly classified deep water which would artificially inflate the Tau value because of a large number of correctly classified deep-water pixels. The error (confusion) matrix (derived above) was fed into a function (Statistical methods for accuracy assessment et al. 2014) to calculate the Tau measure of accuracy.

No accuracy assessment was carried out for the geomorphic reef zone map, as this was digitised by hand.

2.3.9 Habitat patch statistics

The total number of habitat patches (groups of adjacent pixels in the image which were of the same habitat category), and the mean size and standard deviation were calculated using CLASSSTAT in the SDMTools package (VanDerWal et al. 2014). The number of habitat patches and their mean size, and standard deviation is indicative of the spatial spread of benthic habitats (McGarigal and McComb 1995). A large number of patches with a small mean size may be indicative that a particular benthic habitat that only occurs intermittently or indicates that there were high levels of spectral confusion with other habitats resulting in the “salt-and-pepper ” effect during image classification. A high standard deviation is indicative of a habitat that covers a range of patch sizes, and is expected for all benthic habitat categories, given that maximum likelihood image classification operates on a pixel-by-pixel basis (Eastman 2009).

2.4. RESULTS

The results are presented for the three increasingly detailed thematic scales namely geomorphic zones, broad-scale benthic habitat, and fine-scale benthic habitat. The surface area of the reef that was mapped including all four geomorphic zones was approximately 52.9 km². An additional 0.2 km² was under cloud cover, and 0.5 km² was obscured by waves or high reflectance pixels reflecting similar light radiance values to waves. The surface area of classified imagery at broad and fine-scale benthic habitat was very similar, at 51.5 km². The surface area of the geomorphic reef zones was slightly larger because it included the pixels underlying waves and cover where it was known, explaining 0.7 km² of the difference, while the remainder of the difference was a by-product of inaccurate digitising by hand of the outer boundary of the reef platform.

2.4.1 Geomorphic zones

The four geomorphic zones, including the lagoon reef, shallow forereef slope, deep forereef slope, and reef platform encircle Aldabra, and only in the northwest corner was the lagoon reef was absent (Figure 2.17). The surface areas of the seaward lagoon reef and forereef slope were almost identical (approximately 19 km²), and the mapped reef platform included 14.4 km² (Table 2.7). The mapped reef platform including only the area down to approximately 50 m depth and is therefore likely to be an underestimate of its total surface area. The geomorphic reef zones were typically large continues and well-connected habitat, consisting of few habitat patches (Table 2.7). The standard deviation was large relative to the mean patch size a result of many individual pixels which were identified as a single habitat type in contrast to the numerous pixels in large well-connected areas also of a single habitat category.

Table 2.7. The four geomorphic reef zones, number of sampling sites, mapped area, and number of habitat patches at Aldabra Atoll's seaward reefs.

Geomorphic reef zone	Number of sampling polygons (sites)	Mapped surface area (km ²)	Proportional coverage (%)	Number of habitat patches	Mean patch area (km ²)	Standard deviation patch area (km ²)
Lagoon reef	82	19.2	36	28	0.69	2.32
Shallow forereef slope	76	7.8	15	10	0.78	2.01
Deep forereef slope	101	11.6	22	28	0.41	1.24
Platform	65	14.3	27	66	0.22	0.98
Total	324	52.9	100	132		

Note that the number of sampling polygons for which there was geomorphic reef zone data available was more than at the broad or fine-scale, due to lack of sufficiently high-quality video data to analyse at finer scales than the geomorphic reef zone level.

2.4.1.1 The lagoon reef

The seaward lagoon reef at Aldabra is a shallow (1 – 3 m depth) lagoon reef flat, enclosed by land with no backreef. Deep lagoon reef features such as knolls were absent on the outer lagoon reef, and only very small patch reefs of low profile were present in deeper gullies or near to channel mouths. The surface area of the lagoon reef is 19.3 km². The seaward lagoon reef is widest ($\pm$ 400 m) along the leeward west coast, while it is short and not well defined in the windward east coast. The reef crest interfaces the lagoon and forereef slope. Deep surge gullies running perpendicular to the shore connect the lagoon reef to the forereef slope. The reef crest is highly exposed to wave action and very few hard corals (encrusting or low profile) occur here. The interface between the reef crest and the reef flats is dominated by macro and turf algal species, growing on consolidated or medium-sized coral rocks. A seagrass belt, dominated by *Thalassadendron ciliatum*, runs along the west and some parts of the north coast near the breaker line.



Figure 2.14. The shallow seagrass-dominated seaward lagoon reef, with low profile hard-coral and epilithic algal communities, with juvenile grey reef shark at Aldabra Atoll in 0 – 3 m depth.

2.4.1.2 The forereef slope

The Aldabra forereef slope starts between 3 – 5 m depth and extends down to 17 – 45 m, terminating shallowest on the west coast, and deepest along the north coast. The forereef slope was gradual and wide on the east (approximately 500 – 1250 m) and south (approximately 150 – 280 m), and steep and narrow in the west and north of the atoll, approximately 50 – 180 m. In this study, the forereef was classified as shallow forereef slope or deep forereef slope according to the topography: The shallow forereef slope was classified as such at a depth less than 9 m depth, while the deep forereef slope from beyond 9 m.

2.4.1.3 Shallow forereef slope

The forereef front was often inundated with spur and groove formations all along the coast, running perpendicular to the shoreline, which was well defined along the west and north coast. The shallow forereef slope is exposed to wave energy breaking around the Aldabra coastline. The prevailing wave exposure conditions varies around the coast, being greatest in the exposed east coast, and sheltered along the west coast of the atoll, and affects the

benthic cover (See Chapter 3). A sandy terrace at the shelf break separating the reef front and the reef slope was present on some of the reefs of the north coast.



Figure 2.15. The shallow forereef slope (tape at 5 m) on the north coast of Aldabra Atoll's seaward reef.

2.4.1.4 Deep forereef slope

The deep forereef slope has a steep gradient down towards the reef platform and was typically hard substrate comprising hard-coral cover. The forereef slope was shallow along the leeward side of Aldabra's west Grand Terre coast (± 18 m) but extends deeper at Picard (± 30 m) and along the windward south and east coast (30 m). The forereef extended deepest along the north coast (45 m), which was subject to moderate wind and wave exposure increasing from west towards east. The gradient of the forereef slope was steeper in the north and west, where gradients exceed 45° in some parts, than in east and south of Aldabra where gradients are less than 10° over large areas. The width of the forereef slope varies along the atoll and was typically the narrowest in the north of the atoll on Malabar Island near to the Passe Houareau (± 100 m), and along the west coast (± 70 m) while widest in the east of the atoll, offshore from Cinq Cases (1500 m).

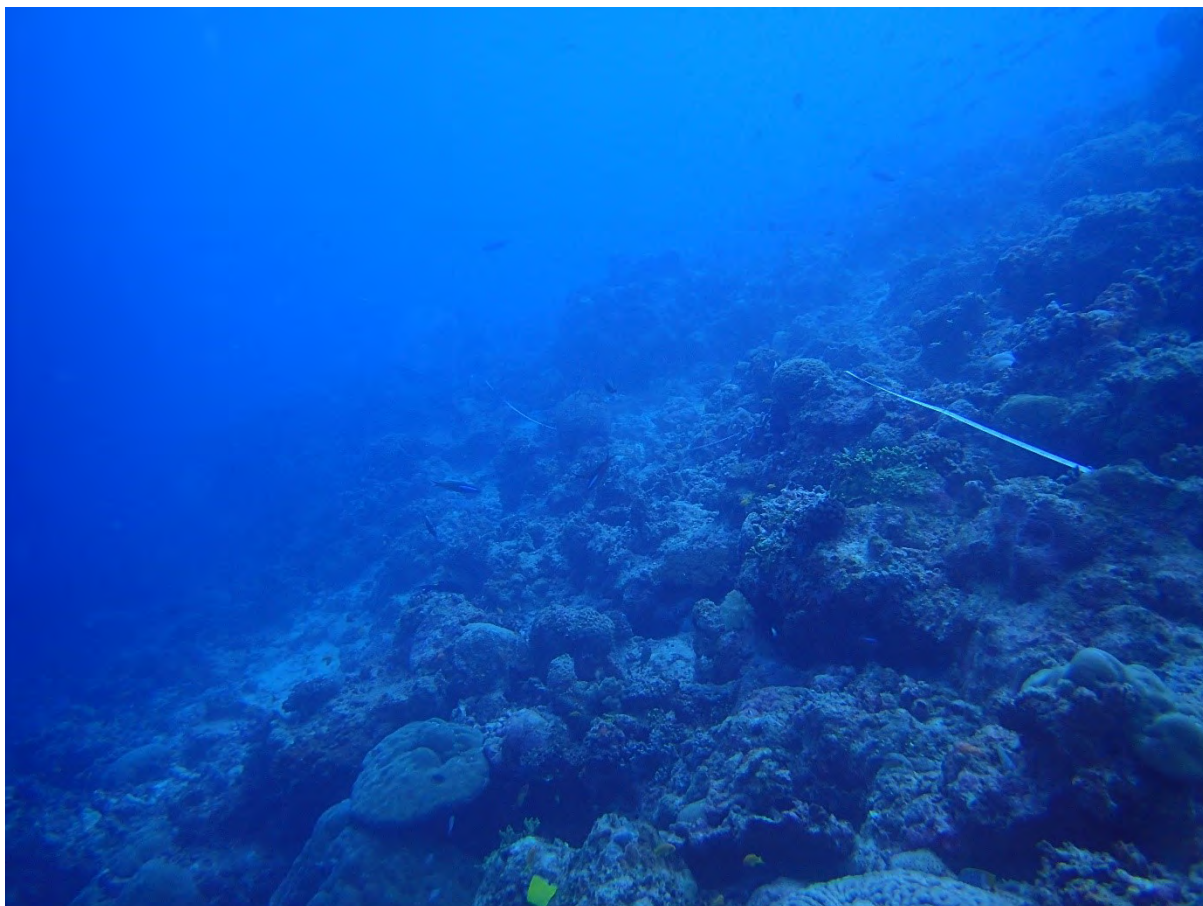


Figure 2.16. The deep forereef slope (tape at 15 m depth) on the northwest coast of Aldabra

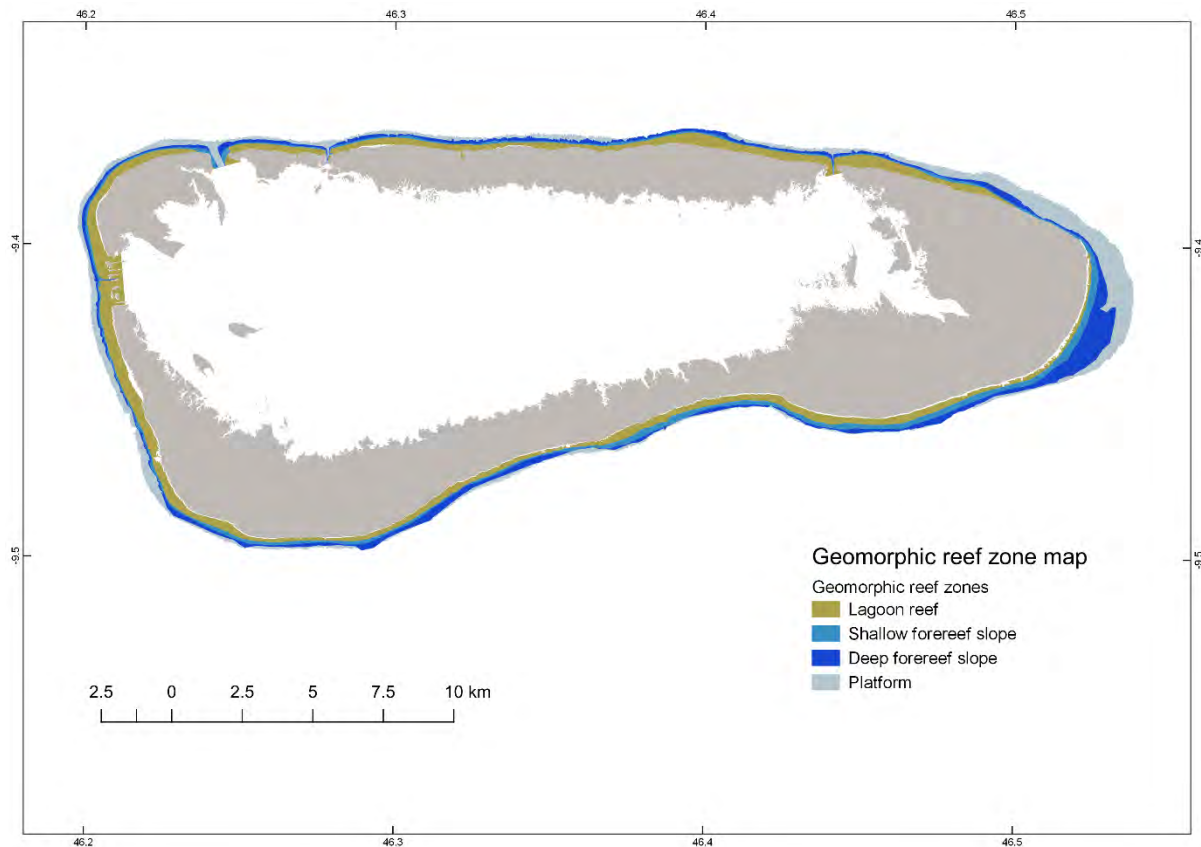


Figure 2.17. Four geomorphic reef zones, including the lagoon reef, the shallow forereef slope, deep forereef slope, and the platform up to 50 m depth around Aldabra Atoll.

2.4.1.5 The reef platform

The reef platform included only the reef apron to approximately 55 m depth, at the limit of the survey depth. The gradient of the non-living platform was gradual from the reef apron becoming steeper towards the drop-off. The total extent of the platform could not be determined from this study, as it extends beyond the depths that satellite imagery can penetrate to, and beyond the depths which the ground truthing survey equipment could operate at.

2.4.2 Broad-scale benthic habitat

Hierarchical cluster analysis resulted in six broad-scale benthic categories to represent the combinations of co-occurring major benthic types on the seaward reefs of Aldabra. The mean composition of the respective six broad-scale benthic habitat categories (percentage benthic cover per benthic type) is shown in (Figure 2.18). Broad-scale benthic category 1 was characterised by a high density of epilithic algal matrix (87 %), which was also abundant (41 %) in category 2, and common in category 3 and 4 (20 % and 24 % respectively) (Figure 2.18). Hard (42 %) and soft coral (10 %) characterised benthic habitat category 2 (See

indicator values for these benthic types Figure 2.19). Rubble (36 %) characterised category 3, Macroalgae (43 %) characterised category 4, Seagrass (70 %) characterised category 5, and category 6 was characterised by high levels of Sand (89 %) (Figure 2.18 and Figure 2.19). The Rubble category was heterogeneous, with a mean hard coral of 18 %.

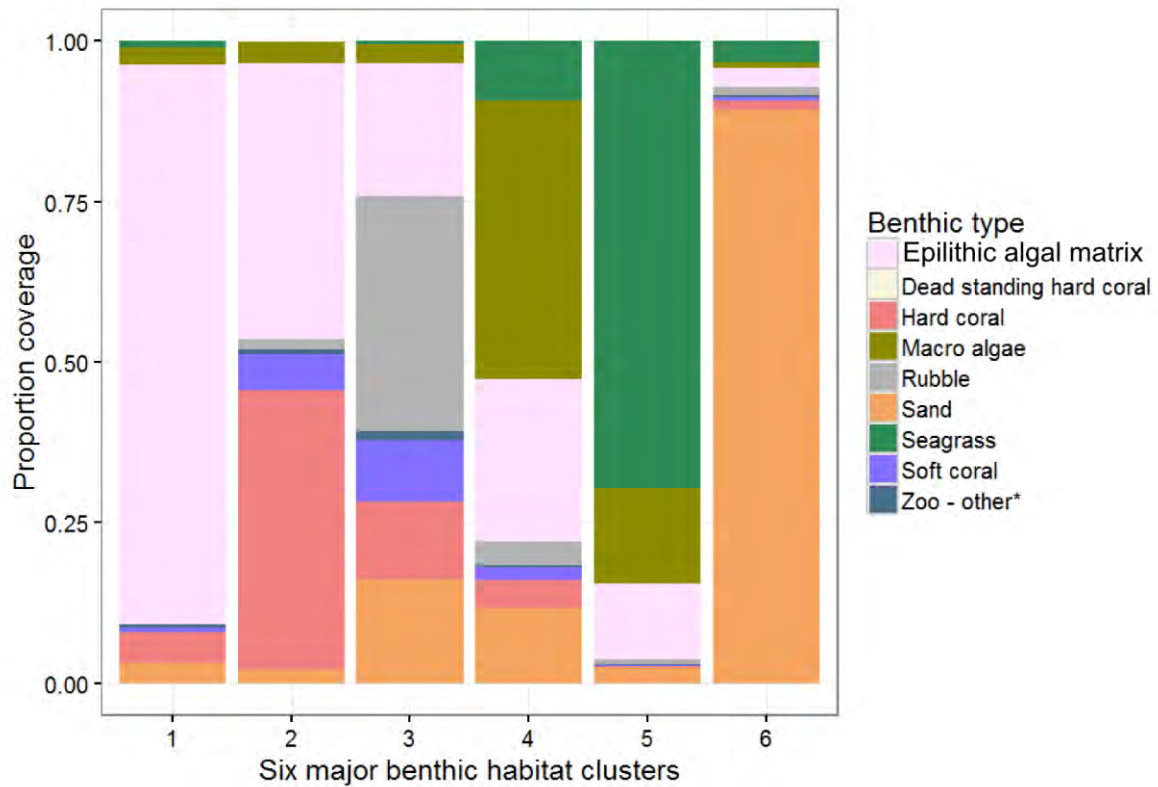


Figure 2.18. The benthic composition of six broad-scale benthic habitat categories, showing the proportion of coverage by major benthic types within each habitat category of the seaward reefs at Aldabra. The following categories, namely, sponge, fire coral, hydrozoan, ascidian, zooanthids, corallimorpharians were grouped together prior to this analysis under 'Zoo - other' for ease of interpretation.

Category names were specified using indicator values (Figure 2.19). Indicator values were consistent with percentage benthic cover type at the broad-scale (Figure 2.18 and Figure 2.19).

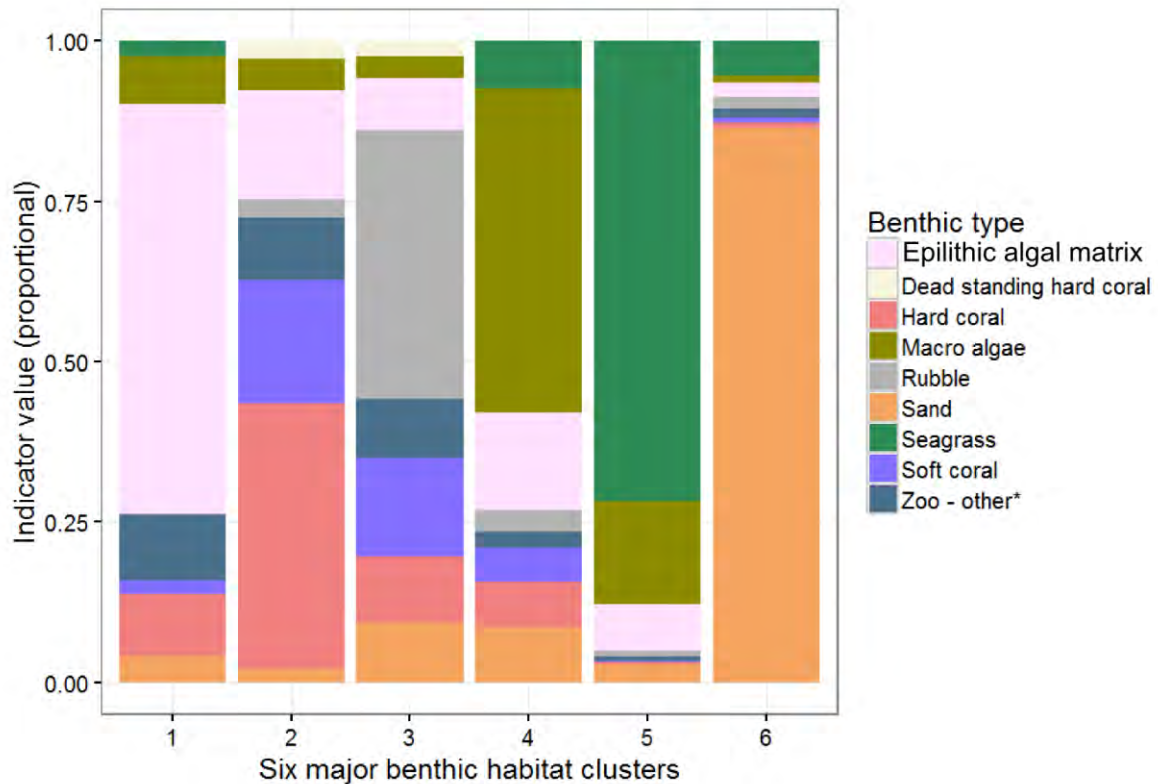


Figure 2.19. The relative contribution of the major benthic types to the distinctiveness of each broad-scale habitat categories of the seaward reefs at Aldabra. The following categories, namely, sponge, fire coral, hydrozoan, ascidian, zooanthids, corallimorpharians were grouped together prior to this analysis under 'Zoo - other' for ease of interpretation.

Every site was assigned to one of the six broad-scale benthic community categories, namely, 1) Epilithic algal matrix (87 %), 2) Hard (43 %) and soft (10 %) coral, 3) Rubble (37 %), 4) Macroalgae (42 %), 5) Seagrass (73 %), and 6) Sand (89 %) (Figure 2.20). The hierarchical cluster plot of the six categories show the samples as terminal branches, coloured per benthic category.

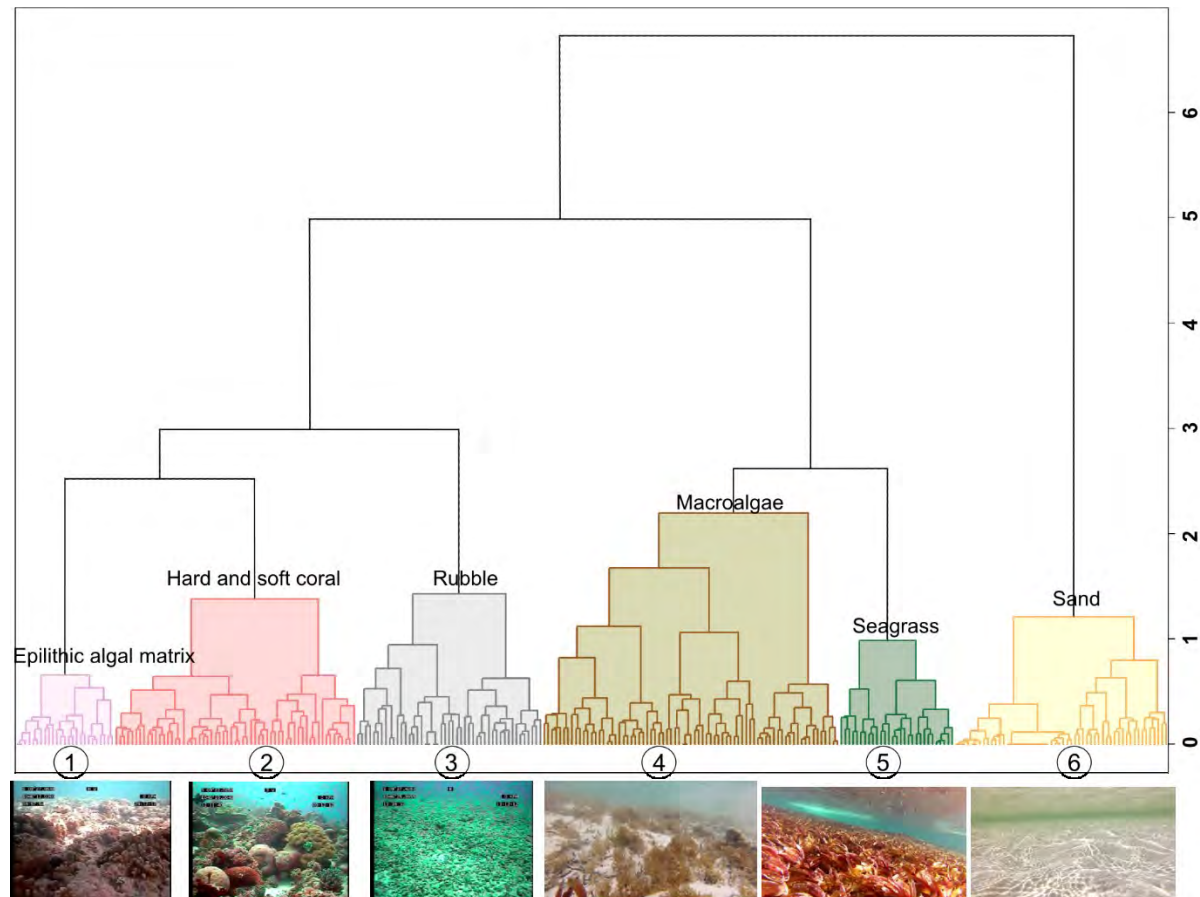


Figure 2.20. Agglomerative nesting of sampling sites based on percentage cover of the major benthic habitat types, which were classified as six broad-scale benthic habitat categories found at Aldabra in 0 to 55 m depth. From left to right, (1) Epilithic algal matrix (87 %), (2) Hard (42 %) and soft (10 %) coral, (3) Rubble (37 %), (4) Macroalgae (42 %), (5) Seagrass (73 %), and (6) Sand (89 %). The coefficient of determination is 0.98 and the height of the tree is 5.3.

All six clusters were represented by 25 or more sampling sites (Table 2.8). Rubble (heterogeneous high rubble content) and Seagrass categories covered the greatest surface area (14.6 km²), followed Hard and soft coral (8.8 km²) categories (Table 2.8). Macroalgae covered the smallest surface area of the broad-scale benthic habitat categories (< 1 km²). Seagrass had the fewest habitat patches, and the greatest mean patch size, indicating that seagrass occurred as a few large well-connected patches. The small number of patches and small mean patch size of Macroalgae shows that this habitat was uncommon and covered only small areas where it did occur.

Table 2.8. The benthic composition of six broad-scale categories, number of sampling sites, mapped surface, proportional coverage and habitat patch statistics for each benthic category at Aldabra in 0 to 55 m depth.

Broad-scale benthic category name	Number of sampling polygons (sites)	Mapped surface area (km ²)	Proportional coverage (%)	Number of habitat patches	Mean patch area (m ²)	Standard deviation patch area (m ²)
Epilithic algal matrix (87 %)	25	5.4	10	63757	339	30966
Hard coral (42 %) and soft coral (10%)	61	8.8	17	8469	4179	169685
Rubble (37 %)	47	14.6	28	28469	2051	231987
Macroalgae (42 %)	75	0.9	2	59441	66	1515
Seagrass (73 %)	29	14.6	28	3136	18568	442309
Sand (89 %)	54	7.2	14	65779	435	66081
Total	291	51.5	100	229051		

The broad-scale benthic habitat map of the six thematic benthic categories is shown below in Figure 2.21. The Rubble category circumscribed the atoll, and together with the Sand category indicates the position of the reef apron on the reef platform. The reef apron was sandier in the west and near absent along the south coast (Figure 2.21). Seagrass was abundant on the reef flats on all sides of the Aldabra coast, but it was replaced by the Epilithic algal matrix and Sand on the north-west corner of Picard Island (Figure 2.21). There is less seagrass on the exposed east coast which corresponds and is consistent with the lack of a well-defined reef crest and reef flats indicated by the geomorphic reef zone map (Figure 2.17 and Figure 2.21). Sand was only common on the reef flats in the lee of Aldabra. Hard and soft coral category dominated the forereef slope all around the coast except on the exposed east coast, where the Hard and soft coral becomes replaced by the Rubble category on the deep forereef slope. The mapped Macroalgae category is visible on the northeastern corner of Aldabra, close inshore, and only a few isolated pixels occurred elsewhere on the lagoon reef.

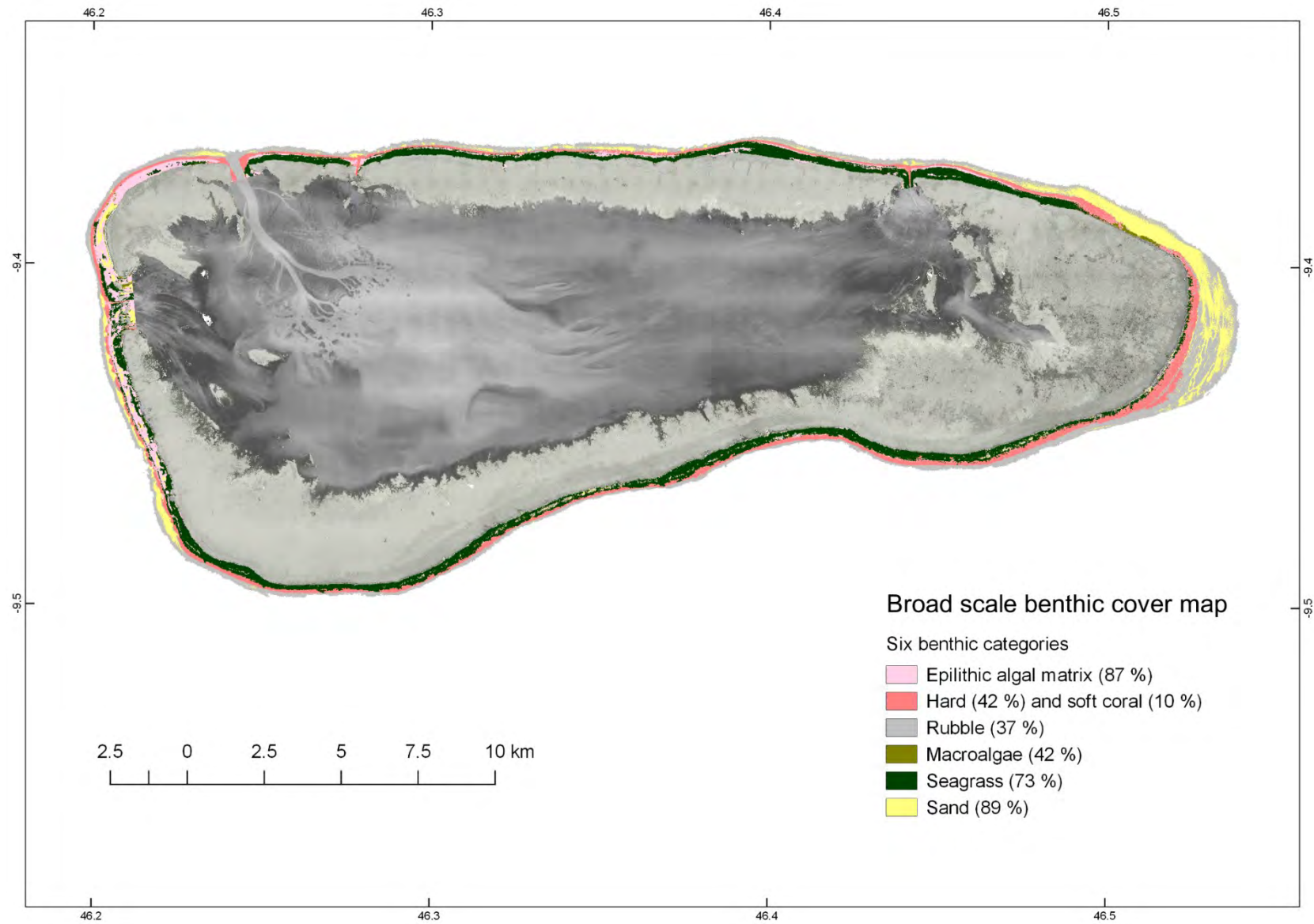


Figure 2.21. Broad-scale benthic habitat consisting of six categories, showing the percentage of the characteristic benthic type for each broad-scale category at Aldabra Atoll between 0 and 50 m depth.

2.4.3 Accuracy assessment of broad-scale benthic habitat map

The accuracy assessment measured the agreement between the reef map produced from 80 % of the data against an unused 20 % of the data in the error matrix. The overall accuracy of the broad-scale benthic habitat map was low (54 %), with an error of $46 \% \pm 0.02$ at the 95 % Confidence Interval (CI_{95}). Sand had the highest classification accuracy, with the lowest user and producer error (15 % and 45 %) (Table 2.9). Seagrass had a relatively low user and producer error (48 % and 50 %). Misclassification of Seagrass arose from incorrectly classifying Seagrass pixels as Macroalgae (error of omission) and classifying pixels as Seagrass which should have been Hard coral or Epilithic Algal matrix (error of commission) (Table 2.9). The prevalence of Macroalgae was significantly underestimated, with an error of omission (producer error) of 97 % (Table 2.9). The error matrix shows Macroalgae was misclassified as Epilithic algal matrix, Hard coral and Seagrass (Table 2.9). High producer error was reported for Sand, which was incorrectly classified as Rubble. Hard coral cover pixels were misclassified as Rubble (Table 2.9).

Table 2.9. Accuracy assessment of six clusters from the broad-scale benthic community at Aldabra Atoll's seaward reefs. Ground truthing values read down the column, and mapped values read across the rows. (Errors of omission and commission expressed as a percentage, and diagonal (grey) elements represent correctly classified pixels)

	Epilithic algal matrix (87 %)	Hard coral (42 %) and soft coral (10%)	Rubble (37 %)	Macroalgae (42 %)	Seagrass (73 %)	Sand (89 %)	Total	Error commission (User error)
Epilithic algal matrix (87 %)	260	10	1	287	139	51	748	65 %
Hard coral (42 %) and soft coral (10%)	199	435	198	320	134	0	1286	66 %
Rubble (37 %)	0	566	776	93	0	537	1972	61 %
Macroalgae (42 %)	0	1	0	28	2	47	78	64 %
Seagrass (73 %)	23	40	0	208	299	28	598	50 %
Sand (89 %)	46	14	74	9	2	801	946	15 %
Total	528	1066	1049	945	576	1464	5628	
Error omission (Producer error)	51 %	59 %	26 %	97 %	48 %	45 %		46 %

The Kappa Index of Agreement (KIA) confirmed the results from the error matrix, and reported low overall KIA value of 0.44, and the lowest KIA values were reported for Macroalgae, while Seagrass and Sand had high KIA values (Table 2.10).

Table 2.10. Kappa Index of Agreement (KIA) per broad-scale benthic habitat category comparing the classified image to the accuracy assessment image.

Category	Classified image	Accuracy assessment image
Epilithic algal matrix (87 %)	0.35	0.49
Hard coral (42 %) and soft coral (10%)	0.34	0.41
Rubble (37 %)	0.39	0.67
Macroalgae (42 %)	0.36	0.03
Seagrass (73 %)	0.5	0.52
Sand (89 %)	0.85	0.54

The relatively low Tau coefficient (T) was 0.35 ± 0.015 overall at the 95 % confidence interval (CI_{95}), confirmed the overall accuracy assessment results from the error matrix for the broad-scale benthic habitat map.

2.4.4 Fine-scale benthic habitat

Twelve fine-scale benthic habitat categories were classified from the ground truthing data which represented the typical minor benthic cover types on the seaward reefs (Figure 2.22). The classification included three coral, two seagrass, two sand, two macroalgal, one epilithic algal matrix, one rubble, and two heterogeneous sand, seagrass and macroalgae dominated categories (Figure 2.22). The indicator values of the characteristic minor benthic cover types which were used to characterise and name the benthic cover categories are shown in Table 2.11 for minor benthic types that contributed significantly to the distinctiveness of each category. For example, category three was characterised by high indicator values for soft coral, namely, *Gorgonia*, *Rhytisma* and other soft coral, as well as two species of hard coral *Physogyra lichtensteini* and *Isopora palifera*. The remaining coral-dominated categories were characterised by high indicator values for either branching growth form coral, or massive corals (Table 2.11). Percentage cover of the indicator benthic types that were used to name the respective fine-scale benthic habitat categories is shown in Figure 2.22. The mean hard coral cover was highest in the fine-scale benthic habitat category 3, namely 'Soft coral (10 %), sponge (2 %), hard coral (44 %) including *Physogyra lichtensteini* (5 %), *Isopora palifera* (5 %)'.

Table 2.11. The benthic habitat composition of fine-scale benthic habitat categories (1-12) at Aldabra's seaward reefs, showing percent minor benthic types per category. (Less than 0.01 only shown as “..” for ease of reading). See footnotes for category names.

Minor benthic type	1	2	3	4	5	6	7	8	9	10	11	12
Sand	0.6	1.5	14	15.2	1.7	5.2	39	3.3	4.5	5.8	98.9	75
<i>Acropora</i> corymbose	0.1	2.7	0.3	..	..	..	..	0.2	..	..	..	..
<i>Acropora</i> digitate	..	0.1	0.3	..	..	..	..	0.2	..	..	..	..
<i>Acropora</i> juvenile	..	..	..	..	..	..	..	..	..	..	..	..
<i>Isopora palifera</i>	0.3	..	5.2	..	..	..	..	..	..	..	..	..
<i>Acropora</i> short branching staghorn	0.4	3.7	0.2	..	..	..	..	0.1	..	..	..	..
<i>Acropora</i> staghorn	..	0.1	..	..	..	..	..	..	..	..	..	..
<i>Acropora</i> tabular	..	..	..	..	..	..	..	..	..	..	..	..
Branching hard coral unidentified	1.4	4.9	1.7	..	0.1	..	..	0.5	..	..	..	0.1
Encrusting hard coral unidentified	5.8	8.7	5.4	0.8	0.2	0.1	0.7	2	0.1	..	..	0.4
Foliose hard coral unidentified	..	0.1	0.1	..	..	..	..	..	..	..	..	..
<i>Fungia</i>	..	..	..	..	..	..	..	..	..	..	..	..
Massive hard coral unidentified	4.6	8	10.7	0.9	0.6	0.2	0.1	2.6	0.1	..	..	0.6
<i>Physogyra lichtensteini</i>	..	..	4.6	..	..	..	..	..	..	..	..	0.5
<i>Porites</i> branching	0.9	0.4	0.3	..	..	..	..	..	..	..	..	..
<i>Porites</i> massive	4.2	2.9	1.3	0.6	0.8	0.1	..	0.1	0.1	..	..	0.1
Submassive hard coral unidentified	1.6	3.2	0.7	0.7	0.1	..	0.1	0.2	..	..	..	0.1
<i>Tubastrea</i>	..	..	..	..	..	..	..	..	..	..	..	..
Unknown hard coral	1.3	5.6	5.6	2.1	0.7	0.1	..	1.5	..	..	..	1.2
<i>Millepora</i>	0.7	0.1	0.4	..	0.2	..	..	0.1	..	..	..	0.2
<i>Gorgonia</i>	..	0.1	0.8	0.7	..	..	0.2	..	..	..	..	3.3
Other soft corals	3.9	5.5	8	1	1.3	0.1	..	6.9	0.1	..	..	0.7
<i>Rhytisma</i>	1.7	0.6	1.6	0.1	..	..	..	0.1	..	..	..	..
Dead standing hard coral recent white	..	0.1	0.1	..	..	..	..	..	..	..	..	..
Seagrass	..	..	1.4	..	3.5	19.8	4.8	..	0.6	73.1	..	4.9
Sponge	0.4	0.3	2.4	0.1	..	0.2	0.9	0.6	0.5	..	..	0.7
Other zoo	0.1	..	0.7	..	..	0.1	..	..	..	..	..	..
<i>Halimeda</i>	1.1	1.1	..	1.1	1.3	4.6	2.8	41.9	0.7	1.4	..	0.3
Rubble	1.8	1.8	12.3	53.9	4.5	4.4	..	0.8	0.2	0.7	..	2.2
Epilithic algal matrix	67.2	38.3	18.7	20	12.3	42.7	24.9	19.2	88.6	9.1	..	6.7
Detritus	..	..	0.3	..	0.1	1.6	1.6	..	0.9	1.3	1	0.2
Fleshy macro algae	1.7	5.4	1.5	2.7	70.1	20.8	20.5	16.6	3.4	8.4	0.1	1.5

Reef fish associations with benthic habitats

1) Hard coral (19 %) including massive and submassive forms (11 %), (1 %) *Millepora* and (2 %) *Rhytisma*, **2)** Hard coral (36 %), including (5 %) branching, (8.7 %) encrusting, and (2.7 %) corymbose and (3.7 %) short staghorn *Acropora*, **3)** Soft coral (10 %), and sponge (2 %), Hard coral (44 %), including *Physogyra lichtensteini* (5 %) and *Isopora palifera* (5 %), **4)** Rubble (58 %), sand (15 %), and (18 %) hard coral, **5)** Fleshy macroalgae (70 %), **6)** Heterogeneous seagrass (20 %), sand (5 %), epilithic algal matrix (43 %), and macroalgae (21 %), **7)** Heterogeneous sand (40 %), macroalgae (21 %), and epilithic algal matrix (24 %), **8)** *Halimeda* macroalgae (41 %) and soft coral, **9)** Epilithic algal matrix (88 %), **10)** High-density seagrass (73 %), **11)** Sand (98 %), **2)** High-density seagrass (73 %), **12)** Sand (78 %), epilithic algal matrix (7 %) and Gorgonian fans (3 %).

Table 2.12. Indicator values for benthic types within the 12 clusters at Aldabra's seaward reefs. (Less than 0.01 only shown as “..” for ease of reading). See footnotes for category names.

Benthic type	1	2	3	4	5	6	7	8	9	10	11	12
Sand	.	..	0.07	0.06	..	0.02	0.14	0.03	0.02	0.02	0.31	0.22
<i>Acropora</i> corymbose	..	0.09	0.03	.	.	.	.	0.04	.	.	.	.
<i>Acropora</i> digitate	..	0.03	0.05	.	.	.	.	0.07	.	.	.	.
<i>Acropora</i> juvenile	.	.	0.04	.	.	.	.	.	.	.	.	.
<i>Isopora palifera</i>	0.06	.	0.29	.	.	.	.	.	.	.	.	.
<i>Acropora</i> short branching staghorn	0.08	0.17	0.03	.	.	.	.	0.05	.	.	.	.
<i>Acropora</i> staghorn	.	0.02	..	.	.	.	.	.	.	.	..	.
<i>Acropora</i> tabular	.	0.03	0.02	.	.	.	.	.	.	.	.	.
Branching hard coral unidentified	0.18	0.33	0.16	.	.	.	.	0.02	.	.	.	.
Encrusting hard coral unidentified	0.24	0.24	0.15	0.02	..	.	..	0.07	.	.	.	..
Foliose hard coral unidentified	.	..	0.10	.	.	.	.	.	.	.	.	.
<i>Fungia</i>	.	..	0.02	.	.	.	.	.	.	.	.	.
Massive hard coral unidentified	0.19	0.21	0.28	0.02	..	..	.	0.07	.	.	.	..
<i>Physogyra lichtensteini</i>	.	.	0.41	.	.	.	.	.	.	.	.	..
<i>Porites</i> branching	0.22	0.02	0.08	.	.	.	.	.	.	.	.	.
<i>Porites</i> massive	0.22	0.12	0.06	0.03	0.04	.	.	.	.	.	.	.
Submassive hard coral unidentified	0.28	0.18	0.05	.	..	.	.	..	.	.	.	.
<i>Tubastrea</i>	.	.	.	.	.	.	.	.	.	.	.	0.06
Unknown hard coral	0.10	0.22	0.21	0.04	0.03	.	.	0.05	.	.	.	0.02
<i>Millepora</i>	0.24	.	0.04	.	0.02	.	.	..	.	.	.	..
<i>Gorgonia</i>	.	.	0.04	0.02	.	.	..	.	.	.	.	0.11
Other soft corals	0.12	0.12	0.17	0.02	0.04	.	.	0.15	.	.	.	..
<i>Rhytisma</i>	0.17	0.02	0.11	..	.	.	.	..	.	.	.	.
Dead standing hard coral recent white	.	..	0.11	.	.	.	.	.	.	.	.	.
Seagrass	.	.	.	.	..	0.19	0.05	.	..	0.55	.	0.02

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Sponge	0.05	0.02	0.26	..	.	.	0.08	0.03	0.03	.	.	0.03
Other zoo	..	.	0.14	.	.	.	.	.	.	.	.	.
<i>Halimeda</i>	0.02	..	.	..	0.02	0.06	0.06	0.53	..	0.02	.	.
Rubble	0.02	..	0.16	0.49	0.02	0.03	.	.	.	..	.	0.02
Epilithic algal matrix	0.16	0.11	0.07	0.07	0.05	0.12	0.08	0.06	0.20	0.03	.	0.03
Detritus	.	.	..	.	.	0.11	0.08	.	0.04	0.07	0.08	..
Fleshy macro algae	0.02	0.03	0.02	..	0.33	0.14	0.15	0.10	0.02	0.05	.	..

1) Hard coral (19 %) including massive and submassive forms (11 %), (1 %) *Millepora* and (2 %) *Rhytisma*, **2)** Hard coral (36 %), including (5 %) branching, (8.7 %) encrusting, and (2.7 %) corymbose and (3.7 %) short staghorn *Acropora*, **3)** Soft coral (10 %), and sponge (2 %), Hard coral (44 %), including *Physogyra lichtensteini* (5 %) and *Isopora palifera* (5 %), **4)** Rubble (58 %), sand (15 %), and (18 %) hard coral., **5)** Fleshy macroalgae (70 %), **6)** Heterogeneous seagrass (20 %), sand (5 %), epilithic algal matrix (43 %), and macroalgae (21 %), **7)** Heterogeneous sand (40 %), macroalgae (21 %), and epilithic algal matrix (24 %), **8)** *Halimeda* macroalgae (41 %) and soft coral, **9)** Epilithic algal matrix (88 %), **10)** High-density seagrass (73 %), **11)** Sand (98 %), **2)** High-density seagrass (73 %), **12)** Sand (78 %), epilithic algal matrix (7 %) and Gorgonian fans (3 %).

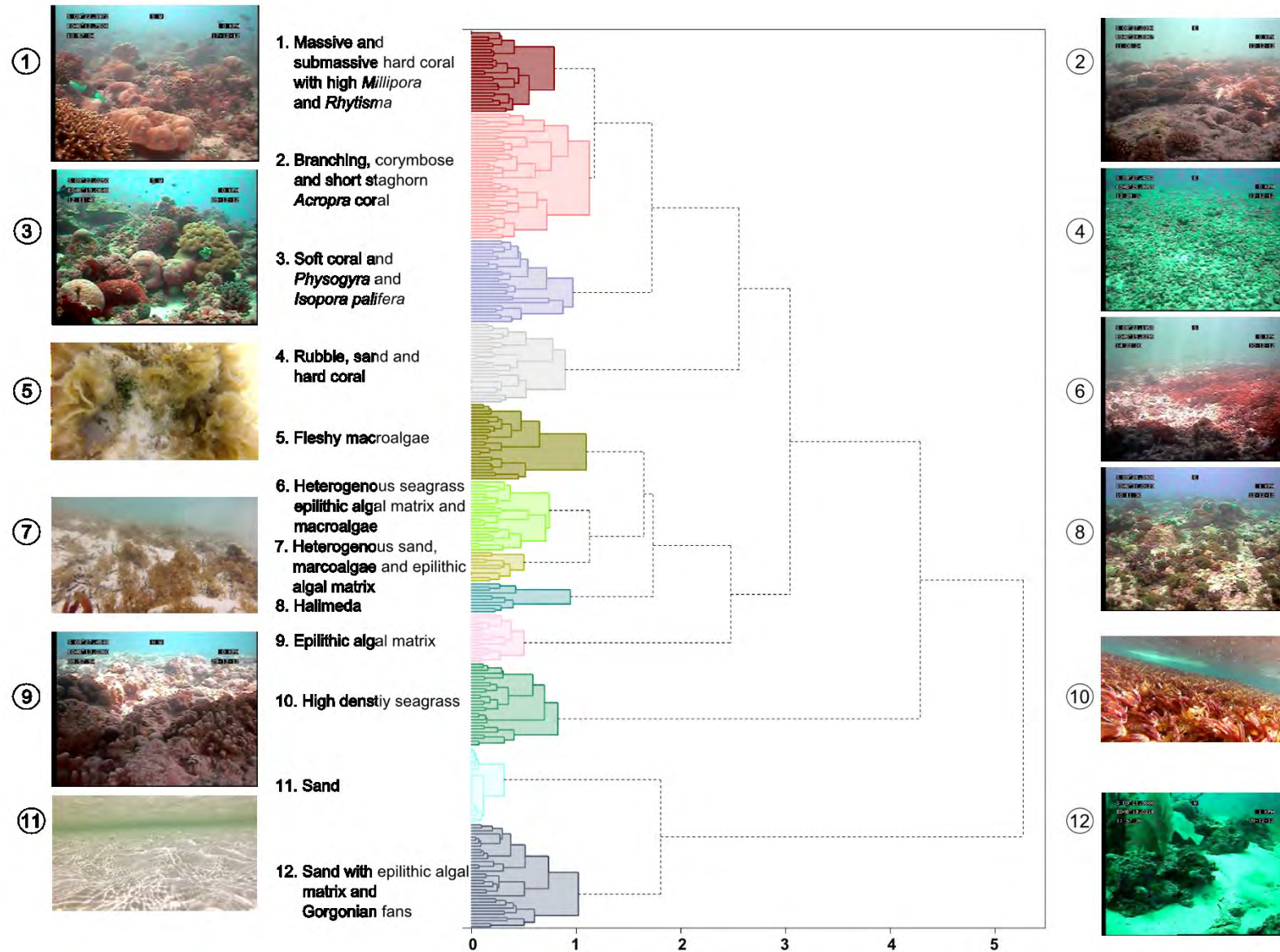


Figure 2.22. The classification tree of the twelve fine-scale benthic categories with representative ground truthing images around the edge from Aldabra's seaward reefs between 0 and 55 m. The coefficient of determination is 0.98 and the height of the tree is 5.3. (Simplified category names used for ease of reading.).

Each of the twelve categories had at least ten representative sites, and High rubble and sand category had 41 representative sites (Table 2.13). Rubble (58 %), sand (15 %), and (18 %) hard coral, and High-density seagrass (73 %) covered the greatest mapped surface area, while Hard coral (36 %), including (5 %) branching, (8.7 %) encrusting, and (2.7 %) corymbose and (3.7 %) short staghorn *Acropora*. was the most prevalent coral dominated category (Table 2.13). Soft coral (10 %), and sponge (2 %), Hard coral (44 %), including *Physogyra lichtensteini* (5 %) and *Isopora palifera* (5 %) and Heterogeneous sand (40 %), macroalgae (21 %), and epilithic algal matrix (24 %) covered the smallest surface area (0.3 km² each).

Epilithic algal matrix (88 %) had the fewest (7757) but largest (7018 m²) habitat patches, which occupied nearly 10 % of the reef area (Table 2.13). Fleshy macroalgae (70 %) had the greatest number of habitat patches (80464), but these were all of a very small size (56 m²), which is likely to be indicative of the misclassification of isolated pixels, rather than a true reflection of the distribution of Fleshy macroalgae (70 %) (Table 2.13).

Table 2.13. The composition of the twelve fine-scale benthic community categories, and the number of samples, mapped area, proportional coverage and habitat patch statistics associated with each category of Aldabra's seaward reefs between 0 and 55 m depth.

Cluster number	Fine-scale benthic category	Number of video samples	Mapped surface area (km ²)	Proportional coverage	Number of patches	Mean patch area (m ²)	Standard deviation patch area (m ²)
1	Hard coral (19 %) including massive and submassive forms (11 %), (1 %) <i>Millepora</i> and (2 %) <i>Rhytisma</i> .	27	3.4	6.6 %	52394	258	13607
2	Hard coral (36 %), including (5 %) branching, (8.7 %) encrusting, and (2.7 %) corymbose and (3.7 %) short staghorn <i>Acropora</i> .	41	5.0	9.8 %	28113	2075	233301
3	Soft coral (10 %), and sponge (2 %), Hard coral (44 %), including <i>Physogyra lichtensteini</i> (5 %) and <i>Isopora palifera</i> (5 %).	27	0.3	0.5 %	45330	444	19912
4	Rubble (58 %), sand (15 %), and (18 %) hard coral.	26	14.6	28.3 %	33247	31	70
5	Fleshy macroalgae (70 %)	25	1.1	2.2 %	80464	56	1254
6	Heterogeneous seagrass (20 %), epilithic algal matrix (43 %), and macroalgae (21 %)	23	0.5	1.0 %	38049	87	622
7	Heterogeneous sand (40 %), macroalgae (21 %), and epilithic algal matrix (24 %)	10	0.3	0.6 %	33960	61	235
8	<i>Halimeda</i> (41 %)	10	0.8	1.6 %	40956	463	36742
9	Epilithic algal matrix (88 %)	16	4.7	9.2 %	7757	7018	258571
10	High density seagrass (73 %)	27	13.6	26.4 %	63178	407	66869
11	Sand (98 %)	34	0.8	1.5 %	27648	42	139
12	Sand (78 %), epilithic algal matrix (7 %) and Gorgonian fans (3 %).	25	6.4	12.5 %	14972	201	6490
Total		291	51.5	100 %	466068		

The twelve fine-scale benthic habitat categories were mapped using the maximum likelihood supervised classification shown in Figure 2.23. Examining the spatial configuration of the benthic cover types indicated that the shallow lagoon reef on the northwest side (at Piccard Island) was dominated by three fine-scale benthic habitat categories, namely 1) Sand (98 %), 2) Heterogeneous sand (40 %), macroalgae (21 %) and epilithic algal matrix (24 %), and 3) Epilithic algal matrix (88 %). The larger part of the lagoon reef was dominated by High-density seagrass (73 %), which was bordered by two heterogeneous benthic categories, namely 1) Heterogeneous seagrass (20 %), epilithic algal matrix (43 %), and macroalgae (21 %), and 2) Heterogeneous sand (40 %), macroalgae (21 %) and epilithic algal matrix (24 %) (Figure 2.23). The location of High-density seagrass (73%) was consistent with Seagrass habitat in the broad-scale benthic habitat map. Beyond the seagrass beds on the shallow lagoon reef, a narrow band comprising of Epilithic algal matrix (88 %) was prevalent, indicating the position of the reef crest (Figure 2.23).

Three fine-scale habitat categories dominated by hard corals characterised the forereef slope (Table 2.14), namely: **1)** Hard coral (36 %), including 5 % branching, 8.7 % encrusting, 2.7 % corymbose and 3.7 % short staghorn *Acropora*, and **2)** Hard coral (19 %) including 11% massive and submassive forms, 1 % *Millepora* and 2 % *Rhytisma*, and **3)** Soft coral (10 %), sponge (2 %), hard coral (44 %), included 5 % *Physogyra lichtensteini* and 5 % *Isopora palifera*. The massive-dominated category typically occurred at greater depth (and further from the coast) than the branching-dominated category) (Table 2.14 and Figure 2.23). The category Hard coral (19 %), which included massive and submassive forms, was more common along the sheltered north and west coast, and was displaced by the *Halimeda* (41 %) habitat category on the forereef slope along the exposed south coast of Aldabra (Figure 2.23). The category Soft coral (10 %), occurred at the greatest depth of the three fine-scale coral dominated categories (Table 2.14 and Figure 2.23).

The reef platform consisted mainly of two habitat categories, firstly, Sand (78 %), epilithic algal matrix (7 %) and Gorgonian fans (3 %), and secondly, Rubble (58 %), sand (15 %) and (18 %) hard coral. (Figure 2.23). The former was prevalent along the west and east coasts of the atoll, while the latter circumvented the sandy reef aprons further offshore. The Sand (78 %), epilithic algal matrix (7 %) and Gorgonian fans (3 %) habitats were also common in chutes that intersect the large reef spurs along the north and west coast of Aldabra (dark blue on Figure 2.23 on north and west coast).

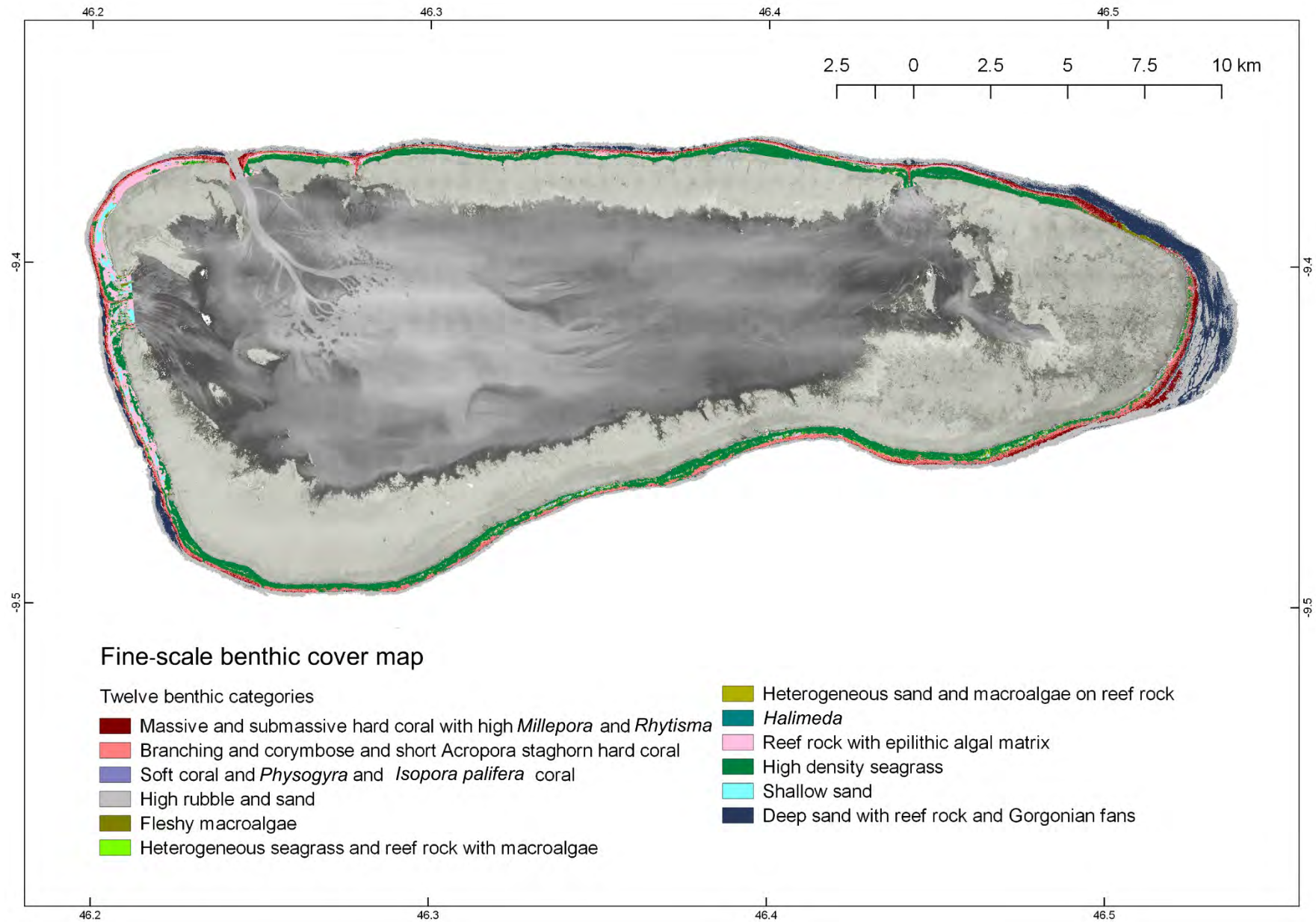


Figure 2.23. Fine-scale benthic habitat map showing the spatial configuration of the 12 habitat categories at Aldabra's seaward reefs between 0 and 55 m depth.

Table 2.14. The composition of the twelve minor benthic habitat categories including the geomorphic reef zones and subzones, mean depth ($\pm$ standard deviation) and abbreviated six broad-scale benthic categories at Aldabra Atoll seaward reefs.

Geomorphic zones	Geomorphic subzones	Depth (m)	Primary underlying substrates	Broad-scale habitat category	Fine-scale benthic habitat category
Lagoon reef, forereef slope, reef platform	Reef flats, forereef slopes and reef apron	18.2 $\pm$ 17.1	Sedimentary	Sand	Sand (98 %).
Lagoon reef	Reef flats	2.9 $\pm$ 2.2	Sedimentary	Seagrass	High-density seagrass (73 %).
Lagoon reef	Reef flats	4.3 $\pm$ 5.6	Heterogeneous sediment and limestone reef rock	Macroalgae and Seagrass	Heterogeneous seagrass (20 %), sand (5 %), epilithic algal matrix (43 %), and macroalgae (21 %).
Lagoon reef	Reef flats	6.2 $\pm$ 9	Heterogeneous sediment and limestone reef rock	Sand and Macroalgae	Heterogeneous sand (40 %), macroalgae (21 %), and epilithic algal matrix (24 %).
Lagoon reef	Reef flats to reef crest	2.4 $\pm$ 1.7	Limestone reef rock	Epilithic algal matrix	Epilithic algal matrix (88 %).
Lagoon reef	Reef flats and patches on forereef slope	8.2 $\pm$ 5.6	Limestone reef rock	Macroalgae	Fleshy macroalgae (70 %)
Lagoon reef and forereef slope	Reef flats, top and deep forereef slope	15.2 $\pm$ 13	Limestone reef rock	Macroalgae	Halimeda macroalgae (41 %).
Forereef slope	Top to deep forereef slope	8.7 $\pm$ 5.9	Limestone reef rock	Hard coral	Hard coral (36 %), including (5 %) branching, (8.7 %) encrusting, and (2.7 %) corymbose and (3.7 %) short staghorn <i>Acropora</i> .
Forereef slope	Top to deep forereef slope	8.2 $\pm$ 4.7	Limestone reef rock	Hard coral	Hard coral (19 %) including 11% massive and submassive forms 1 % <i>Millepora</i> and 2 % <i>Rhytisma</i> .
Forereef slope	Top to deep forereef slope	15 $\pm$ 9.13	Limestone reef rock	Hard coral	Soft coral (10 %), and sponge (2 %), Hard coral (44 %), including 5 % <i>Physogyra lichtensteini</i> and 5 % <i>Isopora palifera</i> .
Forereef slope and Reef platform	Deep edge of forereef slope and reef apron	28.3 $\pm$ 14.9	Heterogeneous sediment and limestone reef rock	Sand	Sand (78 %), with 7 % epilithic algal matrix and 3 % Gorgonian fans.
Reef platform	Reef apron	24.7 $\pm$ 12.5	Sedimentary	Rubble	Rubble (58 %), sand (15 %), and (18 %) hard coral.

2.4.5 Accuracy assessment of fine-scale benthic habitat map

The overall accuracy of the fine-scale benthic habitat map was low, 29 %, with $71 \% \pm 0.012$ (CI_{95}) overall error (Table 2.15). Classification of shallow benthic communities achieved the high producer accuracies (where $100 \% - \text{producer error} > 60 \%$) for shallow benthic communities, for example, Epilithic algal matrix, and Seagrass, and sand dominated benthic habitat categories. The percent coverage of the Epilithic algal matrix was underestimated with an error of omission of 80 %, due to the maximum likelihood algorithm assigning Epilithic algal matrix to the Heterogeneous seagrass and reef rock with macroalgae category. Massive and submassive hard coral with high *Millepora* and *Rhytisma* had the lowest error in producer and user accuracies (77 % and 61 % respectively) of the three-respective hard-coral-dominated minor benthic categories (Table 2.15). There was substantial confusion in the classification between pixels of the two most prevalent minor hard-coral categories, namely, the Massive and submassive hard coral with high *Millepora* and *Rhytisma* category, and the Branching, corymbose and short staghorn *Acropora* category (Table 2.15). Soft coral and *Physogyra* and *Isopora palifera* coral had a very low producer and user accuracy (99 and 93 % respectively) and was substantially underestimated due to spectral confusion with the High rubble and sand content category. This was obvious along the north coast where deep reefs with high *Physogyra* cover were classified as the High Rubble and sand category Figure 2.23. Fleshy macroalgae and *Halimeda* had the greatest error rate, for both user and producer accuracies, with zero ground truthing pixels correctly identified (Table 2.10). There was also confusion between High-density seagrass and Heterogeneous seagrass and reef rock with macroalgae. This indicates the shortcomings of the maximum likelihood model to discern between various benthic communities at the fine-scale, but it provides some confidence that the model may be improved with greater sampling effort, as the confusion was typically between categories of the same major benthic type.

Kappa statistics reflected the same low overall accuracy score (0.26) for the fine-scale benthic habitat map as the error matrix. Shallow benthic habitat categories were more accurately identified than deep water benthic habitat categories, for example, Heterogeneous sand seagrass and reef rock with macroalgae had a KIA of 0.78 while the three coral communities varied between 0.07 and 0.33 (Table 2.16).

The Tau statistic confirmed a low overall accuracy of the spatial configuration of the fine-scale benthic habitat map (0.18 ± 0.012 at CI_{95}).

Table 2.15. Accuracy assessment error matrix of classified image pixels per categories, against the ground-truthed validation set of benthic habitat categories in the top row. The error of omission and commission specifying the types of misclassification errors. Diagonal elements in the table (Grey fill) were correctly classified pixels.

	Massive and submassive hard coral and high <i>Millepora</i> and <i>Rhytisma</i>	Rubble, sand, and hard coral	Branching and corymbose and short <i>Acropora</i> staghorn hard coral	Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> coral	Fleshy macroalgae	<i>Halimeda</i>	Heterogeneous seagrass and reef rock with macroalgae	Epilithic algal matrix	High-density seagrass	Sand with epilithic algal matrix and Gorgonian fans	Heterogeneous sand and macroalgae on reef rock	Sand	Total number of pixels	Error of commission (User error)
Massive and submassive hard coral and high <i>Millepora</i> and <i>Rhytisma</i>	152	100	120	55	202	0	37	0	8	0	0	0	674	77 %
Rubble, sand, and hard coral	0	219	119	663	0	93	0	0	0	80	0	798	1972	89 %
Branching and corymbose and short <i>Acropora</i> staghorn hard coral	151	10	169	13	103	0	72	0	14	0	0	0	532	68 %
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> coral	2	20	16	4	11	0	2	0	0	0	0	0	55	93 %
Fleshy macroalgae	0	0	5	0	0	12	23	0	8	0	0	47	95	100 %
<i>Halimeda</i>	3	2	61	1	9	0	0	0	6	0	0	0	82	100 %
Heterogeneous seagrass and reef rock with macroalgae	0	0	0	0	0	0	18	1	4	0	0	0	23	22 %

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Epilithic algal matrix	81	0	5	0	45	0	9	138	133	0	229	51	691	80 %
High density seagrass	0	0	36	0	0	74	118	22	272	0	0	28	550	51 %
Sand with epilithic algal matrix and Gorgonian fans	0	17	0	32	0	0	0	0	0	353	0	421	823	57 %
Heterogeneous sand and macroalgae on reef rock	0	0	0	0	0	2	3	0	3	0	0	0	8	100 %
Sand	0	1	0	1	9	0	0	46	2	0	0	64	123	48 %
Total pixels	389	369	531	769	379	181	282	207	450	433	229	1409	5628	
Error omission (Producer error)	61 %	41 %	68 %	99 %	100 %	100 %	94 %	33 %	40 %	18 %	100 %	95 %		71 %

Table 2.16. Kappa Index of Agreement (KIA) per category of minor benthic community comparing the classified image to the accuracy assessment image of the benthic habitat categories at Aldabra Atoll.

Cluster	Category	Classified image	Accuracy assessment image
1	Massive and submassive hard coral and high <i>Millepora</i> and <i>Rhytisma</i>	0.2251	0.4615
2	Branching and corymbose and short <i>Acropora</i> staghorn hard coral	0.3172	0.0051
3	Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> coral	0.0717	-0.0001
4			
5	Fleshy macroalgae	-0.0005	-0.0001
6	Halimeda	-0.0002	0.0638
7	Heterogeneous seagrass and reef rock with macroalgae	0.7825	0.6663
8	Reef rock with crustose coralline and turf algae	0.1995	0.6041
9	High density seagrass	0.4942	0.815
10	Sand and epilithic algal matrix with Gorgonian fans	0.4286	0
11	Heterogeneous sand and macroalgae on reef rock	-0.0003	0.0453
	Rubble, sand, and hard coral	0.1105	0.3178
12	Sand	0.5194	0.3902

2.5. DISCUSSION

This study was the first attempt at a detailed, multi-themed benthic habitat classification and mapping of the entire seaward reef system of Aldabra Atoll. In this study, broad and fine-scale benthic habitats were characterised and mapped using a supervised image classification of GeoEye satellite imagery. The Aldabra reef comprised a similar area lagoon reef and forereef slope, of which the forereef slope was widest on the windward side, and the lagoon reef was widest in the lee of the atoll. The variety of benthic habitats supported within the relatively small surface area of the mapped reef (51.5 km²), highlights the ecological value of coral reef habitat of Aldabra. The supervised image classification of the GeoEye imagery was able to resolve variation in the spatial configuration of broad-scale benthic habitats around the atoll, but fine-scale benthic habitats were inaccurate. The design of future ecological sampling and spatial plans should therefore take the distribution of various benthic habitat themes into account. However, the relatively low accuracy with which image classification correctly classified the benthic habitat cover category suggested that care needs to be taken making interpretations around habitat specifics.

The benthic classification system developed in this study complements previous studies which have focussed on a broader geomorphological classification for the Amirantes and builds on the habitat mapping work done for Aldabra (Andréfouët et al. 2009; Hamylton et al. 2010; Andréfouët 2012). The number of benthic categories and level of detail that were characterised and mapped (four geomorphic reef zones, six broad-scale and twelve fine-scale) was similar to previous studies that categorised and mapped benthic habitat in the Caribbean (Mumby and Harborne 1999; Mumby and Edwards 2002), Socotra (Klaus and Turner 2004) and reefs in the Pacific Islands (Phinn et al. 2012). The twelve fine-scale benthic habitat categories determined from field data was not able to resolve fine-scale variation within the broader habitat classification with any accuracy.

The spatial configuration of the broader thematic benthic habitat within respective geomorphic reef zones at Aldabra was typical of a coral atoll, where sand, seagrass and epilithic algal matrix cover types dominate the shallow reef flats, hard coral dominates the forereef slopes, and sand and rubble dominate the reef platform (Blanchon 2011). The reef flats at Aldabra were wider on the leeward western side (ca 420 m) than the windward eastern side (ca 100 m) which lacked a well-defined reef crest, and was consistent with an early descriptive study (Stoddart et al. 1971). In this study, it was shown that high-density seagrass covered the greatest surface area on the shallow seaward lagoon reef flats. Seagrass was not recorded to species level in all samples, but a few observations of seagrass were noted during the survey, including *Thalassodendron ciliatum*, *Cymodocea*

serrulata, *Halodule uninervis*, and *Halophila ovalis* (personal observations). The spatial configuration of seagrass beds was consistent with previous studies which have described seagrass, including species of *Thalassia*, *Halodule* and *Cymodocea*, as forming extensive beds on sheltered shores of the lagoon reef of Aldabra (Taylor 1971). Seagrass is an important dietary component of two of the IUCN Red-List species that occur at Aldabra, namely the green turtle (*Chelonia mydas*) and the dugong (*Dugong dugon*) (Bjorndal 1980; Marsh et al. 1982; Preen 1995). Dugongs feed on most species of seagrass, but preferentially on the more nutritious fast-growing species such as *Halophila ovalis* while green turtles show a preference for a number of species of *Thalassia* (Preen 1995; Fuentes et al. 2007). A change in seagrass assemblage structure may affect the food availability of green turtles and dugongs (de longh et al. 1995). This has important implications for sea-level rise and its impact on the space available within the preferred depth zone for seagrasses, and the species which depend upon seagrasses for food and shelter.

Sand was more prevalent on the western sheltered reef flats of Aldabra, as recorded by Stoddart (1971), while rubble and epilithic algal matrix dominated nearer to the reef crest. Sediment dominated reef aprons were more common on the leeward coast and rubble dominated reef aprons were more common on medium to highly exposed east and south coasts. It is likely that the sediment-dominated reef aprons in the lee of the atoll were a consequence of lower exposure to wave energy. Lower levels of wave energy are associated with lower water flow speeds, which in turn have lower levels of sediment erosion and transport, and higher levels of sediment deposition (Hjulström 1935). The effect of wave exposure as a driver shaping the spatial configuration of the benthic habitat requires further investigation and is the subject of Chapter 3.

In this study, three fine-scale hard-coral habitat categories were classified and mapped on the forereef slope were also recorded in a previous survey which described six forereef zones at Aldabra (Barnes et al. 1971; Drew 1977). The three hard-coral categories and the “Sand (78 %), epilithic algal matrix (7 %) and Gorgonian fans (3 %)” category from this study were also present, forming biological zones on the forereef, in the earlier studies (Barnes et al. 1971; Drew 1977). Despite the benthic cover and benthic community structure having changed since these early surveys following mass bleaching and community succession during recovery (Cerutti et al. Submitted; Stobart et al. 2005), there is a resemblance in the underlying community composition which provides qualitative support for the classification system derived at the fine-scale.

Habitat patch statistics showed that the coarser the habitat scale, the greater the habitat patch size (adjacent pixels which belong to the same habitat category) and the fewer the

number of habitat patches. This relationship between amount of habitat patches and their size to habitat scales, along with the difference in the amount of detail about the benthic community suggests that the ecological niche breadth at coarser habitat scales is greater than within finer scales of habitat definition. The increase in ecological niche breadth with the scale of habitat therefore conforms with previous studies which have shown the relationship between geographical area size and ecological niche breadth (Slatyer et al. 2013). The breadth of the ecological niche may be related to the fish assemblages which are supported within them and is investigated in Chapter 7.

Both the habitat classification and the habitat patch size are influenced by the accuracy with which habitats are assigned to the different habitat categories. The level of accuracy achieved for the respective thematic benthic habitat maps decreased with an increase in the number of benthic categories (and the level of detail provided), with greater accuracy per category at the broad-scale than the fine-scale. The trend of greater accuracy when using fewer categories is consistent with the findings of previous studies (Mumby and Edwards 2002; Andréfouët et al. 2003). An acceptable percentage of misclassified pixels arising from a maximum likelihood classification of four marine habitat categories from satellite imagery including up to four spectral bands should range between 55 – 70 % (Green et al. 2004; Roelfsema and Phinn 2013). The accuracy assessment results of the fine-scale benthic habitat map from this study was similar to another fine-scale benthic map produced using maximum likelihood classification from high-resolution satellite imagery in a previous study, echoing the challenge faced in this study of producing accurate benthic habitat maps at a fine-scale (Table 7 in Phinn et al. 2012).

The high levels of inaccuracy associated with the fine-scale benthic habitat map requires that ecological studies be aware of the risks of making incorrect interpretations when using the mapped data in associating with other spatial data. Assessment of spatial change in benthic habitat cover that use earlier maps requires careful interpretation and an understanding of the accuracy associated with the earlier maps. For example, using the mapped data to detect a phase-shift from a coral-dominated reef to macroalgae dominated reef will have a high level of error associated and results may consequently be unreliable. As in this study, a previous study that used IKONOS satellite imagery to map reef habitat in the Turks and Caicos which also found low levels of accuracy of the resulting fine-scale habitat map cautioned against its use to detect an ecological change (Mumby and Edwards 2002). The inaccuracy of the fine-scale benthic habitat map therefore requires further refinement prior to use for ecological studies at Aldabra.

A key factor that dictates the accuracy with which benthic habitat is mapped is the type and spatial resolution of the imagery (Green et al. 2004). For example, Mumby et al (1997) reported an accuracy of 37 % for low spatial resolution (30 m) Landsat and SPOT satellite imagery, 67 % for very high spatial resolution aerial photography (approximately 0.2 m²), and 81 % for very high spatial resolution (10 – 0.5 m²) CASI airborne imagery for the same area in the Turks and Caicos. Subsequently, Mumby and Edwards (2002) reported 50 % overall accuracy for a classification representing 13 categories using (4 m²) IKONOS satellite imagery, and 81 % for CASI airborne imagery, and Andréfouët et al (2003) report 53 % overall accuracy for IKONOS imagery in the Turks and Caicos islands. Mumby and Edwards (2002) explained that the poor descriptive resolution of satellite sensors being partly due to loss of radiance contrast.

GeoEye satellite imagery has had favourable reviews for benthic classification of tropical marine environments due to its very high spatial resolution (4 m²) and a suitable range of multispectral image bands (Andréfouët 2008). The GeoEye imagery for Aldabra did, however, suffer shortcomings that affected the accuracy of the mapping. The very high spatial resolution was encumbered by variation in the water clarity and amount of shadow behind waves that affected different areas around the coast to a greater or lesser extent depending on the level of wave exposure. The lack of a shortwave Infra-Red band in GeoEye satellite imagery has been regarded as a shortcoming in mapping complex environments, as this waveband is useful to remove surface noise such as shadows produces by waves (Nagendra et al. 2013). More recent studies have reported high accuracy values (> 75 %) but typically used fewer (three to nine) benthic categories than this study (Zhang 2015; Selgrath et al. 2016).

The substantial difference (25 %) in the accuracy of the six-category broad-scale benthic habitat map and the twelve-category fine-scale benthic habitat map, could be explained by the increase in overlap of spectral signatures associated with each habitat category, which is known to increase with the number of categories (Eastman 2009). The more benthic categories used in the classification, the greater the overlap in spectral signatures, which occurs as a result of an increase in the likelihood that multiple benthic habitat categories occur in the same pixel (known as spectral mixing) (Hamylton 2011). It is likely that spectral mixing affected the accuracy of the classification in this study because multiple benthic habitat categories could occur at a finer spatial scale than the resolution of the GeoEye imagery (4 m²). The use of textural filters has been suggested to remove the edges between different benthic habitat types which reduces the number of pixels with a high likelihood of containing multiple benthic habitat types (Mumby and Edwards 2002). Spectral unmixing

procedures have been proven effective to discriminate between pixels with mixed benthic cover types per pixel in hyperspectral imagery analysis and may be useful to apply to the multispectral GeoEye imagery to improve benthic habitat maps for Aldabra in future (Hamylton 2011).

The depth to which this study attempted to classify benthic habitat (50 m) exceeded most benthic habitat mapping studies which typically terminate in 15 – 20 m. Light attenuation with increasing depth limits the image processing to distinguish habitat in depths exceeding 20 m (Green and Edwards 2000), which are often classified as deepwater pixels (Phinn et al. 2012). This supervised classification in this study was able to distinguish reef sandy and rubble dominated reef aprons from the deep-water pixels further offshore, suggesting that GeoEye imagery was able to detect spectral differences for these benthic habitat types beyond the typical 20 m depth limit. The performance at depth was not universal for all benthic habitat types. The classification of the hard-coral dominated forereef slope on the north forereef slope beyond 20 m depth was confused with rubble dominated benthic cover on the reef apron. Improvement in accuracy of deeper benthic habitat categories could be expected if multispectral imagery that includes deeper penetrating blue bands were used (e.g. WorldView 2 imagery) (Nagendra et al. 2013).

Benthic habitat on Aldabra's seaward reefs were mapped using the maximum likelihood pixel-based image classification technique. Pixel-based classification methods have been the standard method used to classify remotely sensed images when using reef mapping techniques (Green et al. 2004). Image classification methods have recently started changing towards OBIA (Object Based Image Analysis) which reports similar or higher accuracy assessment values, which requires further investigation for mapping Aldabra seaward reefs (Phinn et al. 2012; Roelfsema et al. 2014, 2018).

The spatial extent of this study was limited to the seaward reef of Aldabra and did not include the atoll's inner lagoon because this was recently mapped during another study (Hamylton et al. 2012b). Future mapping of Aldabra atoll's marine environment should include a single consolidated benthic habitat map of the lagoon and seaward reefs to provide a more comprehensive basis for studies on the interaction between habitats and species (Potts 1980; Stevens 1984; e.g. Gibson 2003).

A significant limitation to regular updating of habitat maps has been the cost of satellite imagery at a suitable spatial resolution (Mumby et al. 1999; Mumby and Edwards 2002; Green et al. 2004). The recent launch of Sentinel 2 satellites provides (hyperspectral) satellite imagery free of charge with a 10 m² spatial resolution, and improved benthic

classification ability over other satellite sensors with similar spatial resolution, e.g. SPOT-4 and Landsat ETM+ (Hedley et al. 2012). While the spatial resolution of these data is not as fine-scale as the GeoEye imagery (4 m²) used in my study, it provides regular (free) footage which may be sufficient to detect large-scale changes in benthic habitat (Hedley et al. 2012, 2016).

A second major impediment to the regularity with which benthic classification is carried out is the time required to label (annotate) benthic types in ground truthing images in order to train the supervised classification (González-Rivero et al. 2016). The concurrent development of remotely sensed imagery and software that automates the labelling of the ground truthing photographs through artificial intelligence approaches is a powerful combination that enables obtaining ground truthing information far more efficiently than before (González-Rivero et al. 2016). More regular and improved benthic habitat maps will be a useful asset to inform spatial management and ecological studies.

Increased frequency of spatial monitoring of seagrass and coral reefs is becoming an ever-greater need as these habitats are changing rapidly under climate change (Short and Neckles 1999; Loya et al. 2001; Hughes et al. 2010; Jordà et al. 2012; Graham et al. 2015; Hedley et al. 2016). In particular, coral reefs have changed substantially in their spatial coverage and species composition as a result of mass coral bleaching events, at Aldabra and elsewhere (Stobart et al. 2005; Hughes et al. 2010; Graham et al. 2015; Normile 2016; Cerutti 2017). Phase-shifts from coral to macroalgal-dominated benthic communities reduce the biodiversity and fundamentally alter the ecosystem (Hughes 1994; Bellwood et al. 2006; Hughes et al. 2007). I found that the forereef slopes of Aldabra were largely dominated by three fine-scale categories characterised by hard and soft coral, suggesting that at the large spatial scale there was no evidence for a shift towards algal-dominated benthic communities. This finding is consistent with previous surveys of the reef (Sheppard and Obura 2005; Stobart et al. 2005).

However, there was relatively low accuracy with which Hard coral could be distinguished from Macroalgal benthic habitat in my study which was consistent with a previous study using pixel-based habitat classification methods (Mumby et al. 2004b). This questions the validity of using pixel-based classification methods of remotely sensed imagery to detect a change between spectrally similar benthic habitat categories. While the use of pixel-based habitat classification methods may have limited use for detecting spectrally similar habitat changes, it has application for detecting spatial change in habitats categories with distinct spectral signatures, such as a change in the amount of seagrass cover (e.g. Roelfsema et al. 2014). For this same reason, it has been useful to estimate the extent of mass coral

bleaching, as the white coral skeletons have a highly distinct spectral signature (Andréfouët et al. 2002; Mumby et al. 2004b; Yamano and Tamura 2004; Berkelmans et al. 2004; Hedley et al. 2012; Barnes et al. 2015). The continued increase in water temperature as a consequence of climate change will likely bring about more frequent and more intense coral bleaching, and seagrass beds are also likely to change their community structure and distribution (Short and Neckles 1999; Hoegh-Guldberg et al. 2007; Jordà et al. 2012; Hughes et al. 2017). It is recommended that remotely sensed image processing be pursued to update and monitor change to the benthic habitat and detection of coral bleaching in the light of the recent technological advances and impending threats to the marine ecosystem at Aldabra. Declines in Hard coral, in particular “Hard coral (36 %), including (5 %) branching, (8.7 %) encrusting, and (2.7 %) corymbose and (3.7 %) short staghorn *Acropora*” and Soft coral (10 %), and sponge (2 %), Hard coral (44 %), including *Physogyra lichtensteini* (5 %) and *Isopora palifera* (5 %)” categories are highly susceptible to bleaching and should be monitored following bleaching events.

2.5.1 Benthic habitat maps inform expansion of Aldabra’s MPA

The benthic habitat maps created in this study provided critical information which was used to inform the expansion of Aldabra’s existing MPA boundary. From the benthic habitat mapping carried out in this study, it was determined that 3.5 km² of Aldabra’s forereef slope were currently outside the existing MPA boundaries (Figure 2.24). This area included two geomorphic reef zones, including the forereef slope and reef apron, and two broad-scale benthic habitat categories including Rubble (37 %) and Sand (89 %), and two fine-scale benthic habitat categories, namely, “Sand (78 %, epilithic algal matrix (7 %) and Gorgonian fans (3 %),” “Rubble (58 %), sand (15 %), hard coral (18 %)” (Figure 2.25). Data used in the subsequent chapters of the thesis showed that these habitats are unique in combination with the environmental drivers including high wave energy (mean 10639 J/m³) and a depth ranging between 18 and 55 m. Ground truthing surveys from this chapter and data collected using Baited Remote Underwater Video systems (BRUVs) and unbaited Remote Underwater Video systems (RUVs) recorded 21 genera of hard coral and 189 species of fish within the area, respectively. Following the reef mapping at Aldabra, an order for immediate intermittent protection was afforded to the 3.5 km² of reef, which was subsequently expanded to include the entire seamount on which Aldabra rests (See the Outcomes in the General Discussion for more detail on this).

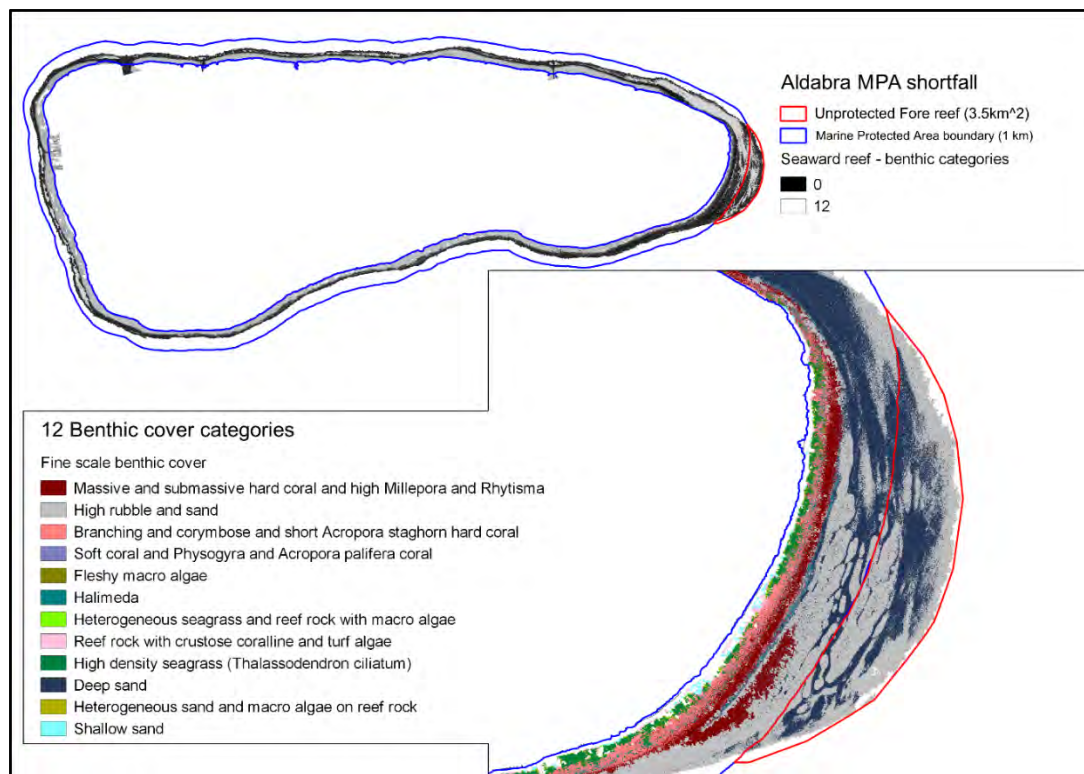


Figure 2.24. An area of 3.5km² of forereef slope was outside of the existing Marine Protected Area (MPA) boundary, shown with fine-scale benthic habitat map.

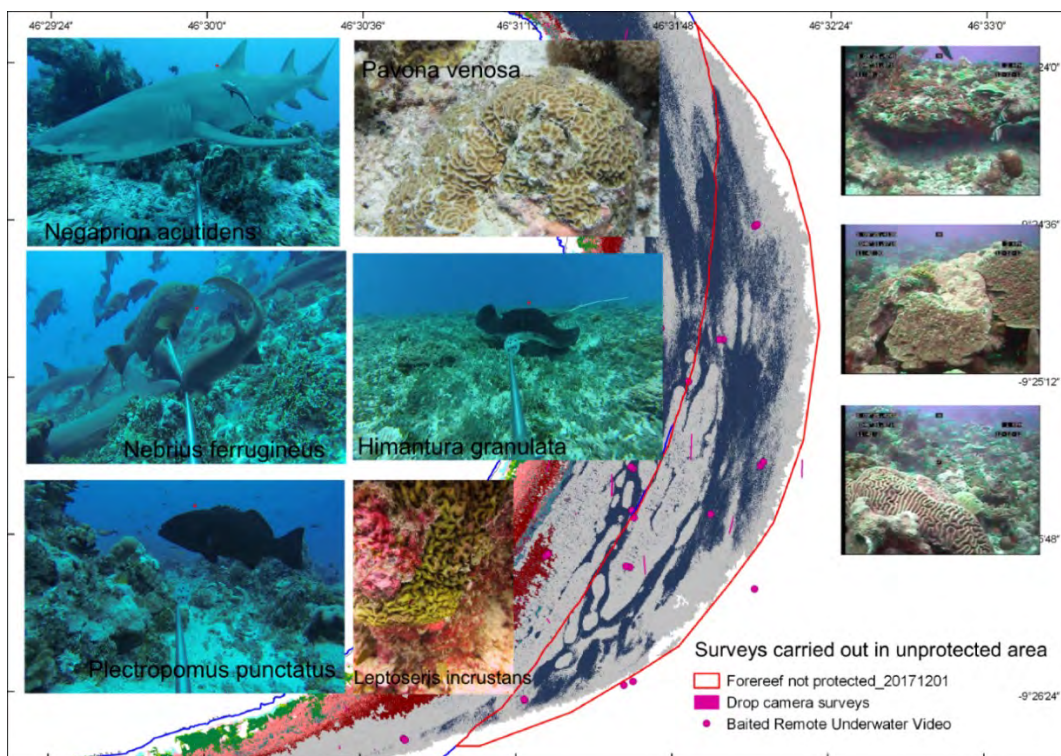


Figure 2.25. The area of 3.5 km² included two fine-scale benthic habitat categories, and several IUCN red-listed species of hard coral and fish species (see examples in inset). On the right reef areas displaying structural complexity are shown

2.5.2 Conclusion

The use of a supervised habitat classification from remotely sensed imagery of tropical reefs provided an efficient means to produce spatially comprehensive habitat maps at multiple scales of classification. The classification produced more accurate results the fewer habitat categories were categorised. Habitat classifications were more accurate for habitat categories that were highly contrasted from other habitat categories, such as sand and seagrass. The results from this study suggested that future investigations of reef habitat should use approximately six categories of benthic habitat to define broad-scale benthic habitats to achieve acceptable levels of producer accuracy when using pixel-based classification methods with four bands of remotely sensed imagery. The habitat classification shows that Aldabra has a diverse variety of habitats, providing a broad range of niches through feeding and sheltering opportunities within these habitats. The acquisition of a benthic habitat map through this study provides the baseline for future change detection and habitat association studies in reef fish and other organisms. Furthermore, the benthic habitat maps derived from this Chapter provided a basis of evidence from which the MPA at Aldabra was expanded to protect previously unprotected sections of reef.

Chapter 3. The modifying effect of wave energy and depth on benthic habitats of Aldabra Atoll



Acropora, Isopora, and Pocillopora hard corals in sheltered waters on the forereef slope of Aldabra Atoll. Credit: Pristine Seas Survey 2015 – National Geographic

3.1. ABSTRACT

The aim of this chapter is to establish the role of environmental drivers on the distribution of benthic habitats at a tropical coral reef. Depth and wave energy are two key environmental drivers of benthic habitat composition on tropical reefs. The objective was to determine how depth and wave energy influence the probability of occurrence of the broad-scale benthic habitats on the seaward reefs between 0.9 and 55 m depth around the entire coastline of Aldabra Atoll. The hypothesis was that depth and prevailing wave energy would dictate the general patterns observed, while storm wave energy would explain stochastic disruptions to the expected habitat distribution pattern. The six broad-scale benthic-habitat categories were associated with 291 benthic habitat sampling sites on Aldabra's forereef and reef flats (derived in Chapter 2). Depth readings were collected from the same sampling sites using an echo sounder and then standardised to mean sea level from tide data. Three years of daily wind speed and direction data were used to construct prevailing and maximum wave energy models over a fetch with 650 km² circumference around Aldabra. The probability of occurrence of the broad-scale benthic habitat categories in response to changes in depth, prevailing and storm wave energy was assessed using Generalised Additive Models (GAMs). The effects of depth and prevailing wave energy were shown to be significant in explaining the biological zoning of the habitat categories, but storm wave energy did not significantly contribute to the GAMs abilities to explain variation in the data. The lack of a significant effect of storm wave energy on the benthic habitat may be explained by the mismatch in the long duration over which significant but infrequent storms take place at Aldabra, and the short (three-year) period for which wind data were available. A wave model which includes a longer duration may be able to detect stochastic disruptions caused by infrequent storms to benthic cover. The interaction between prevailing wave energy and depth had a significant effect on the benthic habitat, showing that higher exposure to prevailing wave energy was associated with the peak probability of occurrence for any habitat to shift to greater depth. The depth-shift with increased wave energy suggests that a change in depth or wave energy levels will lead to change in the benthic habitat. The progressive change in sea level and the intensification of wave conditions arising from global climate change are therefore likely to impact the distribution and composition of benthic habitats and communities of coral reefs.

3.2. INTRODUCTION

The overarching aim of this chapter is to gain an understanding of the environmental drivers that determine the distribution of benthic habitats at a tropical coral reef. The benthic habitat types of tropical marine ecosystems support a multitude of fish and invertebrate species, providing a range of feeding opportunities, refuges and facilitate different stages of life-cycles of many reef fish (Connell 1978; Nagelkerken et al. 2002; Mumby 2006).

Environmental conditions control or modify the composition of the benthic habitat (Sheppard 1982). Understanding how and to what extent environmental conditions modify the composition of the benthic habitat is important as it allows predicting the distribution of benthic communities (Chollett and Mumby 2012; Hamylton et al. 2012b). Furthermore, knowledge of the effects of environmental drivers on the benthic habitat provides an understanding of how ecological functioning may change under different environmental conditions in the future (Freeman and Moisen 2008; Graham et al. 2015).

Environmental conditions that control and modify the benthic community composition include exposure to breaking wave energy, depth, sea surface temperature, salinity, light and sediment, among others (Done 1982; Sheppard 1982; Stoddart 1984; Brown 1997; Hoegh-Guldberg 1999; Dadhich et al. 2011; Chollett and Mumby 2012; Gove et al. 2015). Benthic organisms differ in their tolerance to environmental conditions, producing variations in the combinations of co-occurring species, resulting in benthic communities with different compositions (Marshall and Baird 2000; Schoepf et al. 2015). Over larger spatial scales, the variation in benthic communities determine the benthic habitat composition and their spatial distributions.

Variability in exposure to wave energy and depth are important environmental modifiers that predict the change of species along spatial gradients (Harborne et al. 2006). Depth and wave energy are likely to be effective drivers of benthic community structure at the scale of an atoll, where complex bathymetry and varying levels of exposure on leeward and windward sides of the atoll affects benthic composition (Ponce de León and Guedes Soares 2005; Kench et al. 2006).

Wave action physically erodes the reef by causing structural damage and churning up sediment or rubble that may act to scour the reef and prevent new settlement of coral larvae (Kench et al. 2006; Chollett and Mumby 2012; Perry et al. 2015). As a consequence of this damaging and abrasive interaction of waves on the reef, the leeward and windward side often have a markedly different coral reef communities owing to differences in wave exposure (Perry et al. 2015). Early investigations described how moderate levels of wave

exposure favoured certain types of corals (Stoddart 1969). Past research has shown that coral assemblages in the Caribbean are structurally adapted to tolerate high wave conditions, e.g. *Acropora palmata*, grows its branches into the prevailing wave direction to alleviate wave stress (Sheppard 1982). In Hawaii where strong wave action affects the coral reefs, Dollar (1982) showed that the zonation of coral was related to prevailing wave conditions, with the highest diversity on intermediate depth slopes, with lower diversity on stable upper slopes and deep slopes. Chollet and Mumby (2012) found that wave exposure was the principal driver predicting the distribution of *Montastrea*-dominated forereef habitat throughout the Belize Barrier Reef. In the Indo-Pacific Ocean the algal-ridge is characteristic of the breakwater zone on the reef (Blanchon 2011), and *Porites* colonies are common where water movement is greater, while *Montipora verrucosa* is more common under sheltered conditions (Jokiel 1978; Sheppard 1982).

Coral-reef benthic communities are affected by wave energy at two levels, 1) at prevailing wave conditions and 2) during extreme storm-conditions. Wave energy acts as a stochastic disturbance that interrupts the prevailing conditions by severe impacts on a benthic community (Sheppard 1982). For example, hurricane generated waves caused variability within the distribution pattern predicted by depth and prevailing wave conditions in Hawaii (Dollar 1982). Tropical cyclones cause substantial damage to reefs worldwide (Beeden et al. 2015; Burt et al. 2016), and impacts islands in the Western Indian Ocean (WIO) every year (Turner and Klaus 2005). The inner islands of the Seychelles are close to the equator and consequently do not experience cyclones often. The Seychelles outer islands, including Aldabra Atoll, are further south from the equator, causing them to experience cyclone-induced storm swell more frequently than the inner islands (Stoddart 1968a).

The effect of wave energy on the benthic community is known to change with depth as waves break as a function of their height relative to the substrate depth (Taylor 1971; Drew 1977; Dollar 1982). Breaking waves and the associated water movement exerts a great force on the intermediate to shallow benthos, while deeper benthos is less affected by waves passing over as they typically do not break (Péquignet et al. 2011; Monismith et al. 2015). Depth also regulates a combination of other factors, such as solar radiation (light), nutrients, and temperature, and in turn, regulates their cumulative effects on the benthic community composition (Dubinsky et al. 1984; Dunlap et al. 1986). On a coral reef, depth also influences the composition of the benthic community by altering the distributions of hermatypic and ahermatypic which respond differently to light availability (Marshall 1996). It is therefore important to consider the effects of the interaction of depth and wave energy on the benthic community composition.

Previous studies have suggested that wave energy and depth are environmental drivers affecting the distribution of benthic cover of the seaward reefs of Aldabra Atoll. However, no attempt has been made to quantify the relationship (Taylor 1971; Drew 1977). Hamylton et al. (2012b) used wave exposure as a covariate in a spatial model of benthic cover, but this research was limited to Aldabra's inner lagoon. Thus, there remains a need to assess the effect of wave exposure and depth on the benthic cover of the seaward reefs of Aldabra Atoll.

The aim of the chapter was to gain an understanding of how depth and exposure to inshore wave energy drives the spatial distribution of six categories of broad-scale benthic habitats.

H. 3.1) There are differences in the probability of occurrence of the respective broad-scale benthic cover categories (mapped in Chapter 2) against a gradient of depth and exposure to wave energy along the Aldabra coastline.

The objectives of this chapter were to:

Obj. 3.1) Develop spatial deep-water models of prevailing and storm wave energy over a large fetch with a 650 km radius around Aldabra using daily wind data from the Research Station at Aldabra.

Obj. 3.2) Establish how the probability of occurrence of respective broad-scale benthic habitat categories on the seaward reefs at Aldabra Atoll change with depth, prevailing and storm wave energy using General Additive Models (GAMs).

3.3. METHODS

3.3.1 Study site

The effects of the exposure to wave energy and depth on six categories of benthic habitat were assessed for the seaward reefs at Aldabra Atoll between depths of 0 to 55 m depth. Sampling included all aspects (sides) of Aldabra's coastline to obtain a representative benthic cover set in varying degrees of exposure to wave energy.

3.3.1.1 Wave energy at Aldabra

The prevailing source of wave energy meeting Aldabra is wind driven swell from the Indian Ocean monsoonal trade winds (Stoddart et al. 1971; Stoddart and Mole 1977). Aldabra's geographical position causes it to experience a strong monsoonal shift from the shorter wet northwest-dominated months (Nov-Apr) to the long dry southeast monsoon months (May-Oct) dominating most of the year (Farrow 1971). During the months of southeast winds the air-pressure is high, and winds are strong, while during the months of northwest winds, the air pressure is low, and winds are lighter (Farrow 1971; Stoddart and Mole 1977).

Average wind speeds are generally higher during the SE monsoon, coupled with rough seas, while the NW has calmer seas, with sporadic strong winds, which may be related to tropical storm or cyclones passing nearby. Cyclones or tropical storm events are a second source of wave energy in the region. Aldabra lies north of the south-west Indian Ocean cyclone belt, and only infrequent tropical storms have passed close to Aldabra (Stoddart 1968a). Aldabra is sheltered from Antarctic cold front storms propagating waves through the Indian Ocean, as a consequence of laying in the lee of the southeast coast of Africa, Madagascar and Comoro Islands in the Mozambique Channel.

3.3.2 Benthic cover

Benthic composition at each of the 291 ground-truthing sites (See Figure 2.7 for localities) was determined from video imagery analysed using Coral Point Counts with Excel extensions (CPCe) (Kohler and Gill 2006) as described in Chapter 2. The six broad-scale benthic cover categories are shown in Table 3.1.

Table 3.1. Broad-scale benthic cover categories characterised for Aldabra Atoll's seaward reefs between 0 and 50 m depth.

Broad-scale benthic cover category	Benthic category description
<i>Sand</i>	Sand (89 %)
<i>Hard coral</i>	Hard (42 %) and soft coral (10 %)
<i>Macroalgae</i>	Macroalgae (42 %)
<i>Epilithic algal matrix</i>	Epilithic algal matrix including crustose coralline algae and turf algae (87 %)
<i>Rubble</i>	Rubble (37 %)
<i>Seagrass</i>	Seagrass (73 %)

3.3.3 Depth

Depth was recorded during all boat-based video surveys sampled using the echo sounder on the boat (Garmin 526s), while depth was estimated during surveys on foot. Depth measurements were adjusted to correct for the effect of tide using a tidal water level model (SIF unpublished data). No measurements of light were taken, which is an important predictor variable of benthic communities, but depth serves as a proxy for light to some degree.

3.3.4 Wave energy model

Linear wave theory equations (Ekebom et al. 2003) and significant wave height output from a simplified deep water wave model were used to map wave energy exposure under prevailing (mean) conditions, and storm (maximum) conditions experienced during the three-year period when the field data were collected 2012-04-01 to 2015-03-31. No earlier data collected on site were available.

Existing oceanographic wave model data-output provided online had a spatial resolution that was too coarse to allow for investigating the differences in wave energy around the Aldabra coast. For example, the resolution of NOAA wave watch III data was available at a resolution of 22.5 km², and consequently too coarse to differentiate between the windward and leeward effects of wave exposure at Aldabra, as the study area would include only two wave energy values (pixels). Consequently, a few existing wave energy models were investigated to derive data at a finer spatial scale than currently provided online.

Models using wind speed and direction data within an area of water (known as the fetch) and accounting for the effects of land have been developed for example, NOAA Wave Watch III (Tollman 2007), GREMO (Pepper and Puotinen 2009), SWAN (Booij et al. 1999), and WaveTools2012 (Rohweder et al. 2012). The WavesTool2012 toolbox has previously been

used to assess the ecological effects of wave energy on the benthic community (Graham et al. 2015; Perry et al. 2015). The WaveTools2012 is a deep-water model which provides a good first order estimate of wave energy based on the linear and quadratic approximation of wave energy (Hearn et al 1999 in Williams et al. 2013). The lack of an accurate bathymetry map excluded the use of more sophisticated models like SWAN which can account for the effects of depth on wave energy dissipation.

In this study, Waves2012 was used to model wave energy around Aldabra in ArcGIS (Rohweder et al. 2012; ESRI 2016). The model uses wind velocity and its direction which is cast over a binary map of the water surface in a fetch area, to calculate significant wave height and wave period for each wind measurement. The wind-fetch model is a simplified model which ignores more complex near-shore processes such as shoaling, breaking, reflection, refraction, and diffraction, but provides a good first order estimation of the wave energy within the fetch area calculated (Rohweder et al. 2012). A potential limitation of the simplified wave energy models used in this study was the lack of a detailed bathymetry map and surface roughness which are required to incorporate friction dissipation of breaking waves into models (Monismith et al. 2015). The model does however still provide a valid and useful estimate of the difference in the amount of wave energy experienced along the different aspects of the coastline owing to the sheltering effects of Aldabra, and other islands.

3.3.4.1 Wave model: Input wind data

Wind direction and velocity were recorded daily at the Aldabra Research Station on Picard island. Wind velocity was recorded by an anemometer mounted 8 m above the ground (46.20617, -9.40138) every 15 minutes, but the wind meter did not record direction. Wind direction was recorded, at 8 am every morning, at the synoptic meteorology Research Station on Picard (46.20636, -9.40214) as one of the 16 cardinal and sub cardinal wind directions (every 22.5°) by a trained observer. Fetch-based models use either *in situ* wind data (e.g. Ekeboom et al. 2003; Perry et al. 2015), or satellite data (e.g. Chollett and Mumby 2012; Hamylton et al. 2012b) to estimate wave exposure over a given surface. A shortcoming of using locally measured wind data to estimate wave exposure over a large area is that the wind data may not represent conditions further away from the point where the energy of the wave is generated, and potentially over or under-estimate wave energy. It is, however, a good first order estimation of the relatively stable trade winds that blow within the fetch of Aldabra and has been used like this by others (e.g. Perry et al. 2015).

The wind measurements may also vary in different parts of the atoll. Given the position of anemometer at Picard Island in the lee of Aldabra, it is likely that the strength of the

southeast wind and consequently wave conditions were slightly underestimated. Farrow (1971) reported that localised wind speed at Aldabra measured at the East Channel in October 1968 was considerably higher (+ 1.5 m/s) (compare Farrow 1971; Stoddart and Mole 1977) than that measured at the Research Station. In this study, wind speeds were increased by 1.5 m/s for measurements with a southeast component ($180 \geq \text{wind direction} \geq 90$) to compensate for the under-estimation of south-easterly wind speeds taken at the solar station.

Wind direction recorded at 8 AM in the morning was associated with the maximum wind speed measurements taken during that day. It is acknowledged that the wind direction at 8 AM is likely to underestimate the true variation of the wind direction throughout the day, but by using a crude estimation of wind direction (represented within the 22.5° for each subcardinal wind direction) fine-scale variation would not affect the results. This is further justified as wind direction is known to be consistent, predictable and highly directional in the monsoon climate experienced at Aldabra (Farrow 1971).

The median hourly wind speed recorded over the study period is shown, along with a wind rose indicating the frequency of wind direction and wind speed. The wind rose figure was constructed using COORD_POLAR in GGPlot2 (Wickham 2009), and other graphics were constructed in the STATS package in R statistical software (R Core Team 2016).

3.3.4.2 Wave model: The fetch and resolution

The fetch surface was defined as the area around Aldabra over which wind velocity and direction affects the wave energy experienced at Aldabra (Figure 3.1a). The fetch area was constructed as a 2-dimensional spatial surface within a 650 km radius around Aldabra in GIS (Quantum-GIS-Development-Team 2017). The 650 km radius was based on the area necessary for maximal sea conditions to develop (Sorensen 1977 in Ekebom et al. 2003; Chollett and Mumby 2012; Perry et al. 2015), which has been defined as the length of open ocean required for seas to become fully developed under gale force wind conditions (Hill et al. 2010).

The wave model was constructed to a spatial resolution of 100 m^2 , comparable to a previous study investigating the effects of wave energy on benthic community in Belize which was carried out at 50 m^2 resolution (Chollett and Mumby 2012), and a study on coral reef growth in the Chagos at 100 m^2 under different levels of wave energy (Perry et al. 2015).

3.3.4.3 Wave model: Obstacles within the fetch

As both land and reefs act to slow waves down, both were mapped within the fetch area (Tollman 2003). A binary raster, with a border of pixels outside of the 650 km radius, and

land and reef within this area were assigned 1, while water was assigned 0. Land and reef cover data were obtained from the Open Street Map project as vector shapefiles (Openstreetmap 2016) and the Millennium Coral Reef Mapping Project (Andréfouët et al. 2006). The reef area around Aldabra itself was removed to allow the samples on the reef to be associated with wave energy. (The reefs were used as simplistic obstacles through which wave energy could not move, which would have blocked wave energy reaching the sampling sites if the mapped reef was not removed from around Aldabra prior to running models.). The land and reef vector files were converted to raster format (rasterised) to a resolution of 100 m². Prior to rasterization the area of land and reefs, Aldabra's mapped land was carefully reduced in size by less than 100 m to avoid the process of rasterization converting areas of the sea into the land which overlaps with sampling localities.

3.3.4.4 Wave model: Weighting the fetch according to wind direction probability

The fetch was weighted to account for the frequency of the disturbance from waves which were distributed among each of the 16 cardinal and subcardinal wind directions. The frequency of disturbance was calculated as the proportional number of days that the wind blew from each of the 16 wind directions over the three-year period, referred to as the wind direction probability in the model. The weighted fetch surface was calculated (for every water pixel) for each of the 16 wind directions (Figure 3.1b), by calculating the arithmetic mean of 9 radials spread at 3⁰ increments around the desired wind directions, within the Waves2012 toolbox using the fetch module (Shoreline Protection Manual (SPM) option). This option is recommended when the area of interest is open and not constrained to narrow fetches (Rohweder et al. 2012), and may compensate for some variability in wind direction occurring throughout the day. The approach used in this study was comparable with how the wind direction probability was derived in previous studies using the WaveModel2012 toolbox (e.g. Chollett and Mumby 2012; Perry et al. 2015).

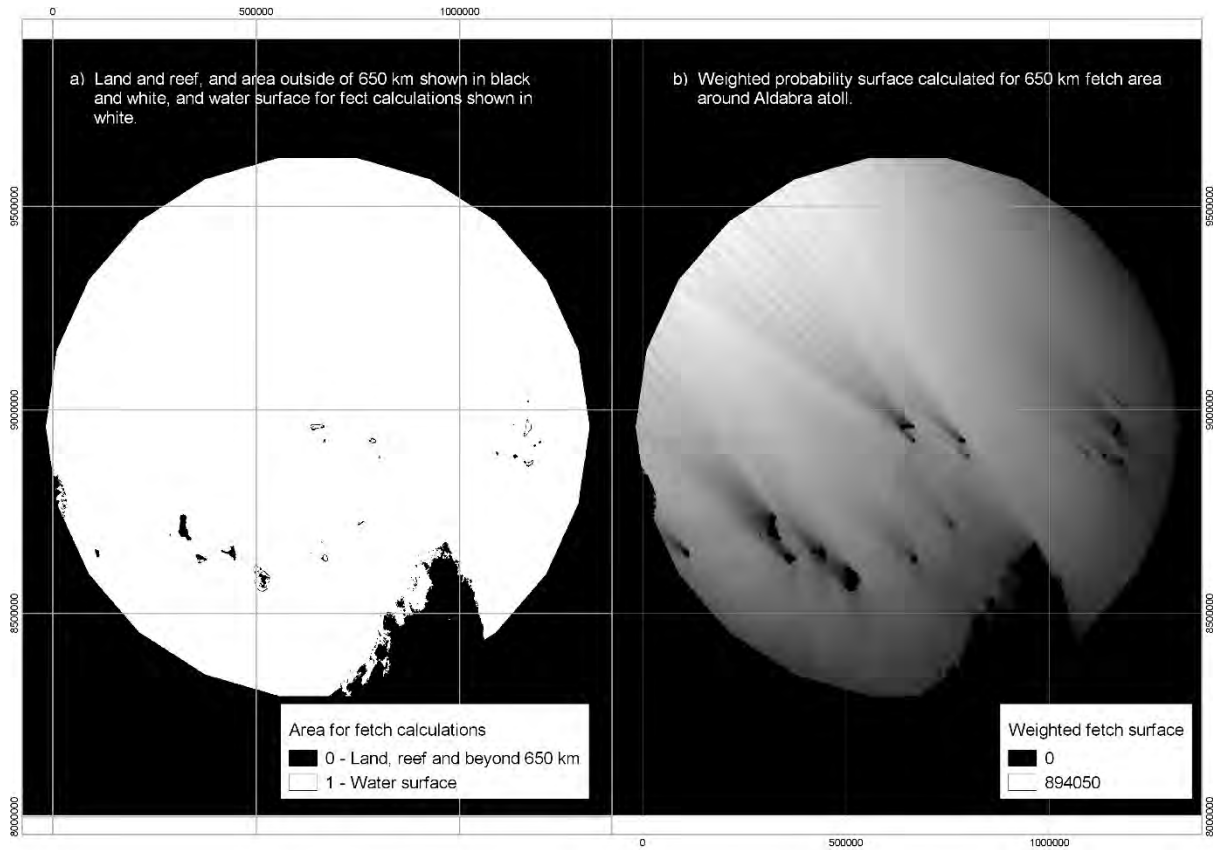


Figure 3.1. Fetch area of 1.13 million km² within wave energy was calculated. a) The land, reefs, and area beyond 650 km away from Aldabra are in black, and the water surface for which wave exposure was calculated is white. b) The weighted fetch probability surface based on the proportion of days in which the wind blew from each of the cardinal and subcardinal wind directions multiplied by distance from source.

3.3.4.5 Wave model: Calculating wave energy from significant wave height

Significant wave height using WaveTools2012 (Rohweder et al. 2012), and the output was used in a wave energy equation, similar to that used in recent studies (Ekeboom et al. 2003; Chollett and Mumby 2012; Graham et al. 2015; Perry et al. 2015), to approximate the wave energy exposure on the nearshore benthic community in the south-west Indian Ocean region around Aldabra. Wave energy exposure was calculated using Equation 3.1 and is expressed as J/m³.

$$E_w = \frac{1}{16} \rho g \cdot H_s^2 \quad (\text{Eqn.3.1})$$

Wave energy (E_w) was calculated using linear wave theory, following Equation 3.1, where ρ = 1023 kg.m⁻³ is approximate sea water density for this region in the Indian Ocean (Morales et al. 1996), g = 9.98 m.s⁻² the gravitational acceleration, and H_s is the significant wave height. Wave height is the distance between the highest point of the wave crest and the

lowest point of the wave trough. Significant wave height is the average height of the largest third of the wave heights (Munk 1944).

3.3.4.6 Wave model: Deriving significant wave height for each wind direction

Significant wave height maps were calculated for each wind direction within the fetch surface for the maximum daily wind strength for prevailing conditions, and the overall maximum wind strength in each direction for the storm condition model, using the waves module in the Waves2012 Toolbox (Rohweder et al. 2012).

These directional significant wave height maps were then overlaid onto each other, and map containing the highest significant wave height value was sampled from that for each pixel, to create a maximum wave energy exposure experienced during the prevailing and maximum conditions respectively.

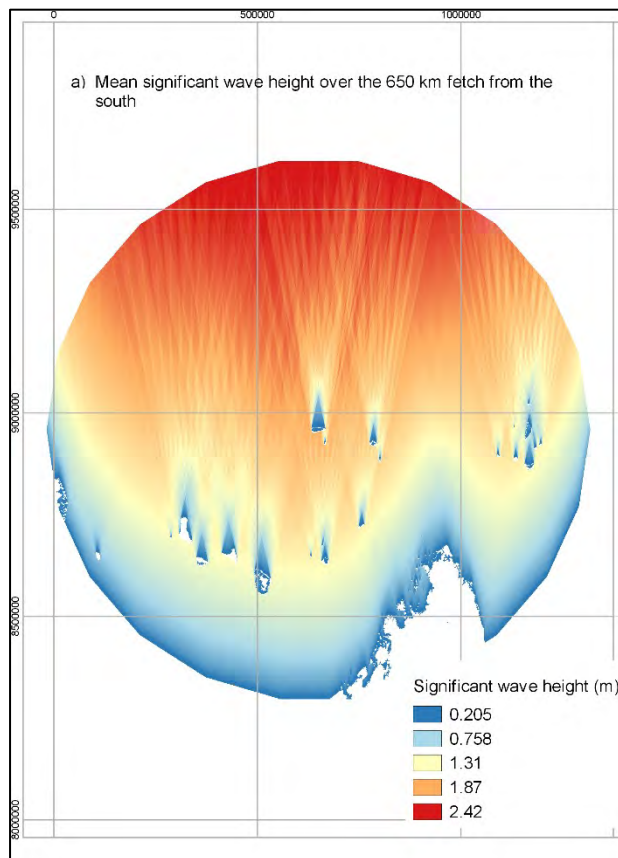


Figure 3.2. An example showing the mean southerly significant wave height within a fetch area of 1.13 million square km around Aldabra Atoll (at the midpoint).

3.3.4.7 Associating depth and wave energy with benthic samples

Direct measurements of depth and modelled wave energy exposure were assigned to the sampling sites using a spatial join ("join attributes by location") in QGIS (Quantum-GIS-Development-Team 2017). Environmental variables were then assessed for their effect on

the probability of occurrence of the broad-scale benthic cover categories derived in Chapter 2.

The effect of environmental variables like slope, current speed and sediment which could affect the distribution of broad-scale benthic cover categories were not included in the GAMs as covariates because the data were not available at the time of analysis.

3.3.5 Statistical analysis

3.3.5.1 The probability of occurrence of the broad-scale benthic cover categories. Binomial generalised additive models (GAMs) were constructed to assess the effects of the wave energy exposure and depth on the probability of occurrence of the six major benthic cover categories defined in Chapter 2 (Table 3.1). Modelling the effects of the environmental modifiers on the probability of occurrence of the 12 fine-scale benthic cover categories was attempted, but a preliminary analysis showed that the data were not suitable in their current form due to zero inflation of the data.

Exploratory analysis revealed a non-linear response in the probability of occurrence to wave energy and depth, and consequently, GAMs were employed because they are well suited to model non-linear and non-monotonic relationship between response and predictor variables (Wood 2011). General Additive Models (GAMs) are a semi-parametric extension of Generalised Linear Models (GLMs), which assume that link functions are additive and that the components in the model are smooth (Guisan et al. 2002). General Additive Models (GAMs) were therefore better suited to model the probability of occurrence of the respective benthic cover categories than GLMs, given their non-linear response to the depth and wave energy. General Additive Models (GAMs) were expressed as:

$$g(E[Y_g]) = X_g^* \theta^* + \sum_h f_h(x_{gh}) \quad (\text{Eqn. 3.2})$$

$E[Y_g]$ is the expected value for the response variable and $g(\cdot)$ is the link function, here defined as the probability of occurrence of the broad-scale benthic cover category. X_g^* is the g^{th} row in the model matrix containing parametric model components. θ^* is the corresponding parameter vector. f_h are the smooth functions for the respective covariates, x_{gh} . (Marra and Wood 2011). Aspect (north, east, south and west) was represented by a parametric model component to which depth, prevailing and storm wave energy were added as tensor product smooths.

Tensor product smooths were used within the GAMs because the units measured by depth (meters), prevailing and storm wave energy (J/m^3) were on scales that differed by several

orders of magnitude. Tensor smooths can deal with variables that are measured values at different scales more efficiently than scaling predictors per unit square can resolve (Wood 2011). Tensor product smooths assume that low-rank bases are available for representing smooth functions for the depth, prevailing and storm energy, and respectively expressed as:

$$f_x(x) = \sum_{i=1}^I \alpha_i a_i(x)$$

$$f_z(z) = \sum_{j=1}^J \delta_j d_j(z)$$

$$f_v(v) = \sum_{k=1}^K \beta_k b_k(v)$$

(Eqn.3.3 a-c)

Where α_i, δ_j and β_k are parameters and $a_i(x), d_j(z)$ and $b_k(v)$ are known basis functions. The smooth function of x and z can therefore be expressed as:

$$\alpha_i(z) = \sum_{l=1}^L \delta_{il} d_l(z)$$

(Eqn.3.4)

which can be expressed as

$$f_{xz}(x, z) = \sum_{i=1}^I \sum_{j=1}^J \delta_{ij} d_j(z) a_i(x)$$

(Eqn.3.5)

The smooth function of all three tensor smooths x, z and v was therefore expressed as:

$$f_{xzv}(x, z, v) = \sum_{i=1}^I \sum_{j=1}^J \sum_{k=1}^K \beta_{ijk} b_k(v) d_j(z) a_i(x)$$

(Eqn.3.6)

The MGCV package was used to generate the GAMs in R (Wood 2011). Models were run using the binomial family and the logit link. An interaction between depth and prevailing wave energy, and depth and storm wave energy were expected given that waves slow down and break as a function of their height relative to bottom depth, and the full model was expressed as:

$$\text{Logit}(Y_i) = \alpha + \text{factor}_1(\text{aspect}) + f_1(\text{depth} \times \text{prevailing wave energy}) \\ + f_2(\text{depth} \times \text{storm wave energy}) + \epsilon$$

(Eqn.3.7)

Y_i is the i^{th} response variable(s) (probability of occurrence for the respective broad-scale benthic categories).

The tensor product smooths were parameterized at a set number of “knots” for each benthic cover category. Setting the number of knots foregoes optimality in the GAM but it avoids over-fitting the model to the data. The k-value was not reduced such that the k'-index fell below 1 (Marra and Wood 2011).

Tensor product smooths were penalised based on a measure of “wiggleness” of the marginal smooths and evaluated using the Un-Biased Risk Estimator (UBRE) statistic (Wood 2011). Smoothing parameters, and their combinations were chosen to minimise the estimate Mean Sum of Errors by minimising UBRE statistic and the Akaike Information Criterion (AIC) (Wood 2011). The fit of models was visually evaluated by comparing the fit of the predicted line to the observed data points and evaluating the values of AIC. The use of both logit and clog-log link function was assessed, given that the data contained many more zeros than ones. The logit link was used as the model fit and AIC score were lower than when using the clog-log link function.

The GAMs were plotted for each aspect of the coastline as the shape of the reef crest varies around the coast (personal observation, and see descriptions in results), and the shape of the reef crest is known to affect wave energy dissipation (Monismith et al. 2015). Predicted results were displayed as panel plots using LATTICE (Sarkar 2008), holding first wave energy constant, and varying depth, and then holding depth constant and varying wave energy.

3.4. RESULTS

3.4.1 Characteristics of environmental variables

3.4.1.1 Wind speed and direction

Wind records yielded a mean of 4.95 m/s at 09:00 AM from May to September between 2012 and 2015. The daily wind speed at Aldabra increased throughout the morning and peaked at 13:00 before it started dropping (Figure 3.3). The maximum wind speeds did not always occur at 13:00 (Figure 3.4).

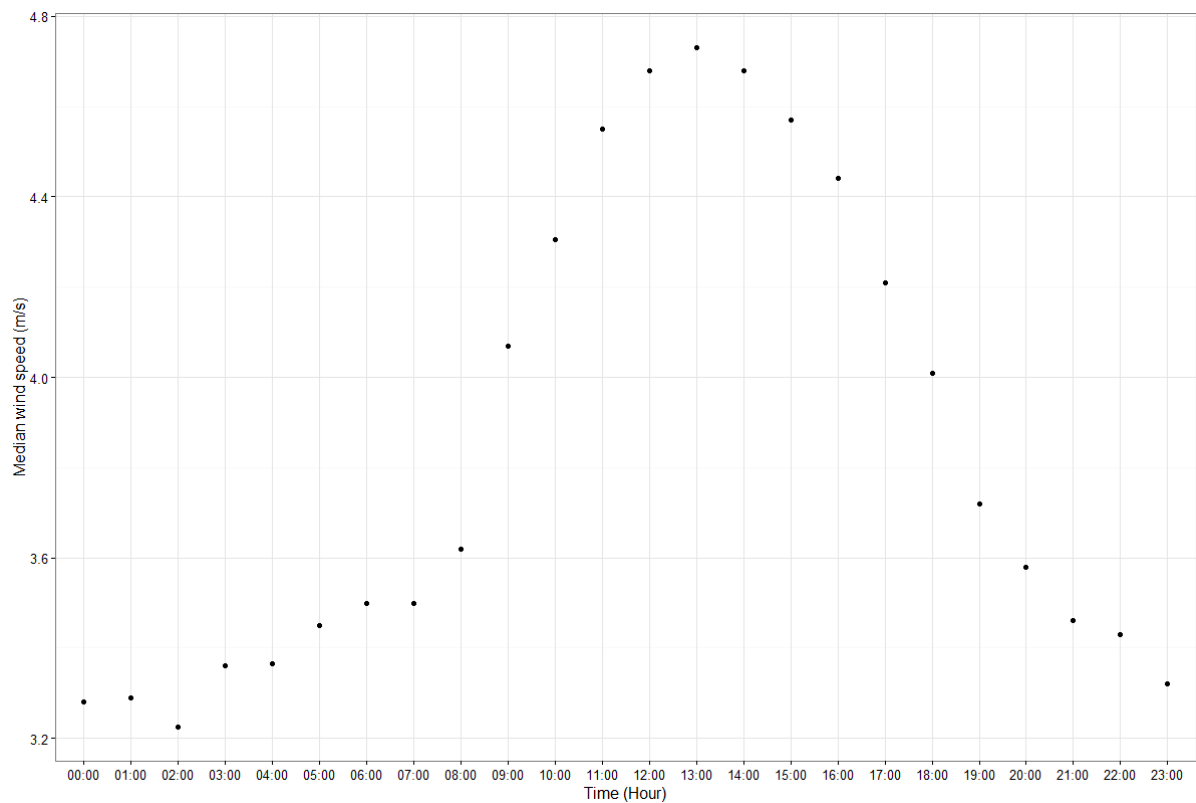


Figure 3.3. Median hourly wind speed from three years data 2012-04-01 to 2015-03-31 showing the change in wind speed throughout the day.

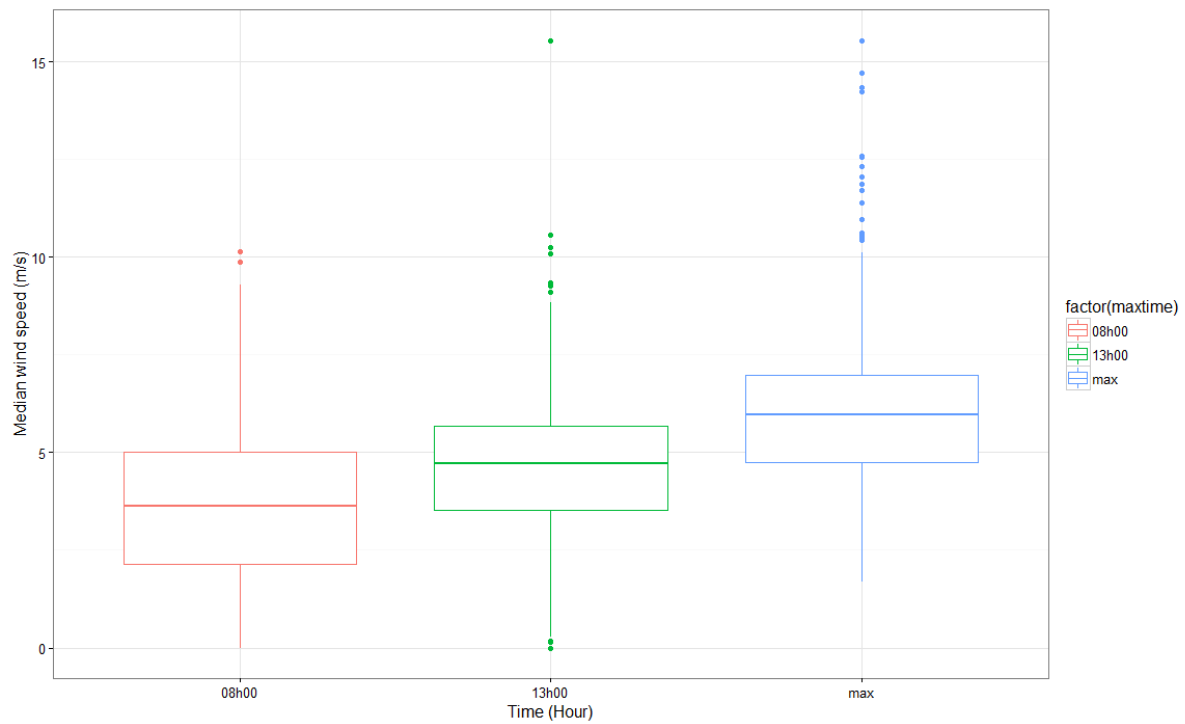


Figure 3.4. Wind speed at 08:00, 13:00 and the daily maximum wind speed record.

Three years' maximum daily wind data are displayed in the wind rose below (Figure 3.5) for measurements from 2012-04-01 to 2015-03-31, showing the temporal dominance of the southeasterly wind component. The highest wind speeds were recorded during storms in the northwest monsoon, as indicated by the red bars when wind speeds exceeded 12m/s (Figure 3.5).

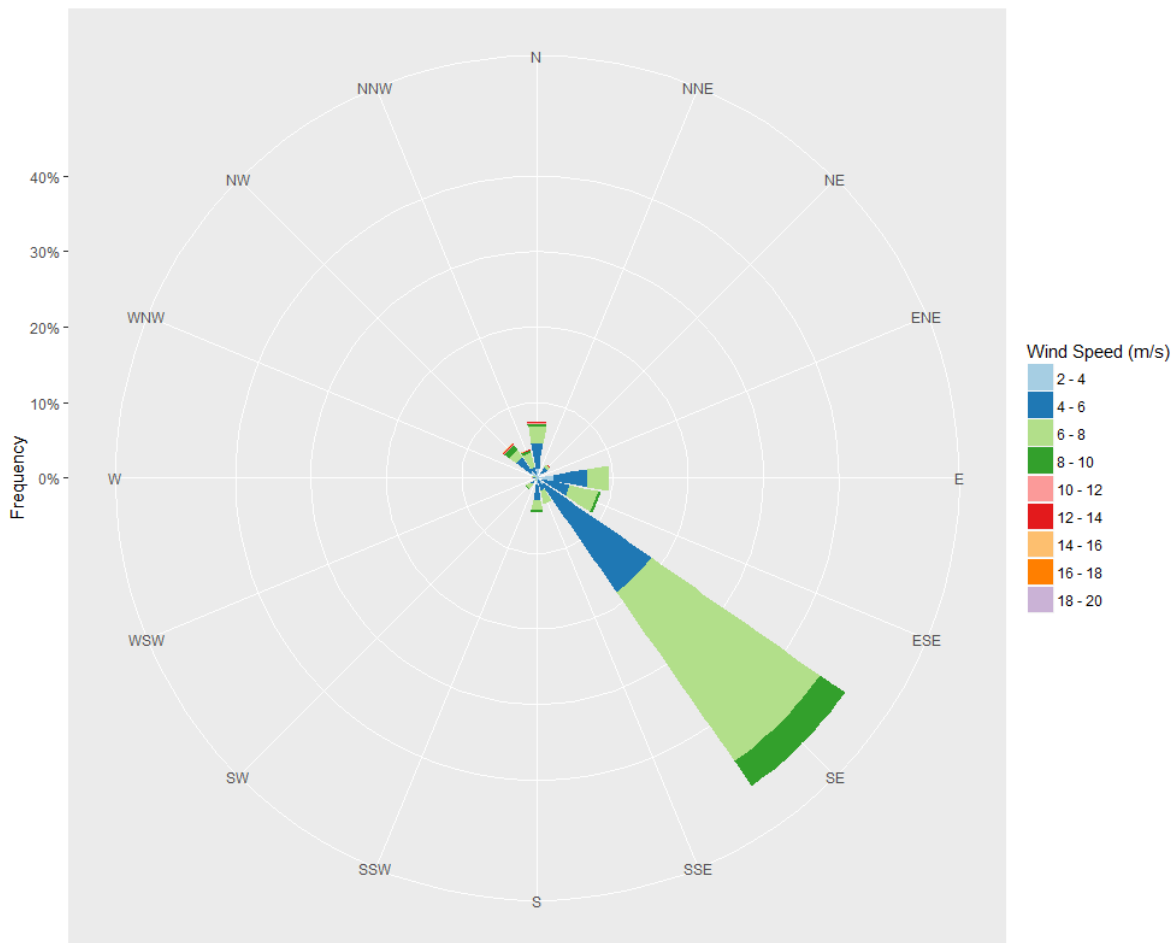


Figure 3.5. Windrose showing the frequency of maximum daily wind speed in each of the cardinal wind directions recorded at Aldabra from 2012-04-01 to 2015-03-31, used to provide an index of wave exposure at different sampling sites.

3.4.1.2 Spatial distribution of wave energy

Due to the strong monsoonal climate, the wind-driven wave energy was highly directional, and consequently, variation in exposure thereto was generated around the island. This resulted in a sheltered west coast, with values ranging between 4 652 and 7413 J/m³ and highly exposed east coast ranging between 9 160 and 11 179 J/m³. Maximum prevailing wave energy was associated with the northeast coast, and the second area with an elevated level of exposure was on the southwestern corner of Aldabra. Minimum prevailing wave energy was distributed to around the west and north coasts. The north coast showed a greater degree of variation in wave energy, from low levels of exposure in the west (4 277 J/m³) to high levels of exposure in the east (10 608 J/m³). The south coast was moderate to highly exposed, ranging between 7 162 to 8 998 J/m³. The spatial distribution patterns of prevailing wave energy were consistent with personal observations made between 2011 April – 2015 May.

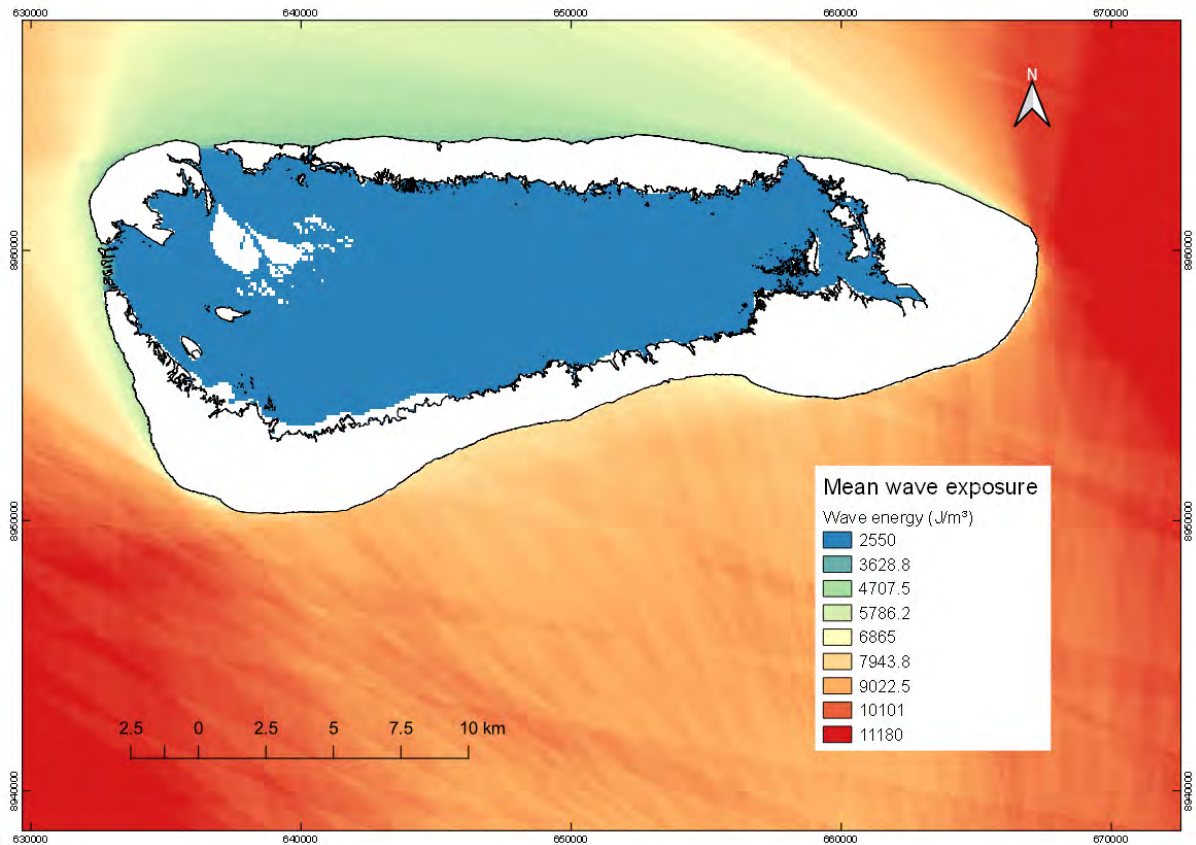


Figure 3.6. Exposure to prevailing wave energy (J/m^2) at Aldabra Atoll, between 2012 and 2015

The map of storm wave energy exposure shows the maximum wave energy experienced within any pixel (100m^2) during the three-year period from April 2012 – April 2015 (Figure 3.7). Storm events at Aldabra were infrequent during this period, and typically in a northerly direction (Figure 3.5). The maximum level of wave energy exposure was consequently experienced on the north coast and was three times greater on north-facing than south-facing coastlines of the atoll. The mean storm wave energy was experienced at the sampling sites was $253\,433.3 \text{ J/m}^2 \pm 5\,528.84 \text{ SE}$, which is 37 times greater than the mean during prevailing conditions.

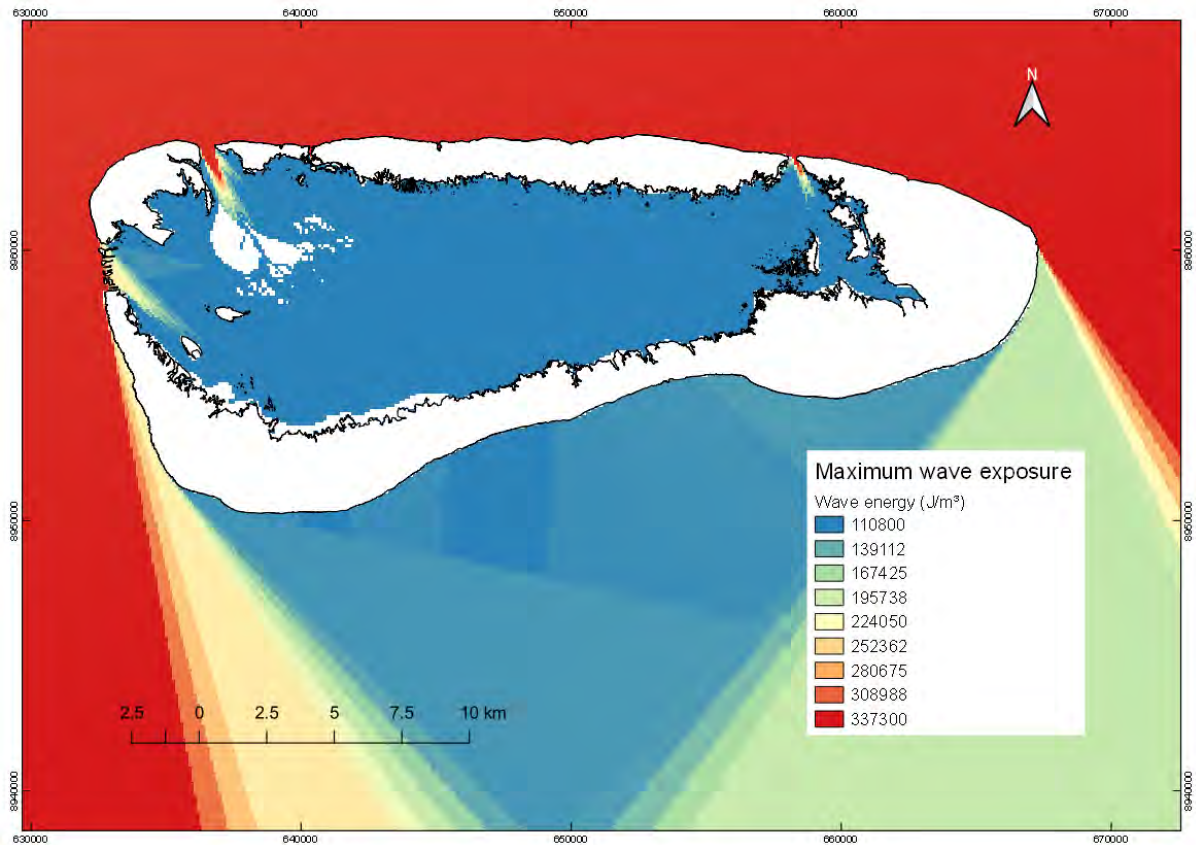


Figure 3.7. Exposure to maximum wave energy (J/m^3) between 2012 – 2015 at the Aldabra atoll was dominated by sporadic northerly storm-driven waves.

3.4.1.3 Summary of environmental variables at benthic sampling sites

Prevailing (mean of daily maximum), and storm (overall maximum) wave exposures were modelled and associated with the sampling sites to establish their effects on the benthic cover categories. The mean prevailing wave energy exposure associated with sampling sites was $6\,805\text{ J/m}^3$ (Table 3.2). The maximum exposure to prevailing wave energy occurred on the north-eastern tip of Aldabra with values of $11\,180\text{ J/m}^3$ (Figure 3.6 and Table 3.2). The lowest value associated with the sampling site localities was at the Main Channel ($2\,550\text{ J/m}^3$), which was an outlying low value, and this sample was discarded prior the data set for analysis, given the disproportionate sheltering it receives by being surrounded by islands. The next lowest value associated with a benthic sampling site was $4\,277\text{ J/m}^3$ which was the north-western side of Picard.

Table 3.2. Summary of the continuous environmental variables at benthic sampling sites on the seaward reefs of Aldabra Atoll between April 2012 and April 2015.

Variable	Mean	Standard error	Standard deviation	Minimum	Maximum
Depth (m)	12.35	0.74	12.62	0.9	50.9
Prevailing wave energy (J/m ³)	6805	105	1785	4277	11179
Storm wave energy (J/m ³)	253433	5529	93990	110780	337336

Sampling sites on the west coast and north coast had a lower mean exposure to wave energy during prevailing conditions than on the south and east coast (Table 3.3). During storm conditions, the mean wave energy was higher on the north and west coast than south and east coast (Table 3.3). Sampling sites on the north and east coast were collected over a greater depth range than on the west and south coast as the forereef slope extended to deeper depths on the north and east coast.

Table 3.3. The mean and standard error of environmental variables for benthic sampling sites from the four aspects of the coast of Aldabra.

Aspect	Depth	Prevailing wave energy (J/m ³)	Storm conditions wave energy (J/m ³)
North	17.2 ± 1.3	5531 ± 142	331139 ± 232
East	13.3 ± 1.5	9800 ± 104	217669 ± 12201
South	9.2 ± 1.1	8024 ± 51	123397 ± 1781
West	7.4 ± 7.4	6024 ± 72	305292 ± 4716

In total of 289 samples were included in the analysis after two outliers (in the Main Channel) were removed from the analysis. The north coast had the greatest proportion (30 %) of sites associated with Rubble, while the south coast had the greatest proportion of Macroalgae (24 %). The leeward west coast had the greatest proportion of Sand (35 %) and sites dominated by an Epilithic algal matrix (11 %). The exposed east coast had the greatest proportion of Macroalgae sites (47 %). The windward east and south coast had very few Sand sites and relatively high proportion of Seagrass sites (17 %) (Table 3.4).

Table 3.4. The number of sampling sites associated with each of the broad-scale benthic cover categories along the four aspects of the coastline at Aldabra.

Aspect	Epilithic algal matrix	Hard coral	Rubble	Macroalgae	Seagrass	Sand	Total
North	10	20	34	13	6	30	113
East	2	7	2	14	5	0	30
South	6	20	8	34	14	2	84
West	7	12	3	14	4	22	62
Total	25	59	47	75	29	52	289

3.4.2 Relationship between environmental variables and benthic cover

The covariates considered for inclusion in the GAMs were aspect, depth, prevailing wave energy and storm wave energy. The inclusion of storm wave energy resulted in a decrease of the AIC values, compared to GAMs without this term, e.g. AIC from 226 to 220 for Hard-coral's GAM with the addition of storm wave energy. However, the inclusion of storm wave energy did not significantly improve the GAMs, (e.g. Hard coral: ANOVA edf = 2.86, $\text{Chi}^2 = 5.23$, $p > 0.226$, and these models tended to overfit the data. As a result, storm wave energy was removed from the analysis for broad-scale benthic cover categories.

The most parsimonious model used for predicting the probability of occurrence of broad-scale benthic cover categories was expressed as

$$\text{Logit}(Y_1) = \alpha + \text{aspect} + f_1(\text{depth} \times \text{prevailing wave energy}) + \epsilon \quad (\text{Eqn. 3.8})$$

Where Y is the response variable (probability of occurrence of the respective benthic cover categories), the aspect is the factor, f_1 is the tensor smooth of depth and prevailing wave energy, and ϵ is the unexplained variability. All models were fit using three knots ($k = 3$), as a greater number of knots resulted in overfitting of the GAMs.

3.4.2.1 Probability of occurrence of the respective benthic cover categories

The most parsimonious GAM for Epilithic algal matrix was able to explain 24 % of the observed variability in the data (adjusted R-square). The aspect significantly altered the probability of occurrence of the Epilithic algal matrix, but neither depth nor wave energy significantly changed the probability of occurrence of the Epilithic algal matrix (Table 3.5, Figure 3.8 and Figure 3.9). See Annex Chapter 3 - Figure 3.21 for three-dimensional plots of the GAMs developed for each of the six broad-scale benthic cover types.

Table 3.5. Generalised Additive Model (GAM) results showing the significance of aspect, and the tensor smooth product (te) of depth and prevailing wave energy in predicting the probability of occurrence for the six broad-scale benthic cover categories. Where edf is the estimated degrees of freedom, and X^2 = Chi-square statistic.

Benthic cover category	Statistic	aspect	Significance	te (depth, prevailing wave energy)	Significance
Epilithic algal matrix	edf	3		7.90	
	X^2	10		13.50	
	p	0.01	**	0.09	
Hard coral	edf	3		7.60	
	X^2	7.5		39.60	
	p	0.057		0.000004	***
Rubble	edf	3		9.40	
	X^2	4.5		41.20	
	p	0.22		0.00003	***
Macroalgae	edf	3		4.20	
	X^2	7.6		8.10	
	p	0.06		0.12	
Sand	edf	1		3.00	
	X^2	0		29.60	
	p	1		0.000002	***
Seagrass	edf	3		3.00	
	X^2	15.6		16.50	
	p	0.001	**	0.0008	***

Significance levels < 0.001 = ***, < 0.01 = **, < 0.05 = *

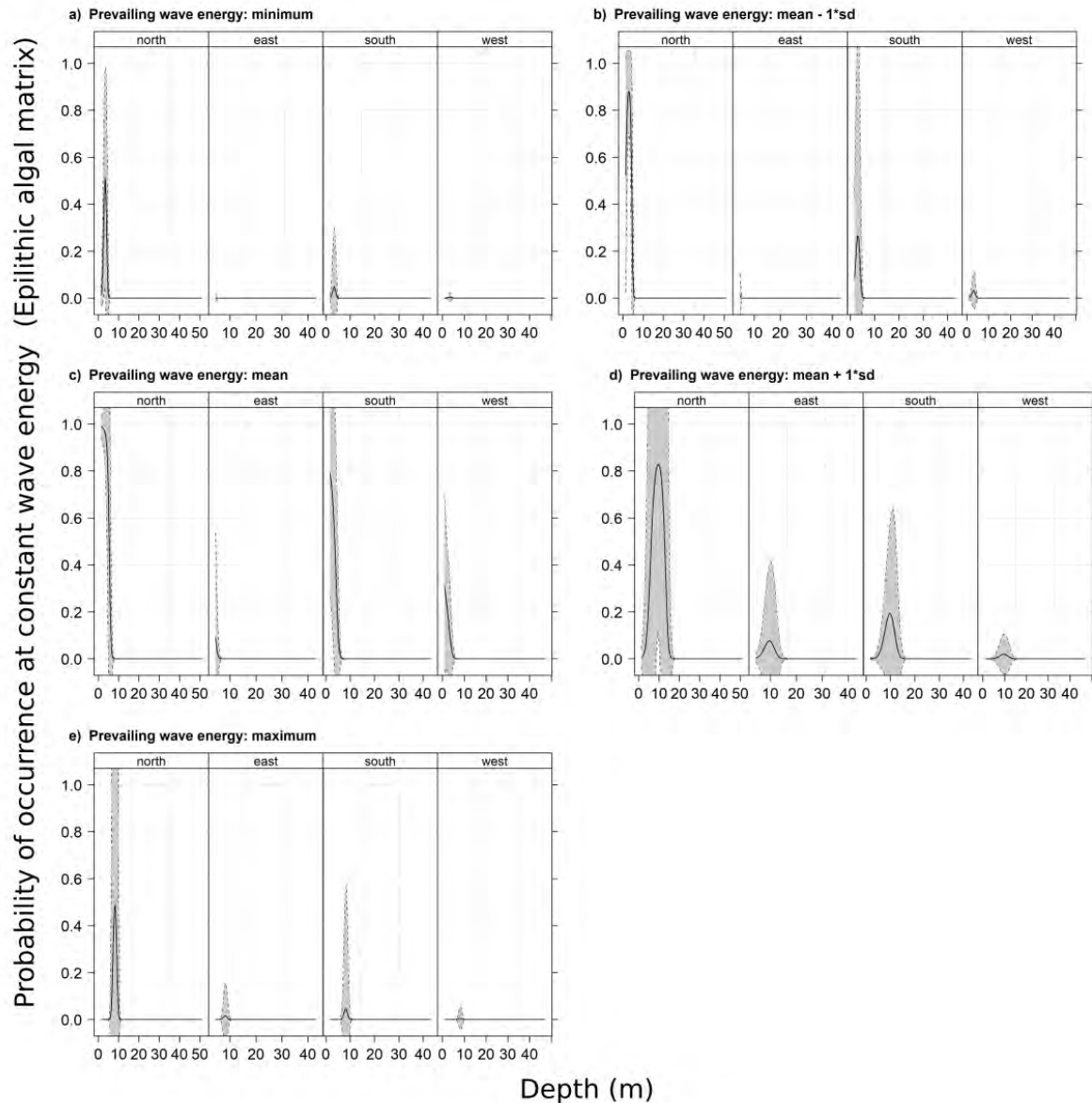


Figure 3.8. Generalised Additive Models (GAMs) showing the probability of occurrence of Epilithic algal matrix (EAM), holding prevailing wave energy constant at a) the minimum, b) mean minus one standard deviation, c) mean, d) mean plus one standard deviation and e) maximum while varying depth. Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

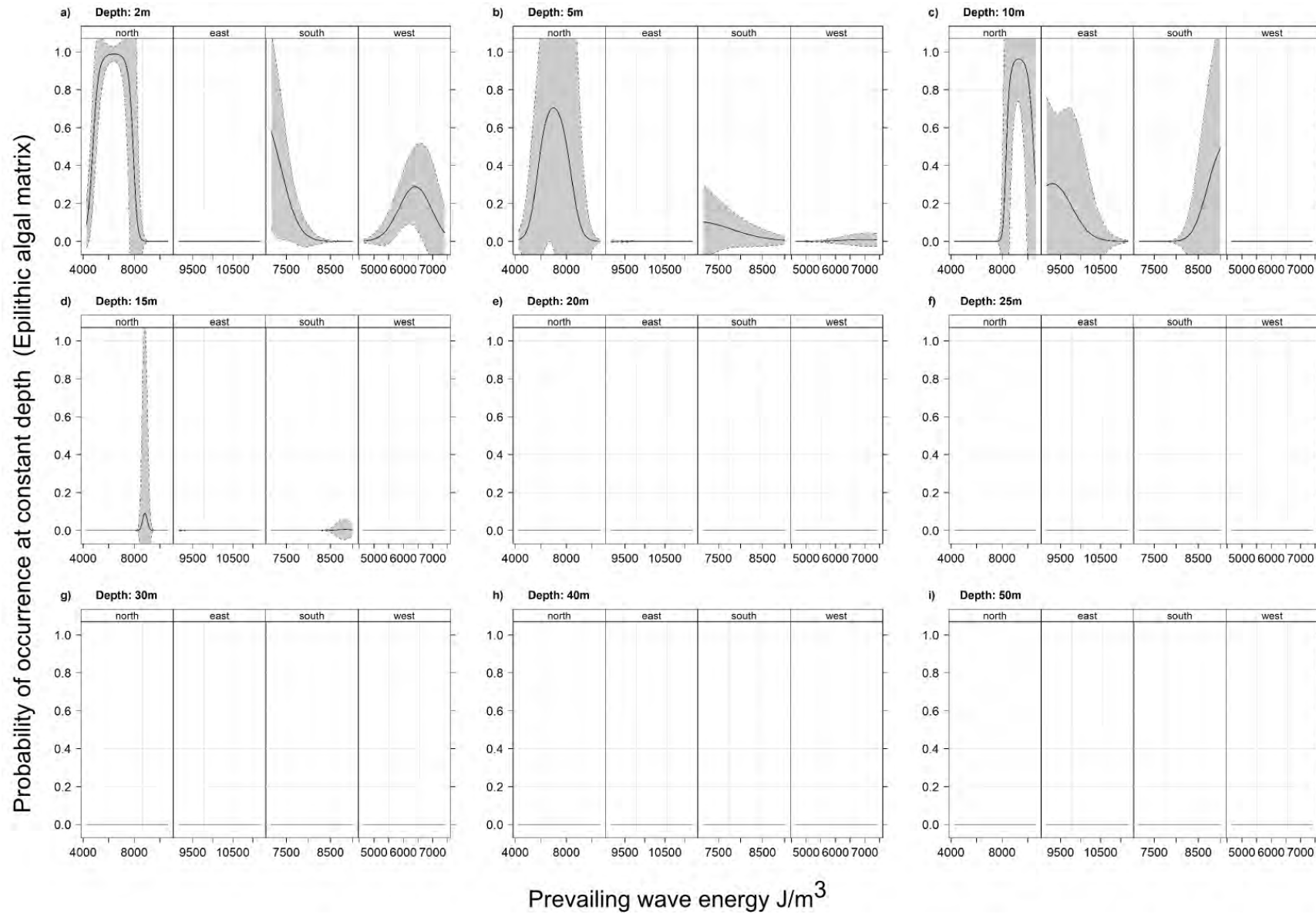


Figure 3.9. Generalised Additive Models (GAMs) showing the effect of wave energy on Epilithic algal matrix while depth was held constant at 2m (a), 5m (b), 10m (c), 15m (d), 20m (e), 25m (f), 30m (g), 40m (h), 50m (i), in the respective plots. The four aspects of Aldabra, north, east south and west are represented in the panels in each plot.

The most parsimonious model of the probability of occurrence of Hard coral was able to explain 29 % of the variability in the data (adjusted R-square). Depth and prevailing wave energy exposure significantly altered the probability occurrence of Hard coral cover, but aspect did not (Table 3.5). The probability of occurrence of Hard coral cover was greatest in water depth between 10 and 18 m, on all aspects of the coast, in all levels of exposure to wave energy (Figure 3.10). Hard coral cover had a greater probability of occurrence in deeper water with an increase in exposure to wave energy, shifting from 10 m depth under 5020 J/m^3 (mean minus one standard deviation) to 18 m under 11179 J/m^3 (maximum wave energy).

The probability of occurrence of Hard coral cover was greatest at low to moderate levels of exposure to wave energy (4000 J/m^3 to 6000 J/m^3) in 2 to 20 m depth on the north and west coast (Figure 3.11). The probability of occurrence of Hard coral cover declined where exposure to wave energy exceeded the mean and mean plus one standard deviation (Figure 3.10). There was an increased probability of occurrence of Hard coral cover with exposure to wave energy on the exposed east coast at 20 m depth (Figure 3.11). The increase in the probability of occurrence of Hard coral with depth at the minimum wave energy exposure level appears to be an incorrect artefact caused by the GAM model (Figure 3.10). This artefact may be explained by a general increase in hard coral with depth, and a lack of samples from the depths between 35 and 50 m where coral cover is significantly reduced along the most sheltered section of the west coast of Aldabra (See Figure 2.7).

The probability of occurrence was not significantly different between the four aspects, and trends appear similar in the four aspects but are shifted to deeper depths in the more exposed aspects (south and east) than the leeward aspects (west and north) (Table 3.5, Figure 3.10, and Figure 3.11).

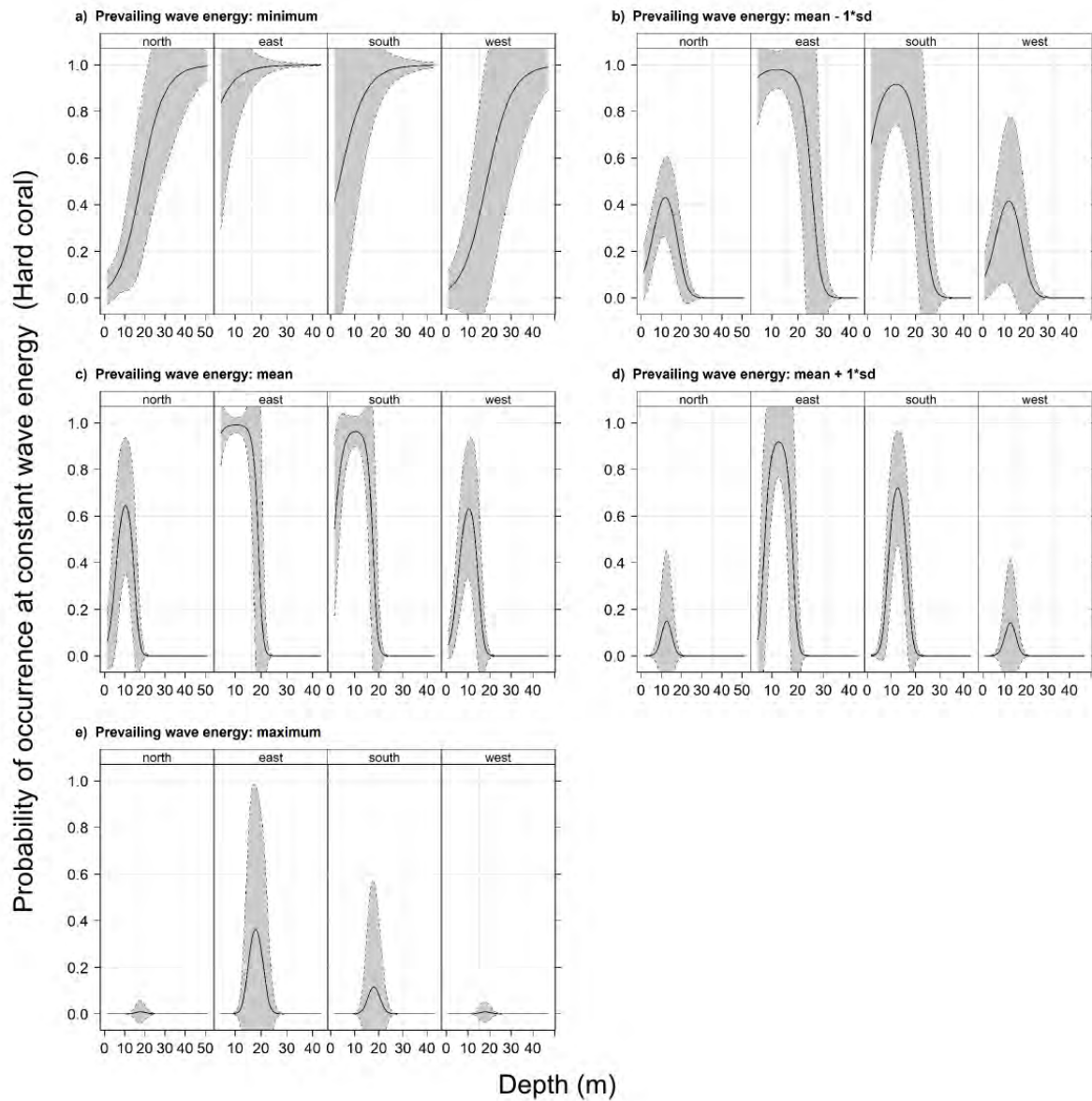


Figure 3.10. Generalised Additive Models (GAMs) showing the probability of occurrence of Hard coral, holding prevailing wave energy constant at a) the minimum, b) mean – 1 standard deviation, c) mean, d) mean plus one standard deviation and e) maximum while varying depth. Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

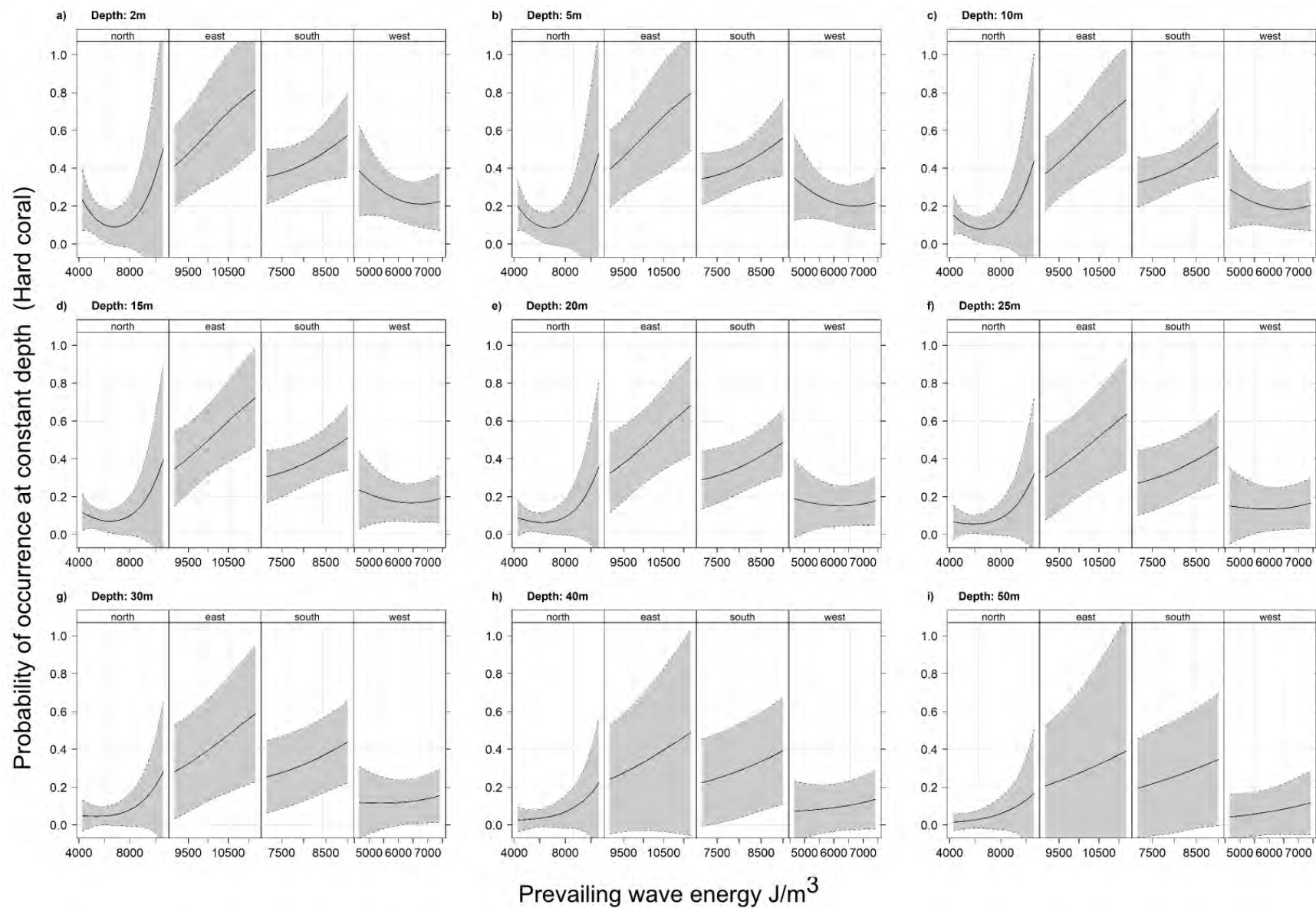


Figure 3.11. Generalised Additive Models (GAMs) showing the probability of occurrence of Hard coral while depth was held constant at 2m (a), 5m (b), 10m (c), 15m (d), 20m (e), 25m (f), 30m (g), 40 (h), 50m (i). Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

The GAM for the probability of occurrence of Rubble cover explained 31 % of the variability in the data (R-square adjusted). The effect of depth and exposure to prevailing wave energy on the probability of occurrence of Rubble cover was highly significant (Table 3.5). The probability of occurrence of Rubble increased with depth, under increasing levels of exposure to wave energy (Figure 3.12): The depth at which the probability of occurrence of Rubble was greatest increased with an increase in exposure to wave energy, shifting in depth from 10 m under minimum levels of wave energy (4277 J/m^3) to 30 m under maximum wave energy (11179 J/m^3).

The probability of occurrence of Rubble cover decreased with an increase in exposure to wave energy in shallow depths (2 to 10 m) but increased on the east coast with increasing levels of exposure at greater depths (15 – 50 m) (Figure 3.13). The patterns were not consistent along all aspects of the Aldabra coastline. The probability of occurrence of Rubble cover on the south coast decreased with an increase in wave energy (Figure 3.13). On the sheltered west coast, Rubble cover had the greatest probability of occurrence was around 6000 J/m^3 and decreased with greater levels of wave energy exposure (Figure 3.13). The very large 95 % confidence intervals (CI) around the predicted mean suggests that there was a high degree of uncertainty in the predicted patterns.

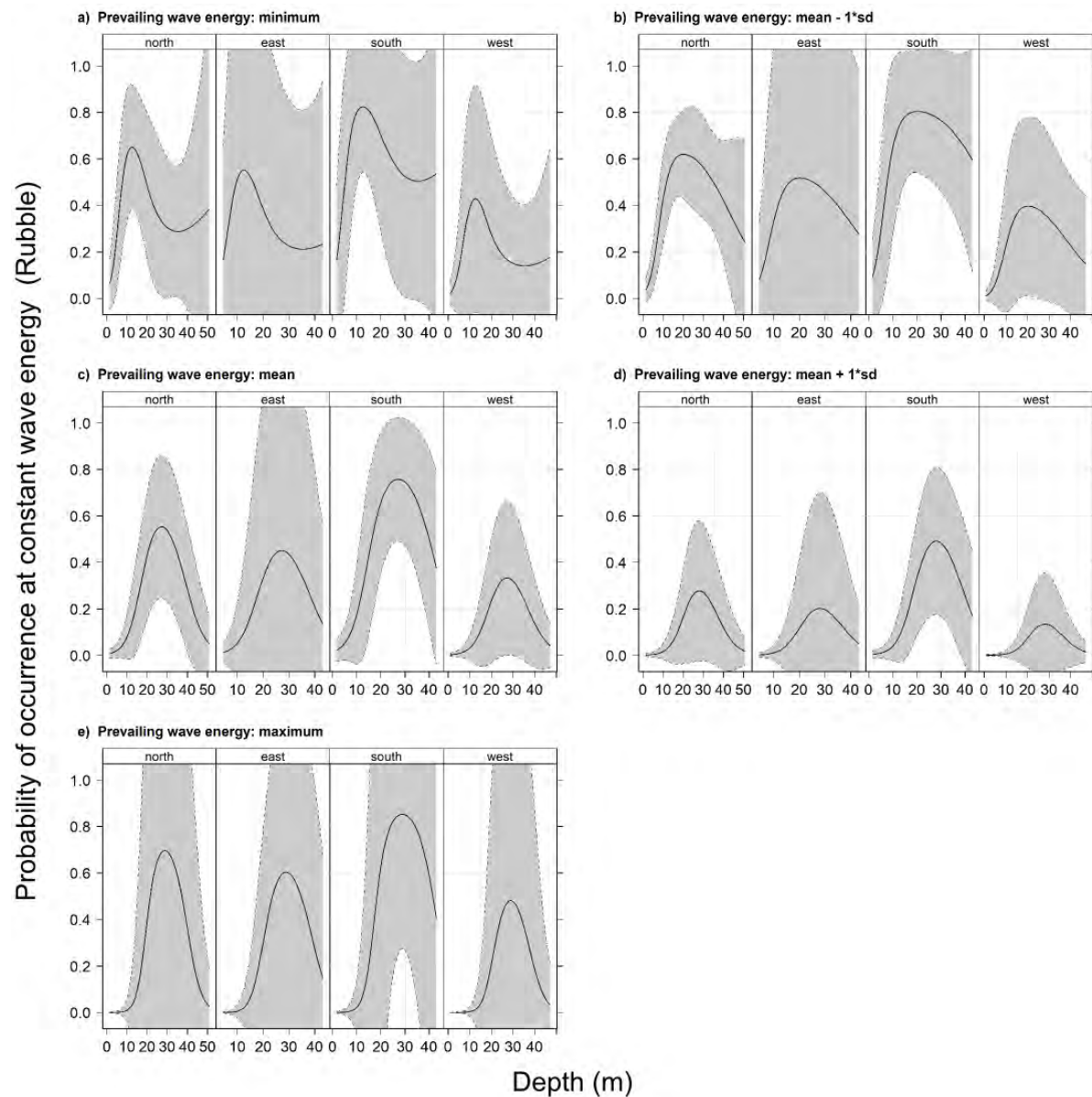


Figure 3.12. Generalised Additive Models (GAMs) showing the probability of occurrence of Rubble, with depth while holding prevailing wave energy constant at a) the minimum, b) mean – 1 standard deviation, c) mean, d) mean plus one standard deviation and e) maximum. Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

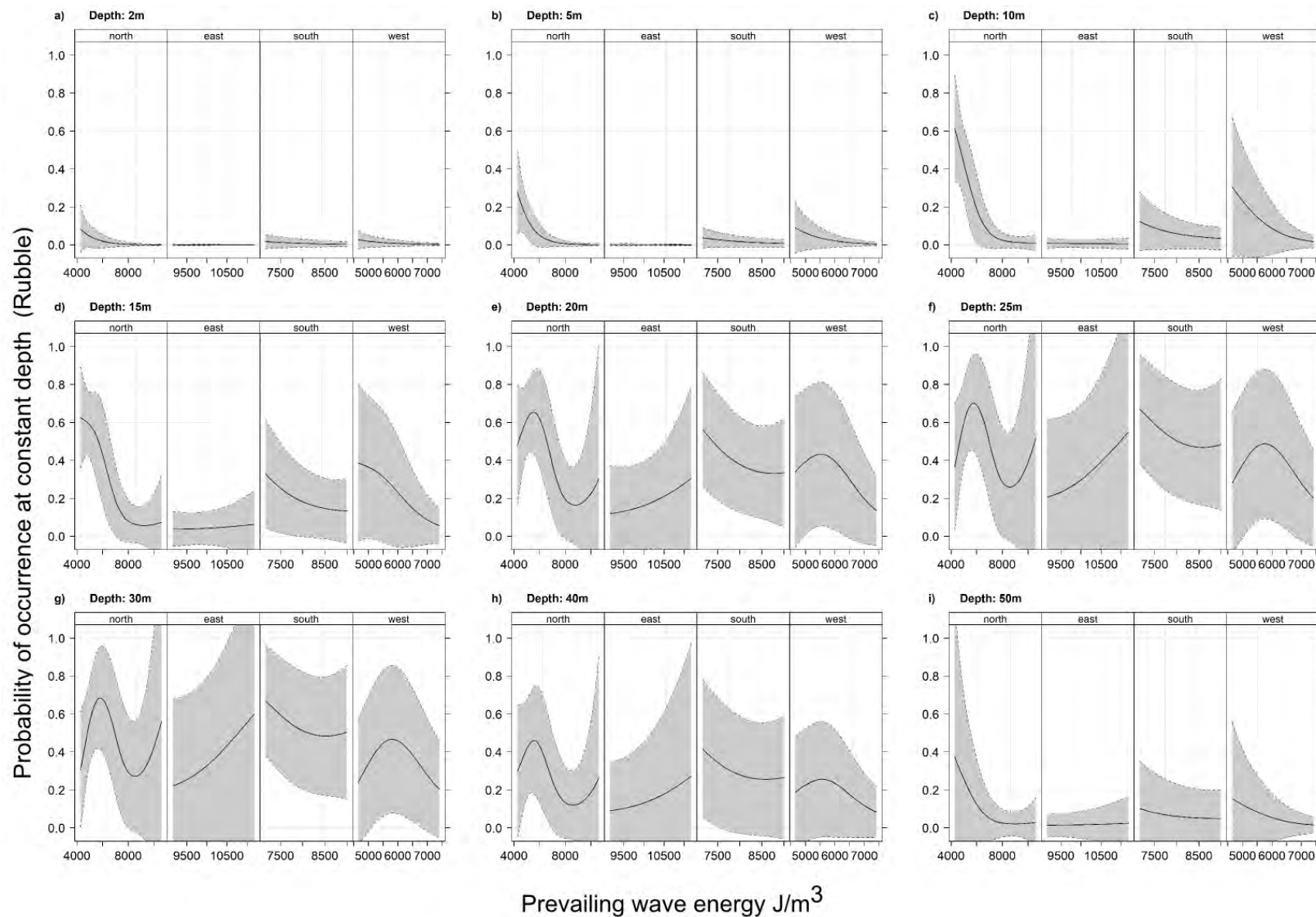


Figure 3.13. The probability of occurrence of Rubble with wave energy while depth was held constant at 2m (a), 5 m (b), 10 m (c), 15m (d), 20 m (e), 25 m (f), 30 m (g), 40 m (h), 50 m (i). Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

The GAM used to investigate the probability of occurrence of Macroalgae cover had a relatively poor fit (R-square adjusted = 0.1) and explained 12 % of the variation in the data. Neither aspect, depth nor exposure to prevailing wave energy significantly altered the probability of occurrence of Macroalgae (Table 3.5). Despite results being non-significant, the trends in the probability of occurrence of Macroalgae were the same on all four aspects in relation to depth and prevailing wave energy: The probability of occurrence of Macroalgae decreased with depth at all levels of wave exposure and its probability of occurrence increased with wave energy (Figure 3.14 and Figure 3.15).

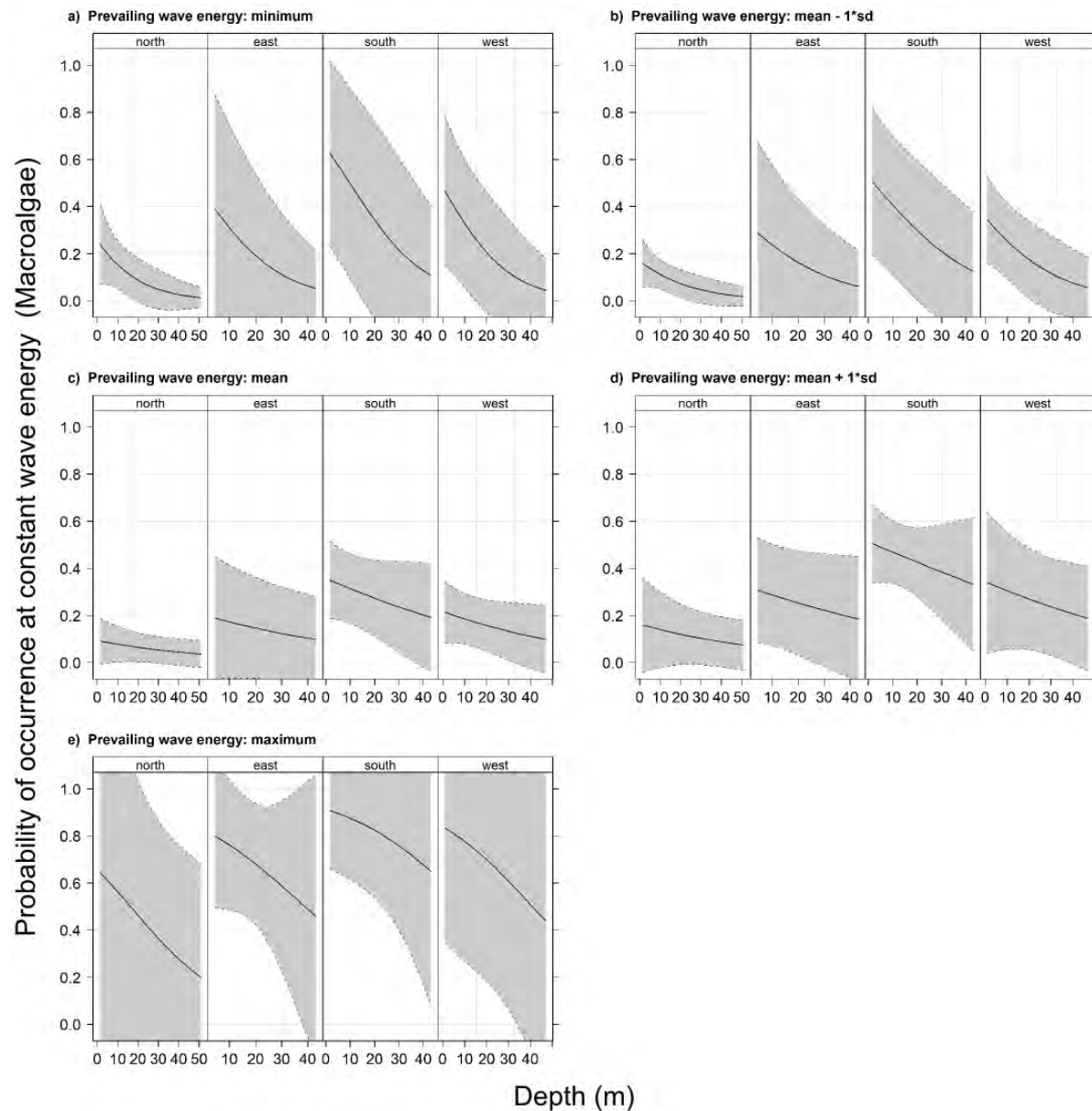


Figure 3.14. Generalised Additive Models (GAMs) showing the probability of occurrence of *Macroalgae*, while holding prevailing wave energy constant at a) the minimum, b) mean minus one standard deviation, c) mean, d) mean plus one standard deviation and e) maximum while varying depth. Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

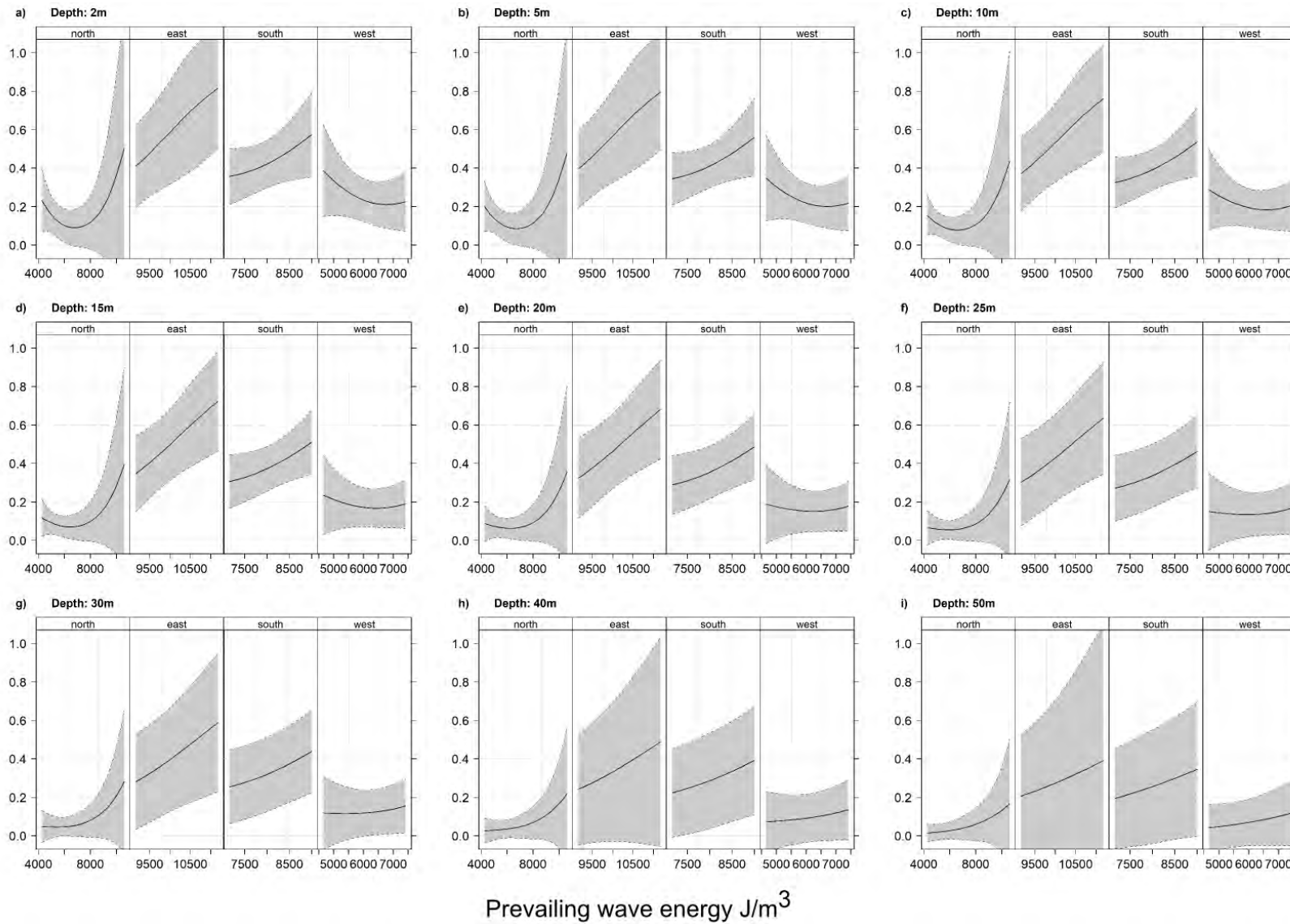


Figure 3.15. Generalised Additive Models (GAMs) showing the probability of occurrence of Macroalgae with wave energy while holding depth constant at 2m (a), 5 m (b), 10 m (c), 15 m (d), 20 m (e), 25 m (f), 30 m (g), 40 m (h), 50 m (i). Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

The GAM investigating the probability of occurrence of Sand cover explained 30 % (R-square adjusted) of the variation in the data. Depth and wave energy were significant in affecting the probability of occurrence of Sand cover, but the effect of aspect was not significant (Table 3.5). The probability of occurrence of Sand cover increased with depth at all levels of exposure to wave energy (Figure 3.16). The probability of Sand cover on the west and north coast was above 0.6 in depths exceeding 30 m. The probability of occurrence of Sand cover increased with an increase in wave energy (Figure 3.17). Sand cover was absent on the exposed east coast and therefore no relationship is shown in the plots of the GAM results (Figure 3.16 and Figure 3.17).

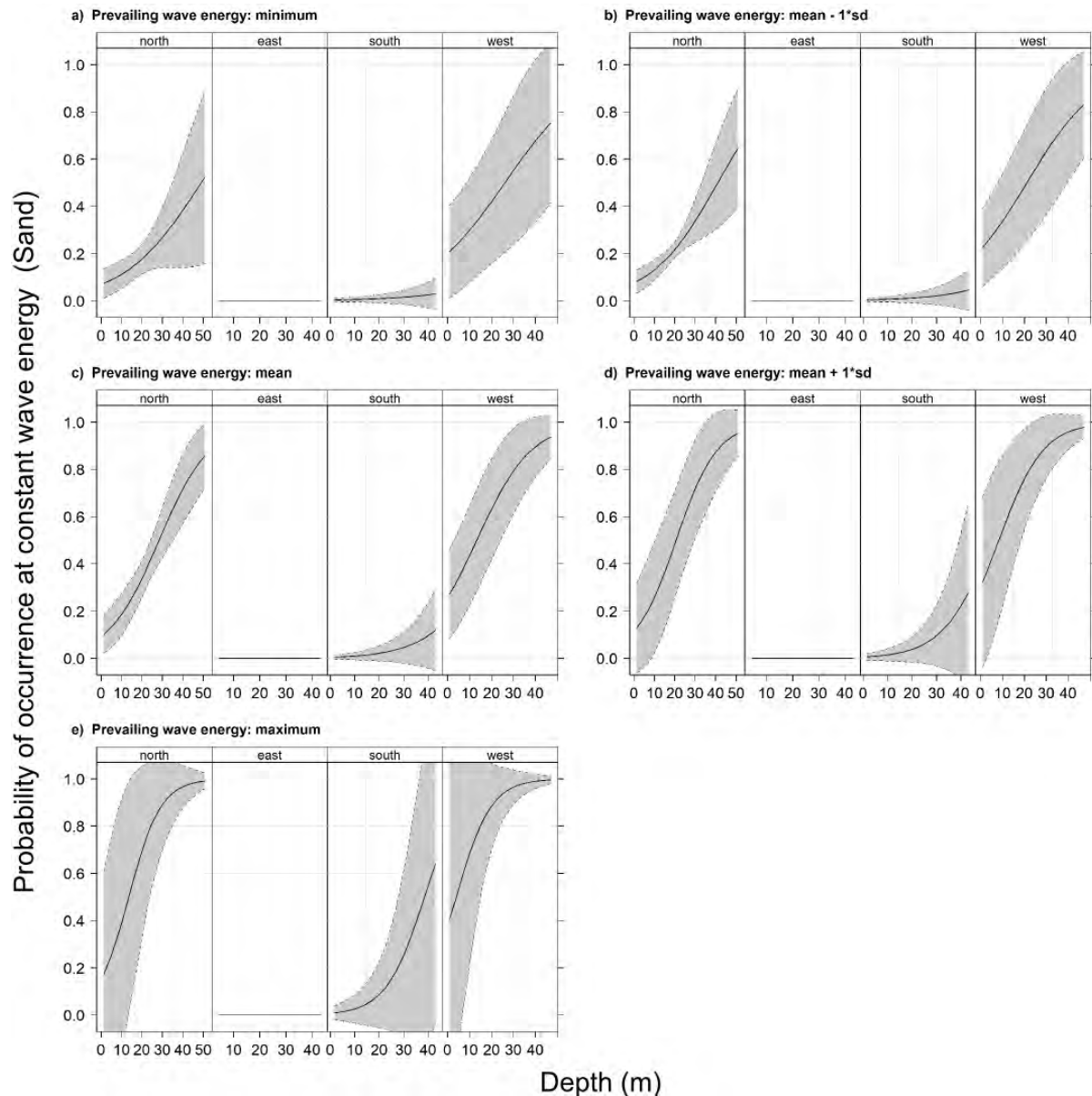


Figure 3.16. Generalised Additive Models (GAMs) showing the probability of occurrence of Sand, holding prevailing wave energy constant at a) the minimum, b) mean – 1 standard deviation, c) mean, d) mean plus one standard deviation and e) maximum while varying depth. Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

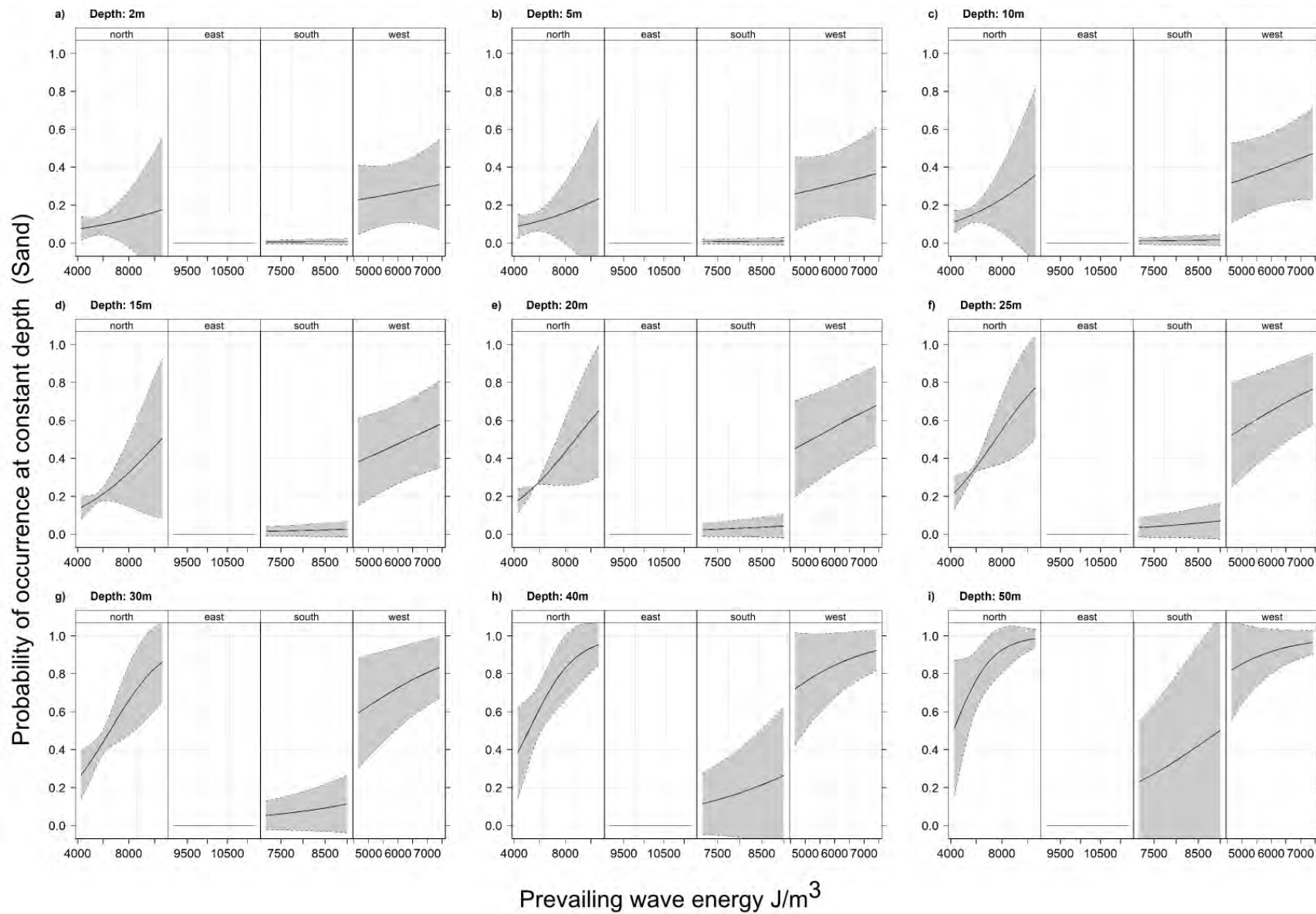


Figure 3.17. Generalised Additive Models (GAMs) showing the probability of occurrence of Sand with wave energy while holding depth constant at 2m (a), 5m (b), 10m (c), 15m (d), 20m (e), 25m (f), 30m (g), 40m (h), 50m (i). The panels on the plots represent the four main aspects of the Aldabra coastline, north, east, south and west.

The GAM for the probability of occurrence of Seagrass cover explained 39 % of the variance in the data. Depth, wave energy and aspect had a significant effect on the probability of occurrence of Seagrass (Table 3.5). The probability of occurrence of Seagrass cover was restricted to depths less than 10 m in wave energy ranging from minimum (4277 J/m^3) to the mean plus one standard deviation (8590 J/m^3) (Figure 3.18). Seagrass had a greater probability of occurring beyond 10 m depth at the maximum level of wave energy (11179 J/m^3) along all aspects of the coast (Figure 3.18). The probability of occurrence of Seagrass became zero along all aspects of the Aldabra coast in depths exceeding 25 m (Figure 3.18). The probability of occurrence of Seagrass cover at 2 m was greatest on the exposed east coast (Figure 3.19). The probability of occurrence of Seagrass cover was increased with wave energy at depths greater than 5 m on the exposed east coast, while the probability of occurrence of Seagrass diminished to nearly zero at depths exceeding 5 m on all other aspects of the coast (Figure 3.19).

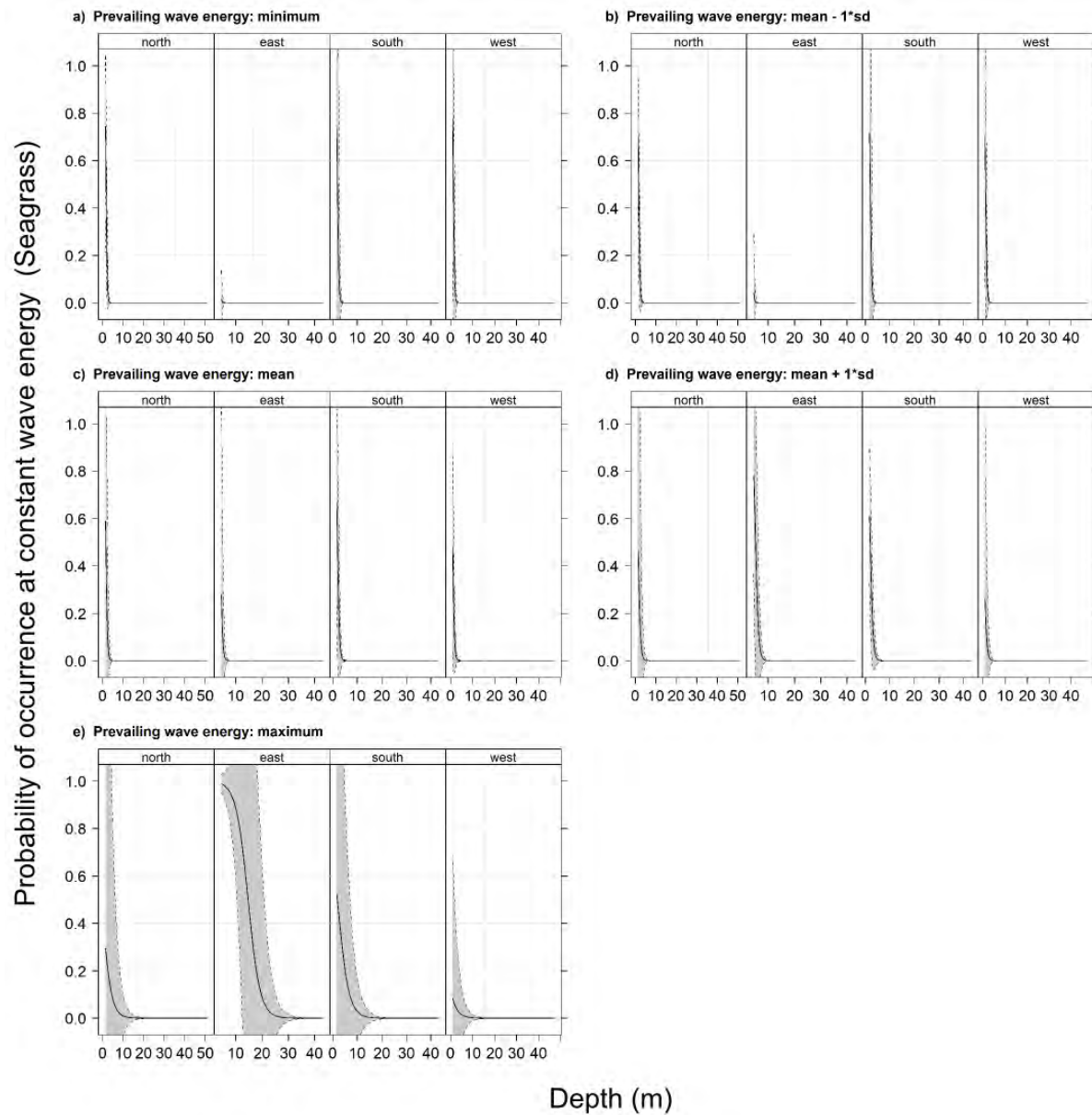


Figure 3.18. Generalised Additive Models (GAMs) showing the probability of occurrence of Seagrass, holding prevailing wave energy constant at a) the minimum, b) mean minus one standard deviation, c) mean, d) mean plus one standard deviation and e) maximum, while varying depth. Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

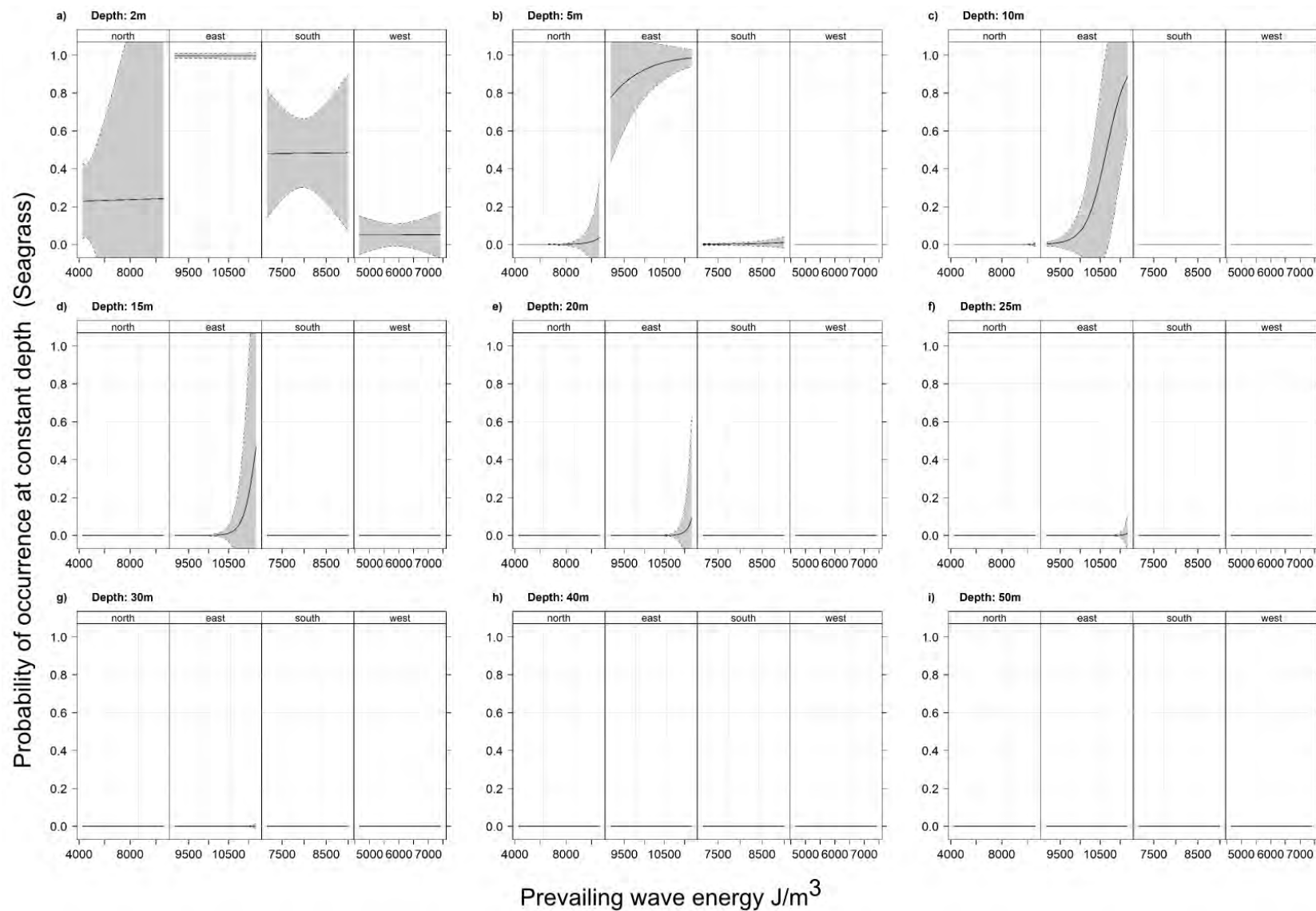


Figure 3.19. GAM Generalised Additive Models (GAMs) showing the probability of occurrence of Seagrass with wave energy while holding depth constant at 2m (a), 5m (b), 10m (c), 15m (d), 20m (e), 25m (f), 30m (g), 40m (h), 50m (i). Plots are divided into panels representing the four main aspects of the Aldabra coastline, north, east, south and west.

3.5. DISCUSSION

3.5.1 The effect of wave energy and depth on benthic cover

Depth and wave energy are integral environmental variables that determine the spatial distribution of broad-scale benthic cover categories (Bradbury and Young 1981; Dollar 1982; Chollett and Mumby 2012). In my study, depth and wave energy were investigated as two principle environmental modifiers of broad-scale benthic cover at Aldabra Atoll using the results from Chapter 2. Wave energy causes structural damage, scours, and affects sediment erosion, transport, and deposition, thereby directly affecting the benthic composition of a reef (Chollett and Mumby 2012; Perry et al. 2015). The effect of wave energy on the benthic substrate is moderated by water depth and the effect of the two variables on the benthic cover was considered together using General Additive Models (GAMs) (Dollar 1982; Sheppard 1982). The GAMs developed in this study showed that depth and wave energy (and their interaction) had a significant effect on the probability of occurrence of the various broad-scale benthic cover categories defined in Chapter 2, thereby shaping the distribution of the benthic habitat around Aldabra Atoll.

The GAMs showed that probability of occurrence of Hard coral, Rubble, Seagrass and Sand benthic cover were significantly altered by the depth and prevailing wave energy, while Epilithic algal matrix and Macroalgae were not significantly affected. The effects of increased wave energy resulted in the maximum probability of occurrence of Hard coral and Rubble to increase towards deeper water, shifting from 10 to 18 m, and 10 to 30 m, respectively. A similar trend was observed from GAMs for Sand and Seagrass, for which the probability of occurrence in deep water increased with increased wave energy. This shift of benthic communities from shallow water to deeper water under greater exposure to wave energy was also noted by Barnes et al (1971) at Aldabra. The shift of shallow water communities to deeper water suggested that increasing water depth shelters benthic communities from high levels of wave energy, and agrees with previous studies suggesting that these two variables act together to generate different benthic zones (Drew 1977; Dollar 1982). Light is a critical variable predicting benthic communities (Chow et al. 2019), not explicitly considered in my study. With an increase in depth, the amount of light reaching the benthic substrate diminishes (Jones and Wills 1956, Chow et al. 2019), thereby changing the amount of energy available to drive photosynthesis which structures the benthic community accordingly. However, the depth shift of benthic communities towards deeper water with an increase in wave energy, suggests that wave energy may be the limiting factor rather light availability. The overriding effect of wave energy on the benthic habitat at Aldabra is likely to

be the dominant environmental variable that structures benthic communities around islands in areas of the WIO exposed to a strong southeast monsoon.

The GAMs predicted the maximum probability of occurrence of Hard coral cover was at depths ranging between 10 and 18 m depth under conditions of low to intermediate levels of wave energy (6000 and 7000 J/m³). The maximum probability of occurrence between 10 and 18 m corresponded with the benthic cover map generated in Chapter 2, which shows hard-coral cover circumscribing the Atoll along the forereef slope. The maximum probability of occurrence of Hard coral was in wave energy conditions that were typical of the west and western half of the north coast of Aldabra, where hard coral occurs in greatest abundance (Haupt et al. 2015b). The peak probability of occurrence of Hard coral at approximately 12 m followed by a drop in probability of occurrence of Hard coral at elevated levels of wave energy (> mean plus one standard deviation [$> 8590 \text{ J/m}^3$]) was consistent with previous studies which have found a greatest percent coral cover at 10 m, decreasing with an increase wave energy at the similarly remote and isolated Kingman Atoll in the Pacific Ocean (Williams et al. 2013).

The same shift of peak probability of occurrence of Rubble and Sand into deeper water with increased wave energy supports the notion of a depth-shift of benthic cover under increased wave energy (Done 1982). The probability of occurrence of Sand and Rubble predicts that these categories would occur in shallow water in sheltered conditions, as observed on the west coast of Aldabra and in deeper water along the wave-swept east coast (Chapter 2). The shift to deeper water of both Sand and Rubble was likely to be caused by increased hydrodynamic transport from waves and currents (Elfrink and Baldock 2002; Harris et al. 2011). The lack of Sand on the east of Aldabra could be explained by high wave energy suspending sand particles in the water column by prevailing south-easterly wind-driven wave energy, which are then transported by currents around the atoll, and fall out of suspension towards the leeward low wave energy west coast of Aldabra, as has been observed in previous studies explaining the sediment distribution at atoll's in response to wave energy (Kench et al. 2006; Harris et al. 2011). Sand being flushed from the lagoon of Aldabra, and transported onto the seaward reefs by currents also contribute to the high occurrence of Sand along the reef apron and reef flats along the leeward west coast (Stoddart et al. 1971; Taylor 1971). The greater probability of occurrence of Rubble than Sand at elevated levels of wave energy could be explained by three factors: 1) High levels of wave energy could lead to greater rates of structural damage to coral leading to more rubble; 2) Wave energy could cause sediment grading causing rubble to be left behind under high wave energy conditions while transporting sand away from high energy sites; 3) At low levels of wave energy sand

may be released from suspension and deposited over the sheltered reef, potentially burying rubble in these areas (Elfrink and Baldock 2002).

The probability of occurrence of Seagrass benthic cover was significantly altered by a change in depth, and Seagrass was limited to depths above 10 m, with a peak probability occurring at a depth less than 2m, which was consistent with mapped Seagrass in Chapter 2. Seagrasses are dependent on light for photosynthesis, which attenuates with depth and thereby limits the distribution of seagrass to shallow light rich waters (Campbell et al. 2007). The slight increase of probability of occurrence of Seagrass with increased wave energy suggests that seagrasses are wave tolerant and may have a competitive advantage over more fragile organisms such as structurally complex hard coral in these dynamic shallow areas. The slightly greater probability of occurrence of Seagrass at depths below 10 m on the east coast compared to other aspects may be a consequence of a lack of a well-formed reef crest allowing for a more continuous spread of seagrass down the reef slope.

The probability of occurrence of Epilithic algal matrix was at a maximum at a depth of less than 10 m but relationships with aspect, depth and wave energy were not statistically significant. Despite the lack of significance, the trends of an increased probability of Epilithic algal matrix under elevated levels of exposure to wave energy is supported by a previous study at Kingman Atoll (Williams et al. 2013). The peak probability of occurrence for Epilithic algal matrix in a shallower water depth than Hard coral suggested that the Epilithic algal matrix outcompetes hard coral in the shallows swash zone, probably as a result of being more wave-tolerant than the structurally complex corals (Sheppard 1982; Williams et al. 2013). Separation of crustose coralline algae and turf algae from within the Epilithic algal matrix category may provide greater insight into the effects of wave energy and depth on this benthic cover category.

The probability of occurrence of Macroalgae in relation to aspect, depth and wave energy was not statistically supported though patterns suggested greater probability of occurrence in shallow water depth and with greater exposure to wave energy. The low levels of occurrence of Macroalgae derived in the broad-scale benthic cover map at Aldabra in Chapter 2 could not be resolved from the GAMs developed in this study. A previous study has suggested that the high levels of heterogeneity and seasonality in macroalgal communities might limit the use of wave energy as a predictor of functional groups within macroalgae (Phillips et al. 1997). However, wave exposure has been successfully used to predict the distribution of macroalgal on a temperate reef ecosystem (Rattray et al. 2015). Relationships between depth and macroalgae may be better assessed at the species level

and should be assessed in future iterations of the relationships of Macroalgae with wave energy at Aldabra.

3.5.2 Wave model

A deep-water wave model as used in this study provided a first-order approximation of the distribution of wave energy derived in the fetch around Aldabra. Deepwater wave models have previously been used for investigating benthic responses to wave energy in recent studies (Chollett and Mumby 2012; Williams et al. 2013; Perry et al. 2015). The spatial distribution of modelled wave energy during prevailing conditions matched expectations from earlier descriptive studies and personal observations, which predicted lower wave energy on the west and northwest coast, and higher wave energy on the east and south coast and maximum exposure to prevailing wave energy between Point Hodoul and Cinq Cases (Taylor 1971).

The deep-water wave models used in this study were limited by a lack of detailed bathymetric information which meant that models were unable to accurately reflect the change in wave energy at intermediate depths where waves interact with the bottom topography. Wave energy changes significantly when waves are slowed down, set-up and break over the reef crest, and then dissipate their energy over the reef flats (Lowe et al. 2005; Péquignet et al. 2011; Monismith et al. 2013, 2015). In addition to detailed bathymetric information, the changes in water level (e.g. tide) have been shown to be important in wave models to understand the effects over shallow reef flats that only become exposed to wave energy during short periods of the day (Péquignet et al. 2011). The rate of wave energy dissipation is a critical factor to understand how wave energy is affecting benthic communities (Williams et al. 2013; Monismith et al. 2015; Rogers et al. 2016) and should be investigated in future iterations of the wave models at Aldabra. The full dispersion equation is required to incorporate these aspects, as well as effects of wave refraction, wave interactions and white capping into the model. Third generation (3G) wave model software, like NOAA's WaveWatch III or SWAN, are able to incorporate these factors (Booij et al. 1999; Tollman 2007) and should be explored in future research of the effects of wave energy at Aldabra Atoll when bathymetric data becomes available.

Detailed bathymetric information for Aldabra will not only improve the understanding of the effects of wave energy distribution and dissipation around Aldabra, but will facilitate predictive modelling of occurrence of broad-scale benthic cover using a combination of wave energy and depth, similar to what has been done for *Montastrea* reefs in the Caribbean (Chollett and Mumby 2012). Predictive benthic cover models may be useful where detailed

and comprehensive benthic cover data are missing (e.g. Hamylton et al. 2012b; Rattray et al. 2015), and to predict the change in benthic cover in response to an increase of wave energy due more frequent and more intense storms (Webster et al. 2005).

3.5.3 Wind data used in wave model

The three-year wind data agreed with general monsoon wind conditions recorded historically at Aldabra (Farrow 1971; Stoddart and Mole 1977). Wind speed measurements were then taken on the most wind-sheltered part of the atoll (Farrow 1971; Stoddart and Mole 1977) and in my study. The correction of an additive 1.5 m/s applied to wind speeds with a southerly component was justified based on the discrepancy between historical wind speeds measurements taken at different localities on Aldabra (Farrow 1971; Stoddart and Mole 1977), but would benefit from a more detailed evaluation of local differences in weather to better understand varying wind conditions experienced around the atoll. Using local measured wind data was therefore a source of error on the scale of the atoll, but may also be problematic at a larger scale (Ponce de León and Guedes Soares 2005; Chollett and Mumby 2012), as it assumed that wind data were representative for the 650 km fetch for which significant wave heights were generated in the wave model. Satellite-derived wind data provides an alternative data set to represent variation in wind speed and direction in the fetch. Chollett and Mumby (2012) used satellite-derived wind data to predict the distribution of *Montastrea* reefs in the Caribbean, and the models used by Williams et al (2013) also relied on satellite-based wind data to estimate wave energy effects on reefs in the Pacific. The strengths of satellite wind data are that it is able to represent variation in wind strength within the study area at one point in time. In future satellite wind data sets, e.g. (<http://marine.copernicus.eu/>), may become available at a spatial resolution suitable to investigate wave energy at the scale of the atoll.

Tropical cyclones are a natural part of reef ecology and have a significant effect in shaping the benthic community on tropical reefs which may cause damage as far as 160 km away (Fabricius et al. 2008; Beeden et al. 2015; Wolff et al. 2016). Storm generated wave energy, in some cases, overrides the benthic distribution patterns created by prevailing wind conditions (Dollar 1982) and therefore it was important to consider during the analysis. The storm wave energy condition models had a near opposite spatial distribution pattern to the prevailing wave energy conditions, which was surprising, as the prevailing tropical storm trajectory passes south of Aldabra (Knapp et al. 2010). This came about as a consequence of the methodology followed to generate a wave model using the directional maximum wave energy from the cardinal and subcardinal wind directions, which were combined in a single

map, where the value associated with each pixel was the maximum wave energy value over the study period.

The wind speeds with the greatest velocity recorded during the study period were recorded from the north-north-west, measured on the morning of the 9 February 2014 (Figure 3.20), when a tropical depression passed 150 km south of Aldabra with wind speeds approximately 62 km/h (Knapp et al. 2010). The variability in wind direction, which was likely to have occurred prior, during and after the storm could not be accounted for using the methods for recording wind direction at the Research Station (a single direction measurement was taken at 8 am in the morning). The storm-wave model was therefore severely limited in its accuracy of wind direction because it was based on data using a single daily wind direction estimate at a fixed point (the Research Station). Storm wave energy from cyclones may be better predicted from ocean scale models such as NOAA's wave watch III which are better able to track the changes in direction (e.g. Moon et al. 2003) and could provide valuable information on the disturbance and distribution of benthic cover around Aldabra in future.



Figure 3.20. The photo was taken during a tropical depression showing the wind blowing through the palm trees on Piccard Island on the 9th February 2014. Photo by Jude Brice.

Wave energy models were further limited by the duration being assessed in this study. The damage caused by a single large storm may last for a longer period than assessed in this study (only 3 years data were available at the time of writing), and in fact, can be detected long after the storm has passed (Grigg 1998; Beeden et al. 2015). Increasing intensity of cyclones in the southern Indian Ocean as a result of increasing sea surface temperatures could mean that this becomes a greater environmental modifier (Elsner et al. 2008) at Aldabra than it presently is, and requires further investigation.

3.5.4 Future directions

Light is a known important variable that predicts benthic communities (Bustamante and Branch 1996). It was not possible to obtain measurements of light levels in my study, but depth serves as a proxy of light as light attenuates with depth in water (Jones and Wills 1956). This is however a fairly crude proxy (Jones and Wills 1956), and future research should consider obtaining measurements of light levels at different depths.

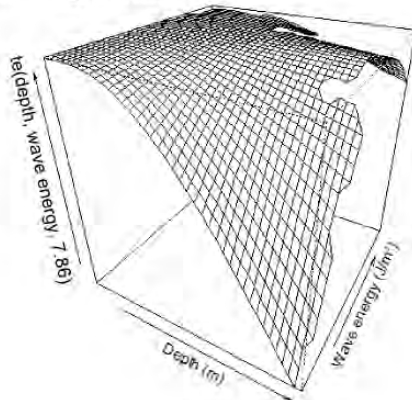
Wave models are improving all the time, but direct measurements of wave energy and other sources of erosion (like currents) in the nearshore environment could improve our understanding of effects of environmental drivers on the benthic community (Carniel et al. 2011).

3.5.5 Conclusion

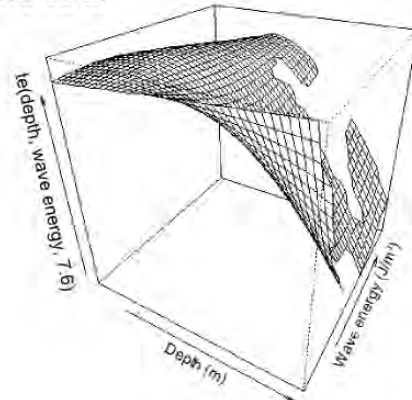
Depth and wave energy explained the distribution of broad-scale benthic habitats around the atoll, with greatest sand and hard-coral cover in the leeward northwestern side while rubble was highest on the windward side of the atoll. It was shown that depth is a critical limitation for the extent of occurrence for benthic habitats such as seagrass which are light dependent. The results from my study confirmed that benthic habitats that are sensitive to wave energy shift towards greater depths with an increase in wave energy. Despite the need for refinement of the wave models and GAMs developed by including more sophisticated wave breaking parameters in the models, the results from this study showed that depth and wave energy were two key drivers that predict the occurrence of broad-scale benthic cover categories at Aldabra. The results from this study sets a baseline for understanding how changes to prevailing wave energy and depth affects the distribution of benthic habitats at Aldabra.

3.6. ANNEX ~ CHAPTER 3

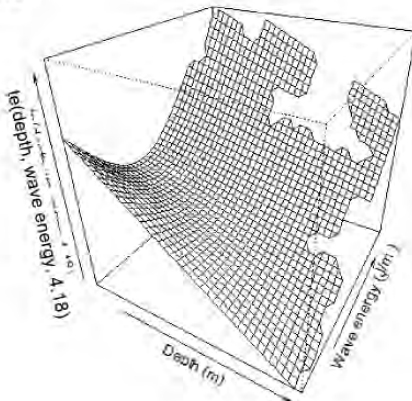
a) Epilithic algal matrix



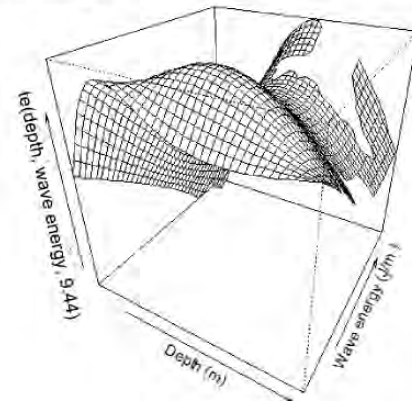
b) Hard coral



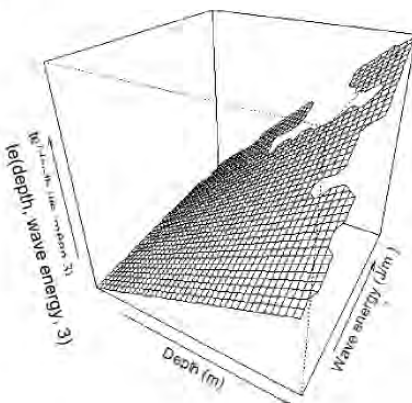
c) Rubble



d) Macroalgae



e) Sand



f) Seagrass

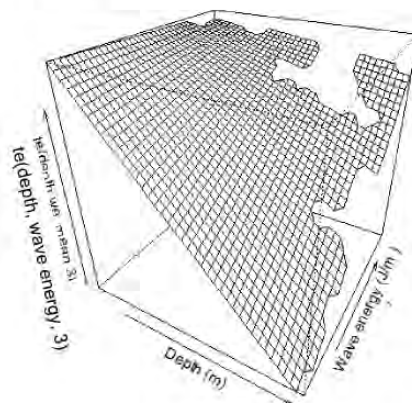
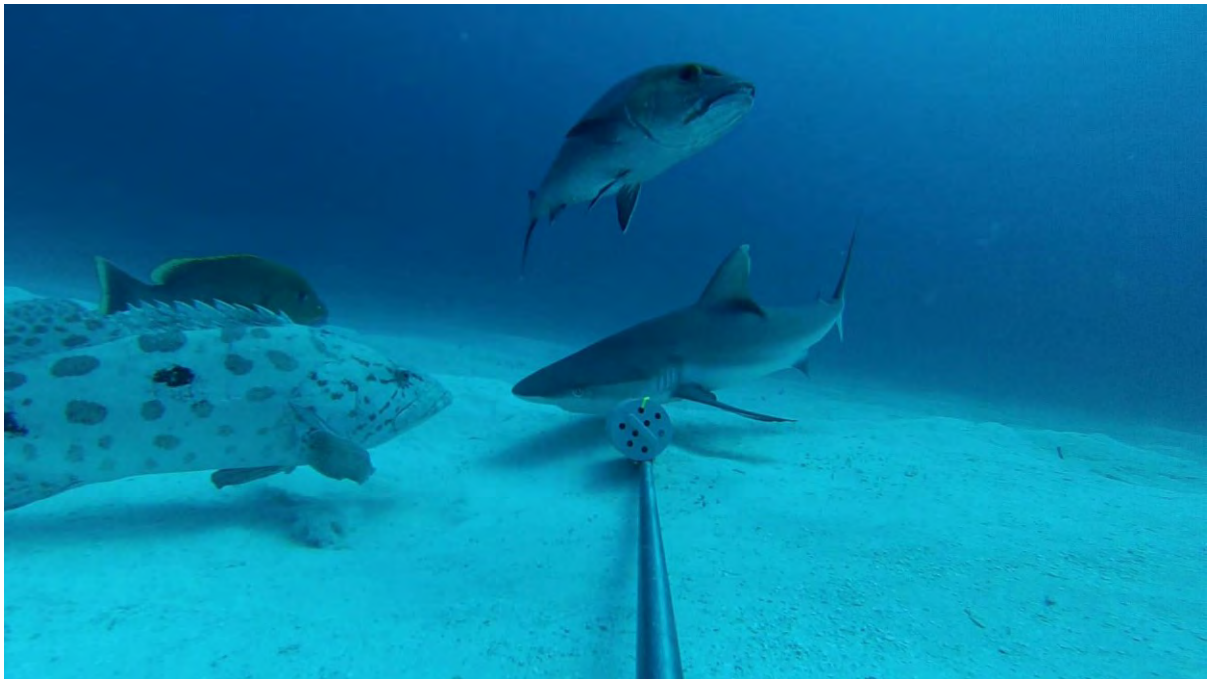


Figure 3.21. Three-dimensional plot of Generalised additive models (GAMs) of each of the six broad-scale benthic cover categories a) Epilithic algal matrix, b) Hard coral, c) Rubble, d) Macroalgae, e) Sand, f) Seagrass. Where “te” is short for tensor smooth, followed by the tensor smooth terms, and the estimated degrees of freedom (edf).

Table 3.6. Wave energy (J/m^3) associated with sampling sites for minimum, mean minus one standard deviation (sd), mean, mean plus one standard deviation (sd) and maximum values for each aspect of the coast.

Aspect	Min (J/m^3)	Mean minus SD (J/m^3)	Mean (J/m^3)	Mean plus Sd (J/m^3)	Max (J/m^3)
North	4277	4027	5531	7035	10608
East	9160	9235	9799	10363	11179
South	7162	7557	8024	8491	8998
West	4651	5463	6024	6584	7413

Chapter 4. Bait significantly alters the observed reef fish assemblage structure across multiple trophic guilds using Remote Underwater Video systems



Several predatory fish at a Baited Remote Underwater Video system, including a grey reef shark, potato grouper, twin spot snapper and a speckled snapper.

4.1. ABSTRACT

The aim of this chapter is firstly to assess the reef fish assemblage structure at a pristine coral reef and secondly to determine the influence of bait on the observed assemblage when using Baited Remote Under Water Video systems (BRUVs). Aldabra's pristine coral reefs provide the opportunity to assess the influence of bait on the observed reef fish assemblage in a system expected to have an intact trophic structure with high levels of large predatory fish. The objectives were to determine and compare the observed species diversity, trophic and size-class assemblage structure of reef fish from the entire Aldabra seaward reef using BRUVs and unbaited Remote Underwater Video systems (RUVs). The hypothesis was that bait would result in an increased abundance of predatory fish, and change species diversity and assemblage structures to be different from those observed under natural (unbaited) conditions. Fish assemblages were sampled, first using RUVs ($n = 61$) and then using BRUVs ($n = 61$), at the same sites between 3 m to 50 m depth, stratified over four geomorphic reef zones. Beta diversity (β), species accumulation curves and a range of multivariate statistics were used to analyse the differences between reef fish assemblages from the two bait treatments within trophic groups and size-class groups. The presence of bait resulted in 1) significantly greater overall abundance of fish being recorded in BRUVs, and 2) altered the assemblage structures within trophic groups and size-classes. These differences between the observed assemblage structures were a result of significantly greater relative abundances and numbers of species of generalist carnivores, piscivores and invertebrate carnivores and zooplanktivores in BRUVs, while RUVs recorded significantly more herbivores and greater species richness of herbivores and corallivores. The differences in the observed fish assemblage structures between the methods could potentially be explained by herbivores and corallivores avoiding baited samples with an elevated abundance of predatory fish. These results indicate that RUVs provide a more comprehensive assessment of the fish assemblage, and more accurate estimates of herbivores and corallivores than in the presence of bait. The strengths of BRUVs were to detect a greater abundance and species diversity of generalist carnivores and piscivores, especially mobile predatory species with naturally low detection rates. BRUVs should be of particular use in areas where fishing activities target predators and have reduced their populations such that detection probability under unbaited conditions requires very large sample sizes. The differences between the observed reef fish assemblage from BRUVs and RUVs highlights the importance of understanding the strengths and weaknesses of survey methodology when interpreting data to inform management decisions. To ensure a representative sample of the reef fish assemblage both RUVs and BRUVs were used throughout this research.

4.2. INTRODUCTION

The overarching aim of this chapter is to assess the reef fish diversity and assemblage structure from a pristine coral reef ecosystem and gain an understanding of the biases of Baited Remote Underwater Video systems (BRUVs) used to record reef fish. Knowledge of abundance and distribution of species is critical to inform decisions on Marine Protected Area (MPA) management and interpretation of ecological studies (Margules and Pressey 2000; Devictor et al. 2010), but abundance and distribution data are highly affected by the survey methods used (MacNeil et al. 2008; Watson et al. 2010). Obtaining accurate estimates of fish population parameters remains challenging (Colton and Swearer 2010), especially of species-rich assemblages in structurally diverse habitat (Harvey et al. 2007), such as shallow coral reefs.

The need for accurate assessments of fish assemblage structure has been met by the development of new survey methods facilitated by advances in technology, e.g. Baited Remote Underwater Video systems. All fish survey methods have their own advantages and drawbacks, and previous studies have described or quantified the biases affecting each (Willis and Babcock 2000; Langlois et al. 2010; e.g. Bernard and Götz 2012; Stobart et al. 2015). Traditional methods like hook-and-line fishing and trap-fishing record only a certain component of the fish population (target species), and may not reflect changes to non-target species (Watson et al. 2010; Harvey et al. 2012b). Extractive methods like trawling, line fishing or trapping may be inappropriate to use in MPAs as they could damage habitat and negatively affect fish populations (Cappo et al. 2004). SCUBA-based methods like Underwater Visual Census (UVC) and Diver Operated Video (DOV) are depth-limited (Harvey et al. 2007), and diver bias affects abundance and behaviour of fish (Watson and Harvey 2007; Colton and Swearer 2010). Underwater Visual Census (UVC) surveys are biased in favour of observing smaller site-attached species over large mobile species, owing to heterogeneity in species detection probability (MacNeil et al. 2015). Differences in divers' abilities to identify fish species could also affect results (Thompson and Mapstone 1997; Bernard et al. 2013). Researchers must therefore consider the biases affecting the respective survey methods to inform decisions on the type of survey method to implement to meet the objectives of their study.

A relatively new survey method, Baited Remote Underwater Video systems (BRUVs), has gained popularity over recent years (Ellis and DeMartini 1995; Cappo et al. 2003; Watson and Harvey 2007; e.g. Bernard and Götz 2012; Stobart et al. 2015) and has been used to assess diversity, distribution and abundance (Brooks et al. 2011; Zintzen et al. 2012). Baited Remote Underwater Video systems (BRUVs) are non-extractive and therefore appropriate to

assess conservation efforts in MPAs (Watson et al. 2007; e.g. Bernard 2012; Bond et al. 2012). Baited Remote Underwater Video systems are also less restricted by depth, and have been used to sample fish assemblages on shallow reefs (Watson et al. 2007; e.g. Bernard 2012), in pelagic and mid-water (Heagney et al. 2007), and deep water (> 1000 m depth) (e.g. Harvey et al. 2012b; Zintzen et al. 2012). Baited Remote Underwater Video systems are not affected by observer bias, as the method makes use of remote (unmanned) cameras, and has the benefit that species identification can subsequently be verified from the video material (Cappo et al. 2003; Bernard and Götz 2012). Using multiple BRUVs allows for simultaneous surveys to be carried out and can collect high volumes of data in a limited time at sea.

However, BRUVs may be biased because they operate on the principle of estimating relative abundance by attracting fish into the field of view (FOV) of a video camera by using bait, in addition to recording the fish species that are either resident or are swimming through the FOV without being attracted to the bait (Bernard 2012). Some of these species may be attracted to the frame on which the video camera is mounted, by bait, or by fish feeding at the bait canister (Harvey et al. 2007). Using bait during sampling may preferentially attract carnivorous or scavenging species into the FOV (Harvey et al. 2007; Ghazilou et al. 2016), which may interact with other species, and potentially decrease the number of herbivores and other prey species that are recorded. The presence of bait may consequently lead to inaccurate conclusions on the diversity and composition of the fish assemblage (Harvey et al. 2007; Bernard and Götz 2012).

Baited Remote Underwater Video systems have been shown to record greater species richness, relative abundance, and biomass, and achieved greater statistical power than DOVs. (Langlois et al. 2010; Watson et al. 2010). A potential drawback of BRUVs is that it may be less effective at sampling herbivores and cryptic species than UVC or DOV methods (Watson 2005; Colton and Swearer 2010), but findings are inconsistent and vary between studies (e.g. Langlois et al. 2010). Eliminating the SCUBA diver from the method allows assessing the effects of bait without the SCUBA-diver bias on observed fish assemblage, and this has been done using baited (BRUVs) and unbaited (RUVs) remote underwater video systems (Cappo et al. 2003).

Studies that have compared fish assemblage diversity and composition sampled using BRUVs to RUVs, found that the use of bait increased the species richness and relative abundance (Watson 2005; Harvey et al. 2007; Bernard and Götz 2012). Harvey et al. (2007) found that bait increased the distinctiveness of fish assemblages between different habitat types. Bernard and Götz (2012) found that in temperate reef systems, baited sampling

increased the precision of abundance estimates of fish, and that abundance estimates from RUVs had higher levels of variability than BRUVs. Baited Remote Underwater Video systems (BRUVs) required smaller sample sizes than RUVs to acquire the same statistical power to detect a change in fish assemblages (Harvey et al. 2007; Bernard and Götz 2012). Previous studies comparing the reef assemblages found that BRUVs recorded a higher relative abundance of generalist carnivores, without significantly decreasing the number of herbivores observed relative to RUVs (Watson 2005; Harvey et al. 2007; Bernard and Götz 2012). Herbivores may or may not be attracted to the systems, but it appeared that the presence of baited systems does not deter them from swimming into the field of view of the BRUVs. Two of the three studies were carried out in temperate waters, namely Tsitsikamma no-take MPA in South Africa (Bernard and Götz 2012), and Hamelin Bay south-western Australia (Watson 2005), and a component of a third study (Harvey et al. 2007) was carried out in the temperate waters of Esperance Bay, Australia. There is potential that the fish assemblage may respond differently to bait in different regions or even at a local scale (Bernard and Götz 2012; Ghazilou et al. 2016). Temperate regions are characterised by lower species diversity than tropical reef habitats (Roberts et al. 2002; Stuart-Smith et al. 2013), and in coral habitats, many of the fish are highly specialised with fine-scale niches and dietary requirements (Wilson et al. 2008). Therefore, it could be argued that tropical fish may respond differently than temperate fish to bait.

Only Harvey et al. (2007) has compared the observed fish assemblage between BRUVs with RUVs in tropical waters specifically. The study by Harvey et al. (2007) on the Great Barrier Reef Marine Park (GBRMP) included pooled fish assemblage data from areas with different levels of protection and exploitation. The surveyed areas included Habitat Protection, Conservation Park, and Marine National Park zones (Great Barrier Reef Marine Park Authority 2016). Extractive uses like trolling, bait netting and invertebrate harvesting are allowed in Habitat Protection zones, which may alter fish assemblages (Ayling and Choat 2008). The effects of bait on the structure of intact reef fish assemblages therefore remains unclear. High predator biomass is associated with intact fish assemblages (Friedlander et al. 2010; McClanahan et al. 2015). The attraction of predatory fish in high abundance to bait and their effect on the reef fish assemblage may therefore be best studied at remote and protected sites which provide the best example of intact fish communities (Pauly 1995; Friedlander et al. 2010; Graham and McClanahan 2013).

Aldabra has historically only had limited exploitation, and has been conserved since 1971 (Stoddart 1971), and officially protected since 1981 as a Seychelles Special Reserve (IUCN 1a). Currently, the only exploitation is a small subsistence handline fishery that supports ca

15 people that work for the management authority on the atoll, but no other extractive uses are permitted (Pistorius and Taylor 2009). The fishery does not permit catching of shark, and zero are landed annually (Seychelles Islands Foundation unpublished data). It was recently described as one of the last remaining intact coral reef ecosystems in the Western Indian Ocean (WIO) region (Friedlander et al. 2015b). Aldabra's remote location and long history of protection makes it an ideal site to study the effects of bait on records of the reef fish assemblage structure.

Fish size is also important for informing site management, such as using size distribution of fish assemblages to evaluate the effect of fishing compared to no-fishing on fish population demographics (Gabelhouse 1984; Graham et al. 2005). The method of sampling is therefore important as it can influence conclusions about fish population structure, and ultimately affect management decisions (Graham et al. 2005; Dorman et al. 2012).

Protected, isolated reefs with lower anthropogenic impacts tend to have different trophic compositions from exploited reefs, often supporting higher predator densities and biomass (Sandin et al. 2008; Graham and McClanahan 2013; Barley et al. 2017; Bradley et al. 2017). A greater density of predatory species may suppress the diversity and abundance of prey species, which could lead to differences in the fish observed between baited and unbaited survey methods. For two reasons it was necessary to investigate the effects of bait on the fish species richness and the assemblage structure. Firstly, the results stand to inform survey methods and data interpretation in the region as this has not been investigated previously in the WIO. Secondly, the high predator density in Aldabra's MPA (Friedlander et al. 2015b) may elicit a greater response from potential prey species than that detected by Harvey et al. (2007) in a study carried out on exploited tropical reefs. The observed fish assemblages using RUVS and BRUVs may therefore differ between study sites, and therefore requires further investigation.

The aim of this chapter is to obtain ecological reference points of the reef fish species richness, diversity, relative abundance and assemblage structure on the seaward reefs of Aldabra Atoll between 0 and 55 m depth using BRUVs and RUVs. All species observed were identified, and the number of species and relative abundances within multiple size classes and functional feeding groups were determined.

The following hypotheses were tested:

H. 4.1.) A greater species richness, diversity and abundance of fish was expected in baited treatments relative to unbaited treatments, as more fish and fish species will be attracted by bait.

H. 4.2) The fish species assemblage structure was expected to be different, at multiple trophic guilds, between baited and unbaited treatments, because differences between species attraction to bait may alter the observed fish assemblage.

H. 4.3) More species and individuals from predatory trophic guilds were expected in baited samples than unbaited samples.

H. 4.4) Fewer species and individuals of lower trophic guilds were expected in baited treatments than unbaited treatments, because increased predatory species may deter potential prey species.

H. 4.5) More observations of species and more individuals of elasmobranch were expected in baited treatments than unbaited treatments, owing to their dietary preference (e.g. King and Fraser 2014).

H. 4.6) I expect a greater species richness and abundance of large-bodied fish in baited treatments than unbaited treatments, because of competition for food (Dunlop et al. 2015b).

The objectives of the study were to:

Obj. 4.1) Assess differences in fish species richness (gamma diversity), diversity (Shannon Index) and standardised relative abundance estimates (MaxN) between paired one-hour samples of BRUVs and RUVs recorded at Aldabra's seaward reefs between 0 and 55 m depths.

Obj. 4.2) Assess the differences in multivariate fish assemblage structure, diversity and relative abundance according to taxonomic, species size-class and functional feeding groups between paired samples of BRUVS and RUVs using univariate and multivariate statistical analysis.

4.3. METHODS

4.3.1 Study area

The fish assemblage within the MPA at Aldabra Atoll was sampled on the seaward reefs from 0.5 m down to 50 m depth, using unbaited remote underwater video systems (RUVs) and baited remote underwater video systems (BRUVs). The seaward reefs that were sampled included the lagoon reef, forereef slope, and reef platform, and samples were collected from various benthic cover types, including seagrass, sand, crustose coralline and turf algae, rubble and hard coral, but these were not explicitly used to stratify the sampling design as no habitat map was available at the time of sampling. The atoll is subjected to strong monsoonal climate, with strong southeasterly dominating April to October and northwesterly winds December to February. Prevailing wave energy varies greatly around the coast, with the highest exposure to wave energy on the east coast, and lowest along the west coast of Aldabra. Water temperature varies between 21 and 30 °C, being warmest between December and April.

4.3.2 Sampling approach

Sampling was conducted between 22 October 2013 and 22 January 2015 in a collaborative project by Seychelles Islands Foundation (SIF), South African Earth Observation Network (SAEON) and South African Institute for Aquatic Biodiversity (SAIAB) under the Global Environment Facility (GEF) project (project ID 3925) and Pangaia project (Cowley et al. 2014). Samples were collected from the same sites (spatially matched pairs of sampling-sites) to compare the species diversity and assemblage structure between the two bait treatments. All sampling sites were sampled using RUVs and BRUVs and were therefore referred to paired samples. All sites were always sampled using RUVs first, and then BRUVs if sampled on the same day. If a baited sample (BRUVs) was collected at a site which has not yet been sampled using RUVs, the unbaited (RUVs sample) was collected at least a day later to avoid the effects of baited sampling influence unbaited sampling. A randomly stratified design was used to determine the localities of paired sampling-sites for RUVs and BRUVs. Stratification was used to collect samples that represent variability in the fish assemblage which may be associated with different depths or differences in wave exposure gradient along the coastline. The atoll was stratified according to aspect orientation of the coastline in four cardinal directions, north, east, south, and west to represent wave exposure gradient, and three depth categories, namely, shallow 0 – 10 m, medium 10 – 20 m, deep 20 – 50 m (Figure 4.1).

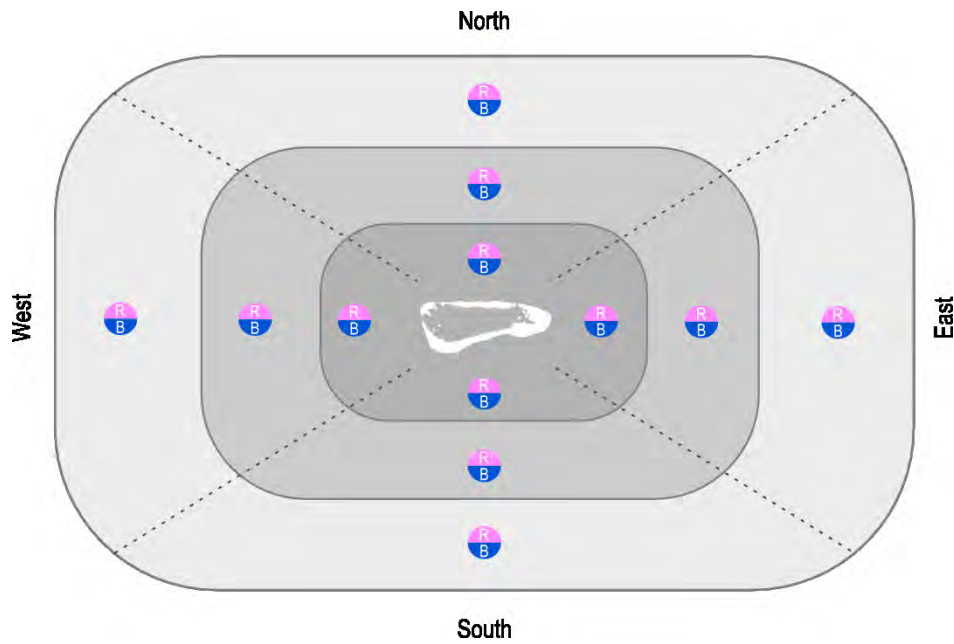


Figure 4.1. The study design was planned to collect data from RUVs and BRUVs from the four aspects of the seaward reefs of Aldabra Atoll to ensure representation of differing wave energy, in shallow (0 – 10 m), medium (10 – 20 m), deep (20 – 50 m) water.

Sampling sites were set to have a minimum distance of 300 m apart within the random stratification design. The RUVs were deployed before the BRUVs when the same sites were visited, to avoid the effects of baited sampling influencing unbaited sampling (Bernard and Götz 2012).

Not all deployments (or video recordings) were successful, and consequently, the sample size was reduced to a total of 61 spatially matched pairs per treatment (Figure 4.2). There were 15 samples per aspect per treatment, other than the west coast where 16 samples per treatment were successfully collected.

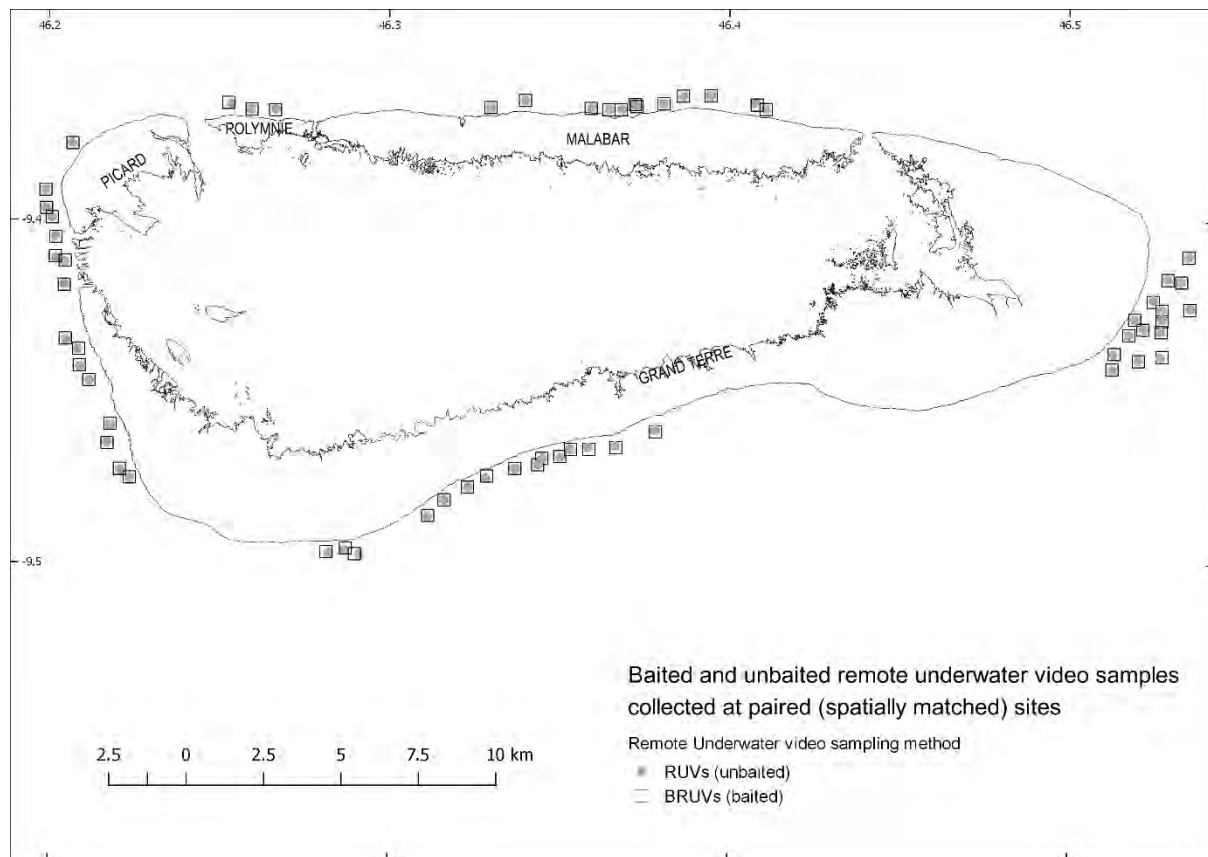


Figure 4.2. Baited Remote Underwater Video systems (BRUVs) and Remote underwater video system (RUVs) were collected from the same 61 spatial locations (spatially matched sampling sites) between 2013-2015.

The sampling areas on the seaward reef covered a similar depth range and total surface area, to allow comparability and adequate levels of sample replication within each sampling area. Three of the four areas sampled were similar in size, but the east was 2 km² larger than other areas because it has a very wide forereef slope that changes depth gradually (consequently a large area needed to be included to obtain depth stratification): East: 6.666 km², South: 3.658 km², West: 4.038 km², North: 3.993 km² (Malabar) + 0.434 km² (Polymnie).

4.3.3 Sampling method

4.3.3.1 Setup

Five remote underwater videos systems were used to collect unbaited samples at the same time, using one system per sampling site. The same sampling sites were then resampled with the addition of bait on a subsequent sampling event. Each system comprised a tripod frame, to which an underwater camera and a rope with a buoy were attached. The frame comprised hollow core (30 mm) marine-grade stainless steel made to an isosceles tripod

shape, consisting of two equal length solid short legs, and one hollow longer leg (Figure 4.3). The tripod design aimed to minimise the number of contact points while the isosceles shape provided stability from a low centre of gravity. The frame was attached to an inflated buoy (size A3), using 6-mm braided floating nylon rope. A GoPro Hero 3 camera in an underwater dive casing (60 m depth rating) was mounted to the frame using a “GoPro handlebar mount” connecting piece, and angled horizontal in the water column (facing forwards), such that the longer leg of the tripod was directly in the FOV. GoPro cameras were set to record videos at 25 frames per second in high definition (HD 1080), in widescreen mode at 11 megapixels in NTSC format, with the LED light and sound functions turned off to avoid attracting fish by these means.

A bait canister was secured to the long leg of the frame, 1.5 m in front of the camera, using cable ties. Bait canisters were made from 110 mm PVC water pipe connectors, into which ca 80 holes were drilled using an 8-mm drill bit, to allow the bait plume to escape into the water column. Approximately 800 grams of bait, comprising of a mixture of fish muscle and offal, collected from the Aldabra subsistence fishery, was used to bait canisters during BRUVs deployments. Offal was chosen as it was a sustainable option at Aldabra to use in SIF’s long-term monitoring programme, given the subsistence fishery on the atoll is not geared towards ensuring a consistent supply of a single species like sardine or bonito. Frozen bait would be taken out early in the morning prior to deployment and bashed with a wooden stump to create a bait-chum. Bait canisters were filled with approximately 800 g bait during baited deployments, while clean bait canisters were used during unbaited deployments. Bait canisters were cleaned or changed after baited deployments to avoid left-over scraps attracting fish in unbaited samples.

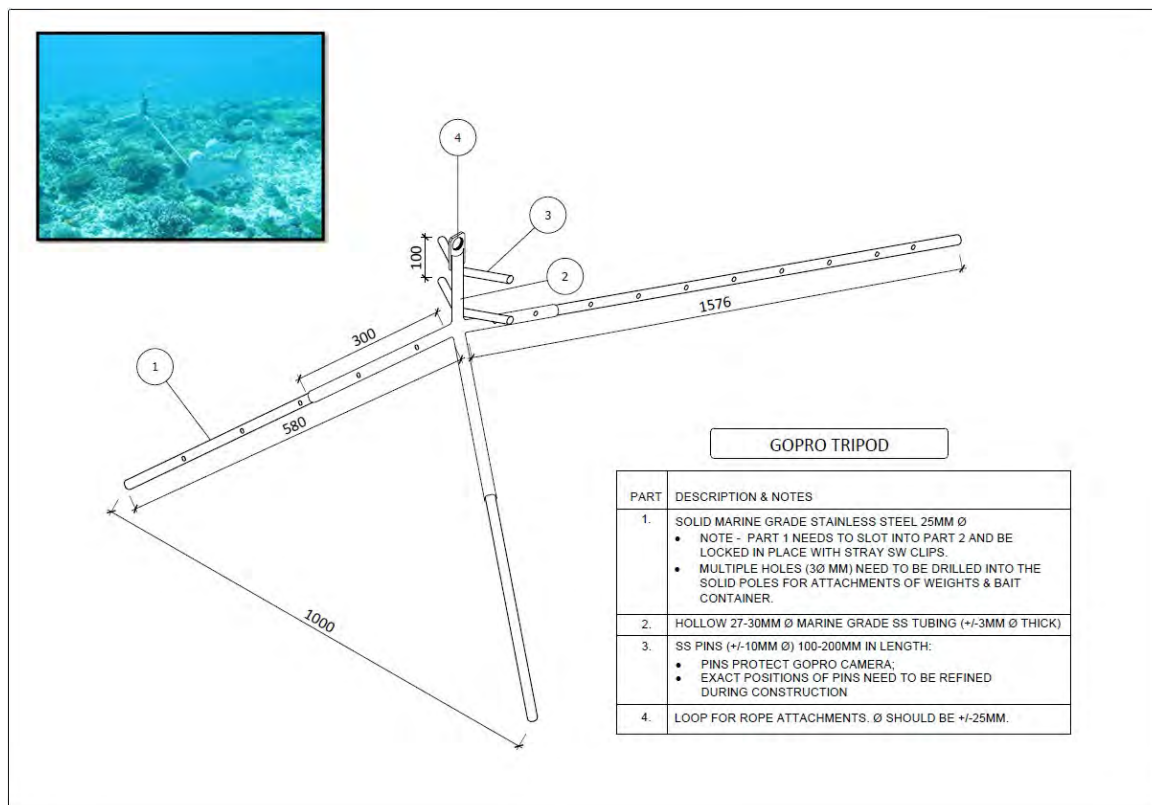


Figure 4.3. Diagram of the remote underwater video system frame, showing the low centre of gravity in the isosceles design. The bait canister was attached to the top of the long leg, 1.5 m from the vertical part of the frame. The camera was attached to the frame between the stainless steel pins facing horizontally in the direction of the long tripod leg. The rope with buoy was attached to the frame at the loop on the top of the frame. SS – Stainless steel.

4.3.3.2 Deployment

The five systems were deployed, one at a time, from a small outboard powered boat at the predetermined sampling sites. A minimum distance of 400 m between sampling stations was implemented to reduce the risk that large mobile species might be recorded at multiple stations during the recordings from the set of five consecutive deployments. While this does not guarantee avoidance of fish movement between sampling stations, this mitigative practice is in line with BRUVs sampling procedures used in other studies (Cappo et al. 2004; Watson et al. 2007; Dorman et al. 2012). Each deployment required a crew member to lower the system over the side of the boat, with the engines turned off to avoid snagging the buoy line in the propeller. The length of rope used to attach to the buoy was roughly three times the depth to ensure enough slack such that systems would not be overturned by strong currents. Care was taken to slowly lower the system to the bottom, as this increased the chance of the system landing upright and minimised the chance of damaging the sensitive coral reef habitat. A minimum of three crew members was used during deployments,

including the skipper, data recorder, and crew member handling the frame and bait. Once deployed, the boat moved onto the next site, or away from the deployment site to avoid boat-based interference in the sample. Each deployment lasted just over 60 minutes to standardise recordings to 1 hour for subsequent analysis. Over the course of a day, this routine would be repeated to collect approximately 20 samples per day.

4.3.4 Sample processing

Videos recorded from the same sampling site (spatially matched pairs) were processed consecutively. The order in which the series of spatially matched pairs were processed was randomised to avoid learning effects biasing species identification accuracy. All videos analysis was carried out by the same person to avoid observer bias. Video imagery was processed using EventMeasure software (www.seagis.com.au). Videos were played back and analysed at normal frame rate but were slowed down to improve detecting fish when many individuals were present in the same frame. One hour of video footage was analysed for each video recording. All fish were identified to species level as far as possible, and sex and life cycle phase when possible. Fish species were identified from field guides specific to the WIO (King and Fraser 2014; Walton 2015), and other field guides (Allen et al. 2003), FishBase (www.fishbase.org), and a photo library constructed during the study.

Fish were counted for each species during the video analysis, and the maximum abundance determined using the MaxN method. MaxN is the maximum number of individuals of a species recorded in a video frame over the duration of that video (Cappo et al. 2003). MaxN is a standardised measure used during analysis of remote video techniques (Cappo et al. 2006) and avoids double counting individual fish that revisit the camera (Cappo 2010). MaxN offers a conservative estimate of abundance as not all individuals will always be visible in the same frame at the same time (Bernard 2012).

4.3.4.1 Mitigating dominance by abundant schooling species

Relative abundance (MaxN) counts for schooling species with counts exceeding 44 were reassigned to 44, based on the mean MaxN plus two standard deviations, to dampen the dominating effect of schooling species in the analysis, but retain the species in the analysis. This method was preferred to removing records for these species, which would incorrectly imply the absence of the species in some of the samples. Root-root and log transformations were tested prior to this but were unable to remove the dominating effect of schooling species.

4.3.4.2 Assigning fish to trophic feeding guilds

Fish were assigned to one of eight trophic feeding guilds according to their predominant feeding preferences (Table 4.1). Fish dietary and feeding information from the Ecology (http://www.fishbase.org/manual/fishbasethe_ecology_table.htm) and FoodItem (http://www.fishbase.org/manual/FishbaseThe_FOOD_ITEMS_table.htm) data tables in FishBase (www.fishbase.org) were obtained via the RFISHBASE library in R (Boettiger et al. 2012). The information was supplemented by local fish guides and literature (Stevens 1984; King and Fraser 2014), and unpublished data compiled from various resources held by SAIAB. Nine species had no referenced information regarding feeding preferences or trophic score in FishBase and were assigned the same trophic guild as similar species within the same genus. (Trophic score in the FishBase table is an indicative score of a species trophic level). Fish diets are often varied, including food items corresponding to more than one trophic guild. The prevalence of food items in the fish's diet was used to inform trophic guild assignment, based on "CommonessII" column from the "FoodItem" FishBase table. For fish with mixed diets, species were assigned to trophic guilds (), using the following rules: If food items were rare (<6%) while other items were very common (21-50%) or dominant (>50%), the species was assigned to the trophic guild associated with dominant food. If multiple food items corresponding to different trophic guilds were common (6-20%), very common (>20%) or dominant (>50%) in a fish's diet, it would be assigned to the corresponding trophic guild with mixed food items (Table 4.1). For example, if algae and invertebrates were both very common in the fishes' diet, it was assigned to algae/invertivore as opposed to herbivore or carnivore invertebrate. Where food items in a fish's diet were present but quantitative prevalence data were absent, descriptions from the aforementioned sources of a species' diet were interpreted to assign trophic guild. If there were insufficient data to determine predominance of food items, and only one item was present, the fish would be assigned to the trophic guild corresponding to that item (Table 4.1). Species with mixed diets that lack information on the prevalence of those food items were assigned to the mixed or generalist groups corresponding to the mixture of food items in their diet. The assigned trophic guilds were cross-checked with the descriptive published dietary information for each species from the aforementioned references and Fishbase website.

Table 4.1. Description of food items corresponding to trophic guilds used in this study.

#	Trophic guilds	Typical food items
1	Herbivore	Algae, detritus, diatoms, phytoplankton, benthic algae/weeds, dinoflagellates, and blue-green algae.
2	Corallivore	Coral and coral polyps, hard corals, including a mixture of coral and other invertebrates.

3	Zooplanktivore	Zooplankton, planktonic invertebrates, planktonic crustaceans, copepods, euphausiids, mysids, jellyfish/hydroids, cladocerans, and fish eggs and larvae and early stages of fish life stage.
4	Piscivore	Nekton, fish, bony fish, finfish. Squid and cephalopods regarded as nekton.
5	Invertivore carnivore	Zoobenthos, benthic invertebrates, echinoderms, sea urchins, sea stars, brittle stars, molluscs, worms, polychaetes, annelids, terrestrial insects, crabs, sea urchins, lobsters, octopi, shrimp, prawn, stomatopods, gastropods, amphipods, isopods, ostracods, bivalves, and mysids.
6	Algae/Invertivore	Combinations of herbivore and invertivore items.
7	Sponges/Invertivore	Sponges, ascidians and tunicates and other invertebrates listed above.
8	Generalist carnivore	Carnivores fish feeding on mixtures of food items listed as invertivore and piscivorous but may include turtles, herps, mammals, pinnipeds, dolphins, and seabirds.

4.3.4.3 Assigning body size classes

Fish species were assigned to one of the following size classes based on common length estimates obtained from FishBase and selected reference materials (King and Fraser, 2014). Fish species were assigned to a size class by calculating length bins from species-size data using Kernel Density Estimates (KDE) using KernSmooth (Wand 2015). Plots of KDE were respectively compiled for Actinopterygii and Elasmobranchii to inform the five size class categories used in this chapter (Figure 4.4). The five size class categories were very small, small, medium, large and very large, for Actinopterygii and Elasmobranchii, respectively, as shown in Figure 4.4.

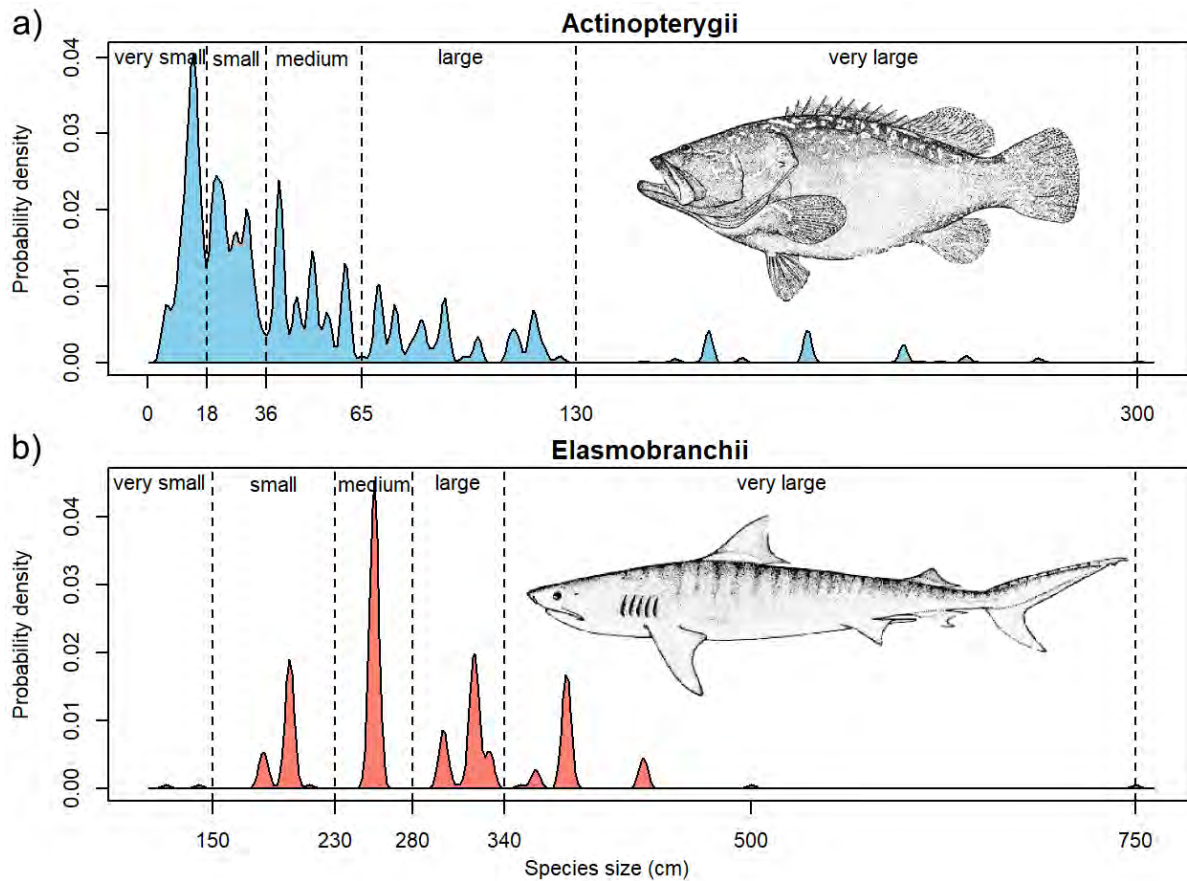


Figure 4.4. Species size class categories for Actinopterygii and Elasmobranch fish recorded using Baited Remote Underwater Video systems (BRUVs) and RUVs. Size class categories were based on kernel density estimates from fish species maximum size data. (Drawings FAO).

4.3.5 Covariates

Covariates included bait treatment, which is a factor of two levels, baited or unbaited. The environmental predictor variables included depth (m), water temperature ($^{\circ}\text{C}$), and wave energy (J/m^3). Other predictor variables included, sample area (m^2), and percentage water column (%), which were all real numbers.

Depth and wave exposure are important in structuring the fish assemblage (Bell 1983; Clark 1997; Friedlander and Parrish 1998; Friedlander et al. 2003) and were included in the analysis. Temperature variation is important over large latitudinal change (Floeter et al. 2005) and varies with depth with deeper water being colder than surface water. Larger areas in view would suggest that one would be able to observe more fish that would otherwise be hidden from the Field Of View (FOV), and was included to account for its effect (Bernard and Götz 2012). The “percent water column” variable refers to the area in the FOV that only includes water, and no visible benthic substrate. The percent water column in the FOV is

related to the angle at which the camera is facing in the water column when the system settled on the seabed. An increase in the water column may result in observing more pelagic and mid-water species, while a lower percentage water column may result in observing more demersal reef species, and consequently an important variable to include in the analysis. Habitat is often important in structuring fish assemblages (Harvey et al. 2007) but was not included in this analysis as paired sites had similar habitat, and this is the subject of subsequent analysis in Chapter 6.

4.3.5.1 Depth

Depth was recorded as meters below sea level measured by echo sounder mounted to the boat (Garmin 520s) when the system reached the seabed.

4.3.5.2 Wave energy

Wave energy was assigned to samples by overlaying the georeferenced localities of samples onto a map of the prevailing wave energy. Wave energy values were then associated with samples using a spatial join in QGIS. See Chapter 3 for wave energy calculations and mapping. Wave energy was not affected by the date of sampling, as it represents the mean prevailing conditions between 2012 and 2015, and not daily variation.

4.3.5.3 Water temperature

Onset HOBO Pro V2 water temperature data loggers were affixed to the system frame and set to take a reading every 10 minutes during a deployment. The first and last water temperature readings taken during the 60-minute deployment were discarded to avoid variability introduced as an artefact of temperatures experienced out of the water. The remaining four logs per deployment were averaged to produce a single temperature record for each sample. There were not enough loggers to attach one to each system frame, therefore not all samples had in situ data. The temperature data were interpolated for samples without readings, which were taken from the nearest system that had a logger attached on the same date and time.

4.3.5.4 Habitat, visibility, sample area and percentage water column analysis

A still image (screen grab) was taken during video review, at the point when the system reached the seabed. Underwater visibility was estimated as the distance in meters from the video, drawing on site knowledge and SCUBA diving experience. Vidana software (Hedley 2003) was used to calculate the percentage benthic habitat, water column, and obstructions in each image. Percentage water column was the area in the image only consisting of water, with no visible benthic habitat, or obscured by obstructions. Obstructions were typically vertical benthic reef structures or live growth, like gorgonian fans, that were directly in front of the camera, and less than 1.5 m from the camera, which obscured the view of the benthic

landscape and water column further away (1.5 to 15 m). Sampled surface area in the horizontal plane was calculated as a wedge of the circular area. The area of the wedge was calculated from the angle of the FOV, and the radius which was the estimated visibility (Figure 4.5).

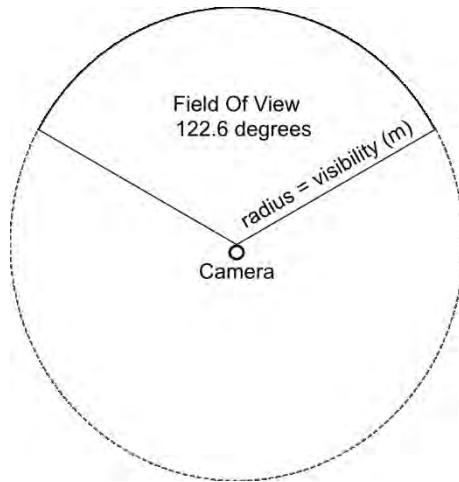


Figure 4.5. The annotated segment in a circle explains the calculation of surface area of the wedge shape Field of View (FOV), where the camera is the GoPro Hero 3 lens position, viewed from above, camera facing to the top of the page.

The wide FOV setting for the GoPro Hero 3 is at an angle (α) = 122.6°, (<https://gopro.com/support/articles/hero3-field-of-view-fov-information>).

$$Area = \frac{r^2}{2} \left(\left(\alpha \times \frac{\pi}{180} \right) - \sin \left(\alpha \times \frac{\pi}{180} \right) \right) \quad (\text{Eqn.4.1})$$

$$Visible\ area = Area - (Area \times Percentage\ obstruction) \quad (\text{Eqn.4.2})$$

In Equation 4.1 the area of the segment in the FOV was calculated. Angle was converted to radians for calculations, as shown in the formula. The second equation (Eqn.4.2) calculates the visible area by subtracting the area obscured (percentage multiplied by the area) from the FOV area calculated in Equation 4.1. The R code developed to calculate the area in the FOV is available as an R function and can be downloaded from https://github.com/philiphaupt/bruv_area. The user supplies the estimated visibility, and the angle of the FOV of the camera used.

4.3.6 Statistical analysis

The statistical analysis primarily was carried out in R (R Core Team 2016), and Primer with the PERMANOVA extension (Clarke and Gorley 2006; Anderson et al. 2008) as indicated.

4.3.6.1 Covariates

Differences in covariate values across treatments were assessed using boxplots and statistical significance tested using Pairwise Wilcoxon with Holm adjustment of p-values, as the data had a non-parametric distribution (Bauer 1972; Holm 1979; Crawley 2007).

Independence of variables was assessed using draftsman plots and significance of correlations between variables was tested using Spearman's rank correlation.

Each covariate was standardised using DECOSTAND (Oksanen et al. 2016), where the mean of the covariate is scaled to zero and variance to a margin of ± 2 . The data were not transformed prior to standardisation, as transformation did not remove non-parametric structure in the data. Outliers were identified using a Multi-Scale Dimensional (MDS) plot of the Euclidian distance of the standardised covariate data. METAMDS (Oksanen et al. 2016) was used with 50 random restarts to converge on a solution. Outlier samples were identified as samples outside the 99 % confidence interval (CI) and were removed prior to multivariate analysis because some analysis is known to be sensitive to the effect outliers (Anderson et al. 2008). Note that the outlier analysis was first carried out using 95 % CI to identify outliers. The outlying samples were further assessed for differences between covariate values across spatially matched pairs of samples. At 95 % three outliers were identified, but two of the three matched pairs were not very different in the values causing them to be outliers, e.g. One outlier was identified because it had a depth of 55 m, while its spatially matched opposite treatment had a depth of 49 m. A CI of 95 % appeared overly conservative in this study, and therefore the CI was relaxed to 99 %. Three outlier samples were identified as samples which fell outside of the 99 % confidence interval for the respective treatments. The outlier's spatially matched opposite treatment sample was also removed to balance the sampling design prior multivariate analysis.

4.3.6.2 Fish assemblage data aggregation

Five levels aggregation of two data sets (presence/absence, abundance) were assessed for species richness and diversity, and fish assemblage composition, as follows: 1) species level, 2) trophic guild and 3) a combined group of the trophic guild, taxonomic class, and species size class. Species assemblages were also assessed within their respective 4) trophic guilds, and within their respective 5) combined guild-class-size groups.

4.3.6.3 Species richness and diversity

The number of species (N_{sp_i}), and relative abundance ($MaxN_i$) were summed, respectively, to obtain sample totals. Shannon-Wiener diversity index was calculated from relative abundance ($MaxN_i$) values for each sample using the DIVERSITY function in the VEGAN community ecology package (Oksanen et al. 2016) with a logbase to 10 parameter setting.

Statistical significance of differences of Nsp, MaxN and Shannon-Wiener diversity between baited and unbaited samples were tested using pairwise Wilcoxon at 95 % confidence interval (CI), as data were non-parametric (Bauer 1972; Hollander et al. 2013).

4.3.6.3.1 Beta diversity

Beta diversity (β) or species turnover is a measure of ratio of the regional and local species diversity. Beta diversity was used to represent the variation in diversity of assemblages between treatments. Whittaker's (1960) Beta diversity equation (Eqn.4.3) was used to calculate species turn over between treatments, as the ratio of gamma diversity (γ) to alpha diversity (α), where γ is overall number of species from all sites in the study and α is the number of species at a sampling site.

$$\beta = \frac{\gamma}{\alpha} - 1 \quad (\text{Eqn.4.3})$$

Statistical significance was assessed using multivariate dispersion test (Anderson 2006), and is described below under *Multivariate dispersion tests of variation in assemblage structure*.

4.3.6.3.2 Species accumulation curves (SAC)

Species accumulation curves (SACs) record the rate at which new species are added with increasing sampling effort (Thompson et al. 2003). SACs were fitted to the respective data sets (BRUVs and RUVs) using SPECACCUM (Oksanen et al. 2016). A two-tailed Kolmogorov-Smirnoff test was used to detect significance in the difference of distribution between bait treatments (Marsaglia et al. 2003; R Core Team 2016).

4.3.6.4 Multi-variate assemblage analysis

4.3.6.4.1 Data transformation and ecological distance resemblance matrix

Fish assemblage data had a non-parametric data distribution, and consequently, multivariate statistics were used to analyse the data. Prior to analysis, the abundance ($MaxN_i$) data were $\log_{10}(x+1)$ transformed to avoid high abundance values dominating results, which may potentially mask out the effects of other species (Anderson et al. 2008). Modified Gower dissimilarity matrix was calculated from transformed values as it is an appropriate ecological distance measure for dealing with multi-variate heterogeneity (Anderson 2006). Lingoes transformation was applied to the dissimilarity matrices within respective multivariate data analyses to avoid negative eigenvalues incorrectly inflating the contribution of axes to the distribution of points (Legendre and Anderson 1999; Legendre and Legendre 2012). Jaccard distance was taken for presence/absence data (Anderson et al. 2008; Oksanen et al. 2016).

4.3.6.4.2 Multi-variate assemblage structure

One way non-parametric permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001a, 2006) was used to assess the difference in fish assemblages (number of species and relative abundance) between bait treatments. PERMANOVA is permutation-based, and consequently, the data are distribution free and enable any ecological distance to be applied during analysis (Anderson et al. 2008). The analysis was carried out using ADONIS2 (Oksanen et al. 2016). Permutation of residuals under the reduced model was required as the model included multiple covariates (Anderson et al. 2008). Sequential sums of squares, with fixed effects summing to zero for mixed terms, were run under 4 999 permutations, corresponding to a 99 % confidence interval (Anderson et al. 2008). Model designs were treated as unbalanced because environmental covariates were used in the analysis (Anderson et al. 2008). The covariates were fitted to the model in a specific order. Covariates over which there was the least control in terms of sampling design were fitted first, and those over which there was the most control fitted last, as follows: sample area, percentage water column, temperature, wave exposure, depth, and treatment. This was done to ensure conservative estimates of the significance of the effect of bait treatment by first accounting for the explained variance resulting from covariates (Anderson et al. 2008).

4.3.6.4.3 Multivariate dispersion tests of variation in assemblage structure

Dispersion of variance in the multivariate data was tested for homogeneity using BETADISPER (Oksanen et al. 2016). Dispersion of variance informs underlying causes of dissimilarity (Anderson et al. 2008), and when used with presence/absence data (number of species) informs the statistical significance of Beta diversity (Anderson 2006). Samples grouped according to bait treatment to provide a mean and standard error of the distance to the centroid. An ANOVA-based permutation test, PERMUTEST (Oksanen et al. 2016) with 4 999 permutations, was used to calculate the statistical significance of the differences across the treatment of the sample distances to group centroid.

4.3.6.4.4 Ordination analysis of fish assemblages

Distance matrices of multivariate abundance ($MaxN_i$) data were submitted to unconstrained Principal Coordinate Ordination (PCO) and constrained Canonical Analysis of Principal coordinates (CAP) analysis to visually compare fish assemblages identified by BRUVs and RUVs. Analyses were carried out at species-level, combined taxonomic-class-guild-size groups, trophic guilds, and within-trophic guilds. Within-combined taxonomic-class-guild-size groups were not submitted to PCO as there were too many classes: 38 PCO and 38 CAP plots were deemed overwhelming to aid visual interpretation.

Unconstrained ordination maximises the differences between sample points, and then fits independent variables to the data, providing an objective view of the greatest dissimilarities

between samples, while CAP defines the axes that best discriminates among *a priori* groups (treatments) in the data (Anderson and Willis 2003; Anderson et al. 2008). CAP analysis finds linear combinations of predictor and response variables that are maximally correlated with one another (Anderson et al. 2008).

4.3.6.4.4.1 Principal Coordinates Ordination

Principal Coordinates Ordination (PCO) were calculated from the respective resemblance matrices using WCMDSALE (Oksanen et al. 2016). Standardised values of covariates were fit to the PCO ordination plots using ENVFIT (Oksanen et al. 2016) to gain an understanding of their effect on the assemblages, and potential causes resulting in differences between assemblages. Covariates were overlaid onto the ordination as vectors in the direction of maximal change of a given variable. The average of eigenvalues was used to obtain centroids per treatment (central point within a cloud of PCO points of the same factor) (See Oksanen et al. 2016 for detailed description).

4.3.6.4.4.2 Canonical Analysis of Principal coordinates (CAP analysis)

Canonical Analysis of Principal coordinates (CAP) was performed to test the hypothesis that fish assemblages were different between baited and unbaited treatments (Anderson and Willis 2003).

Only treatment and covariates found to significantly explain the variance observed were used in CAP analysis. The significance of covariates was determined using a permutation test, ORDISTEP, in VEGAN (Oksanen et al. 2016). The effect of bait treatment was then tested while accounting for the effect of significant covariates from the CAP model, by removing their effect on the data prior to testing the effect of treatment on CAP analysis, using the “Condition” parameter in CAPSCALE in VEGAN (Oksanen et al. 2016). The significance of CAP models and the contribution of individual terms were tested using a permutational ANOVA, using ANOVA.CCA in the VEGAN package with 4 999 permutations (Oksanen et al. 2016). Weighted orthogonal species scores were added to CAP plots to illustrate the relative contribution of species to the observed differences in fish assemblages across bait treatments.

4.3.6.4.4.3 CAP cross-validation

Linear discriminant analysis was used to predict the bait treatment group allocation of 4 999 permutations of the principal coordinate samples obtained during CAP analysis, using (CAPDISCRIM) CAPDISCRIM function in the BIODIVERSITYR package in R (Kindt and Coe 2005). The number of correct predictive assignments were tested by comparing the permuted output with the actual treatments associated with samples. The significance of models was estimated by dividing the number of times the randomisation generated a larger

percentage of correct predictions than the ordination model (Kindt and Coe 2005). This is similar to the method of validation as the “leave-one-out” approach used by Anderson and Willis (2003), used in similar studies (Harvey et al. 2007; Dorman et al. 2012). The significance of cross-validation was tested using MANOVA as part of the CAPDISCRIM function (Kindt and Coe 2005).

4.3.6.4.5 Species dissimilarity between BRUVs and RUVs

Similarity percentage (SIMPER) analysis was used to determine species that characterise BRUVs and RUVs assemblages. The method decomposes Bray-Curtis dissimilarity into individual species contribution to overall dissimilarity and was carried out using SIMPER in R (Oksanen et al. 2016).

4.3.6.5 Univariate assemblage analysis within trophic and combined taxonomic-class-guild-size groups

The differences between fish abundance and the number of species were assessed across bait treatments using one-way permutational ANOVA within specified trophic guilds, and within the combined taxonomic-class-guild-size groups (Anderson and Millar 2004). As the fish assemblages here represent univariate data (a single variable), dissimilarity was based on the Euclidian distance between samples (Anderson and Millar 2004). The analysis included the same covariates as in the multivariate analysis to account for their effect on fish assemblages. Permutation of residuals was run under reduced models with 4 999 permutations and sequential sums of squares calculated.

The dispersion of variance data was tested using BETADISPER (Oksanen et al. 2016), with data grouped according to bait treatment. The mean and standard error of sample distances to the centroid of the group were calculated from the Euclidian distances, and significance assessed PERMUTEST with 4 999 permutations (Oksanen et al. 2016).

4.4. RESULTS

4.4.1 Description and assessment of covariate data structure

A total of 122 samples was collected, consisting of 61 BRUVs and 61 RUVs. Samples covered a depth range from 3 to 50 m depth, with temperatures that ranged between 23.1 and 29.5 °C (Figure 4.6). Samples were collected on the four aspects of the coastline ranging from low mean wave energy (4 444J/m³) on the west to high wave energy (11 191 J/m³) in the east. The sampled area within the Field of View (FOV) of the videos ranged 6 to 166 m², and the percentage water column also varied substantially from 0 to 84 %. The means of the respective covariates were not significantly different across bait treatments (Pairwise Wilcoxon, Holm adjusted $p > 0.05$) (Figure 4.6).

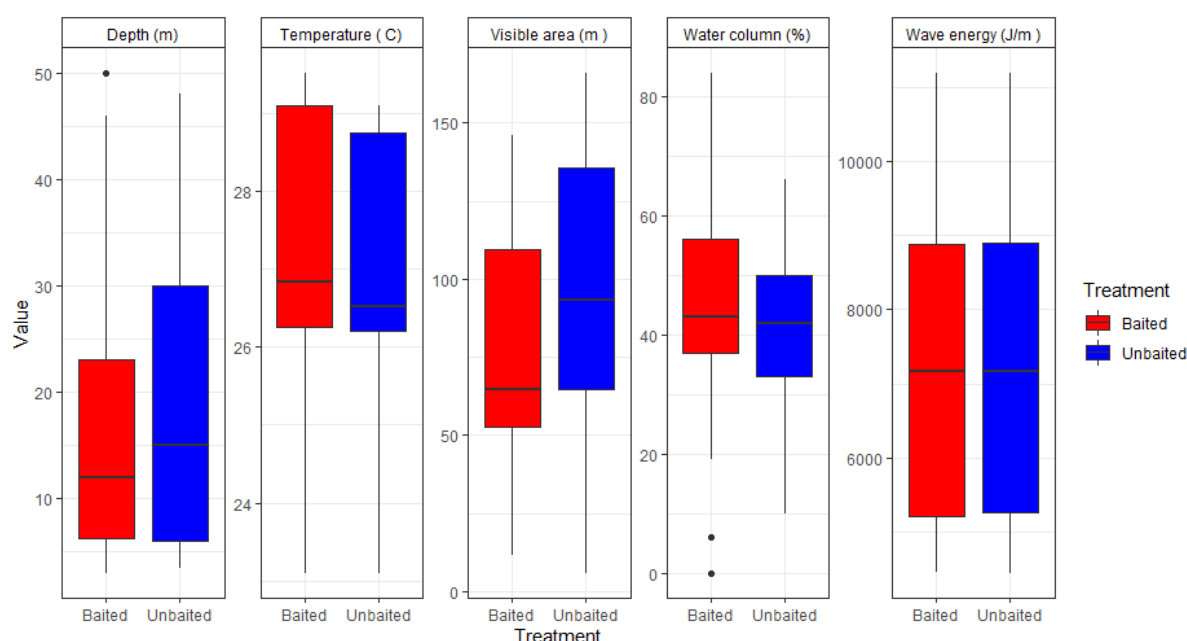


Figure 4.6. Boxplot of environmental and bias covariates showing the spread of values among treatments. Mean values are indicated by a middle bar, and outliers by dots (which were removed from the multivariate analysis).

4.4.2 Species richness

In total, 303 species from a diverse set of 51 families, including 17 species from 7 families of Elasmobranchii (cartilaginous fishes), and 286 species from 44 families in the Actinopterygii (bony fish) were recorded using spatially matched pairs of RUVs (unbaited) and BRUVs (baited) samples. Eight species of shark and nine species of ray were recorded. The most frequently observed Actinopterygii fish was the bluefin trevally, *Caranx melampygus*, which was observed in 98 out of 122 (80.3 %) samples, *Labroides dimidiatus* was observed 90

times, and *Variola louti* 81 times. Frequently observed elasmobranchs included *Carcharhinus amblyrhynchos* (67), *Nebrius ferrugineus* (34), *Carcharhinus melanopterus* (27) and *Negaprion acutidens* (27), and *Himantura fai* (7) was the most frequently observed ray.

4.4.3 Species diversity

Mean Shannon-Wiener diversity was not significantly greater (Wilcoxon signed rank test with continuity correction: $V = 894$, $p > 0.05$) in BRUVs (4.131 ± 0.094) than RUVs (4.152 ± 0.119). The baited mean distance to group centroid was 5.17, and unbaited mean distance to group centroid was 5.13 and was not significantly different from each other (BETADISPER F-ratio 0.07, and $p > 0.05$). Beta diversity (Table 4.2) was therefore not significantly different between treatments.

4.4.4 Mean number of species and relative abundance

The number of fish species and families were recorded in baited and unbaited treatments were very similar, with 265 fish species from 47 families recorded in baited samples, and 266 species from 47 families in unbaited samples (See Table 4.2 for a summary). There was substantial overlap in species recorded, with 228 shared species from 43 fish families in both RUVs and BRUVs videos. Baited treatments included two more elasmobranchs and three fewer Actinopterygii fish species (Table 4.2).

Table 4.2. A summary of the number of species, number of individuals, and diversity indices recorded in Baited Remote Underwater Video systems (BRUVs) and RUVs (baited and unbaited treatments) of the reef fish assemblage recorded at Aldabra.

	BRUVS (Baited)	RUVS (Unbaited)
Number of families	47	47
Number of Elasmobranchii species	14	12
Number of Actinopterygii species	251	254
Number of species (Gamma diversity) (γ)	265	266
Mean $\pm$ SE number of species per sample (Alpha diversity) (α)	41.33 ± 2.37	39.34 ± 2.43
Beta diversity (β)	5.41	5.76
Mean $\pm$ SE Shannon-Wiener diversity (H)	4.131 ± 0.094	4.152 ± 0.119
Mean $\pm$ SE number of fish per sample	118.8 ± 7.11	92.03 ± 6.56

SE (Standard error)

The number of species per sample in BRUVs (41.33 ± 2.36) was not significantly different (pairwise two-sided Wilcoxon signed rank test, $p > 0.05$, CI 95%, degrees freedom = 120) to

RUVs (39.43 ± 2.43). The most species recorded in a single baited sample was 73, while 71 species were recorded in a single unbaited sample.

Overall, 15 366 fish were recorded, based on total MaxN values, with 8 652 individuals counted in baited samples, and 6 714 in unbaited samples. Of these, 8 445 Actinopterygii fish and 207 elasmobranchs were recorded in BRUVs, and 6 657 Actinopterygii fish and 57 elasmobranchs in RUVs. The mean of total relative abundance (MaxN) per sample was significantly greater in BRUVs (118.8 ± 7.11) than RUVs (92.03 ± 6.56) (pairwise Wilcoxon test at 95 % CI, $p < 0.0001$).

4.4.5 Unique species and families per method

Several unique species were recorded per method. There were 37 species from 19 families recorded in BRUVs that were not in RUVs, and 38 species from 19 families in RUVs that were not recorded in BRUVs (

Table 4.3). The fish families Atherinidae, Grammistidae, Megalopidae, and Rhinobatidae, were sampled in BRUVs but not in RUVs, while the families Apogonidae, Microdesmidae, Molidae, and Ophichthidae were sampled by RUVs but not in BRUVs. Species unique to BRUVs include large eels such as *Gymnothorax flavimarginatus*, *Gymnothorax javanicus*, *G. meleagris* and *G. undulatus*, and large-invertebrate-carnivore-elasmobranchs including, *Rhynchobatus djiddensis*, *Dasyatis brevicaudata*, *Taeniura meyeni*, *Himantura granulate*, *Pastinachus sephen*, and groupers, *Epinephelus fuscoguttatus*, *E. malabaricus*, *E. hexagonatus*, *Plectropomus pessuliferus*, *Cephalopholis leopardus*. Notable species present in samples from unbaited treatment (RUVs) but not baited treatments (BRUVs) include single observations of large zooplanktivores rays, *Manta (Mobula) alfredi*, *Mobula kuhlii*, a white tip reef shark, *Triaenodon obesus* (See

Table 4.3 for species list). Most species unique to either treatment were observed only once, but *Anampses lineatus* and *Oxycheilinus digramma* were observed seven and eight times, respectively, in unbaited samples only. *Epinephelus fuscoguttatus* was observed 11 times, in baited samples only.

Table 4.3. Unique species that were recorded using RUVs (unbaited) or BRUVs (baited) treatments, and their frequency (number of samples in which species were present).

RUVs unique species	Frequency	BRUVs unique species	Frequency
<i>Abudefduf sexfasciatus</i>	1	<i>Amphiprion akallopisos</i>	1
<i>Acanthocybium solandri</i>	1	<i>Arothron mappa</i>	1
<i>Aluterus scriptus</i>	1	<i>Aspidontus tractus</i>	1
<i>Amphiprion allardi</i>	2	<i>Atherinomorus lacunosus</i>	1
<i>Anampses lineatus</i>	7	<i>Caesio caerulaurea</i>	1
<i>Arothron immaculatus</i>	3	<i>Caesio teres</i>	2
<i>Arothron meleagris</i>	2	<i>Caesio xanthonota</i>	1
<i>Arothron stellatus</i>	2	<i>Caranx lugubris</i>	1
<i>Canthigaster smithae</i>	1	<i>Cephalopholis leopardus</i>	1
<i>Carangoides fulvoguttatus</i>	3	<i>Cephalopholis sonnerati</i>	1
<i>Cephalopholis boenak</i>	1	<i>Cetoscarus bicolor</i>	2
<i>Cheilinus fasciatus</i>	1	<i>Chaetodon vagabundus</i>	1
<i>Chromis opercularis</i>	3	<i>Cheilodipterus macrodon</i>	1
<i>Exallias brevis</i>	1	<i>Chromis pembae</i>	1
<i>Gunnelichthys curiosus</i>	2	<i>Chromis ternatensis</i>	1
<i>Gunnelichthys monostigma</i>	2	<i>Cirripectes auritus</i>	1
<i>Hologymnosus annulatus</i>	3	<i>Dasyatis brevicaudata</i>	4
<i>Lutjanus ehrenbergii</i>	1	<i>Elagatis bipinnulatus</i>	1
<i>Lutjanus fulviflamma</i>	1	<i>Epinephelus fuscoguttatus</i>	11
<i>Lutjanus lutjanus</i>	1	<i>Epinephelus hexagonatus</i>	1
<i>Manta alfredi</i>	1	<i>Epinephelus malabaricus</i>	1
<i>Mobula kuhlii</i>	1	<i>Euthynnus affinis</i>	1
<i>Myrichthys maculosus</i>	1	<i>Grammistes sexlineatus</i>	1
<i>Myripristis violacea</i>	1	<i>Gymnothorax flavimarginatus</i>	2
<i>Ostorhinchus angustatus</i>	1	<i>Gymnothorax javanicus</i>	1
<i>Oxycheilinus digramma</i>	8	<i>Gymnothorax meleagris</i>	1
<i>Paracaesio xanthura</i>	1	<i>Gymnothorax undulatus</i>	1
<i>Paraluteres prionurus</i>	2	<i>Heniochus acuminatus</i>	1
<i>Petroscirtes breviceps</i>	1	<i>Heniochus monoceros</i>	3
<i>Pomacanthus chrysurus</i>	3	<i>Himantura granulata</i>	1
<i>Pomacentrus trichrourus</i>	1	<i>Lutjanus bengalensis</i>	1
<i>Pseudobalistes fuscus</i>	2	<i>Megalops cyprinoides</i>	1
<i>Ptereleotris evides</i>	2	<i>Pastinachus sephen</i>	1
<i>Sargocentron diadema</i>	1	<i>Plectropomus pessuliferus</i>	1
<i>Scarus globiceps</i>	1	<i>Rhynchobatus djiddensis</i>	1
<i>Thalassoma hardwicke</i>	1	<i>Siganus argenteus</i>	1
<i>Trachinotus blochii</i>	1	<i>Taeniura meyeri</i>	2
<i>Triaenodon obesus</i>	1		

4.4.6 Species accumulation curves

There was no significant difference in the rate of new or additional species being observed by increasing the sample size between baited and unbaited treatments (Two-sample Kolmogorov-Smirnov test data: $D = 0.033$, $p \gg 0.05$) (Figure 4.7).

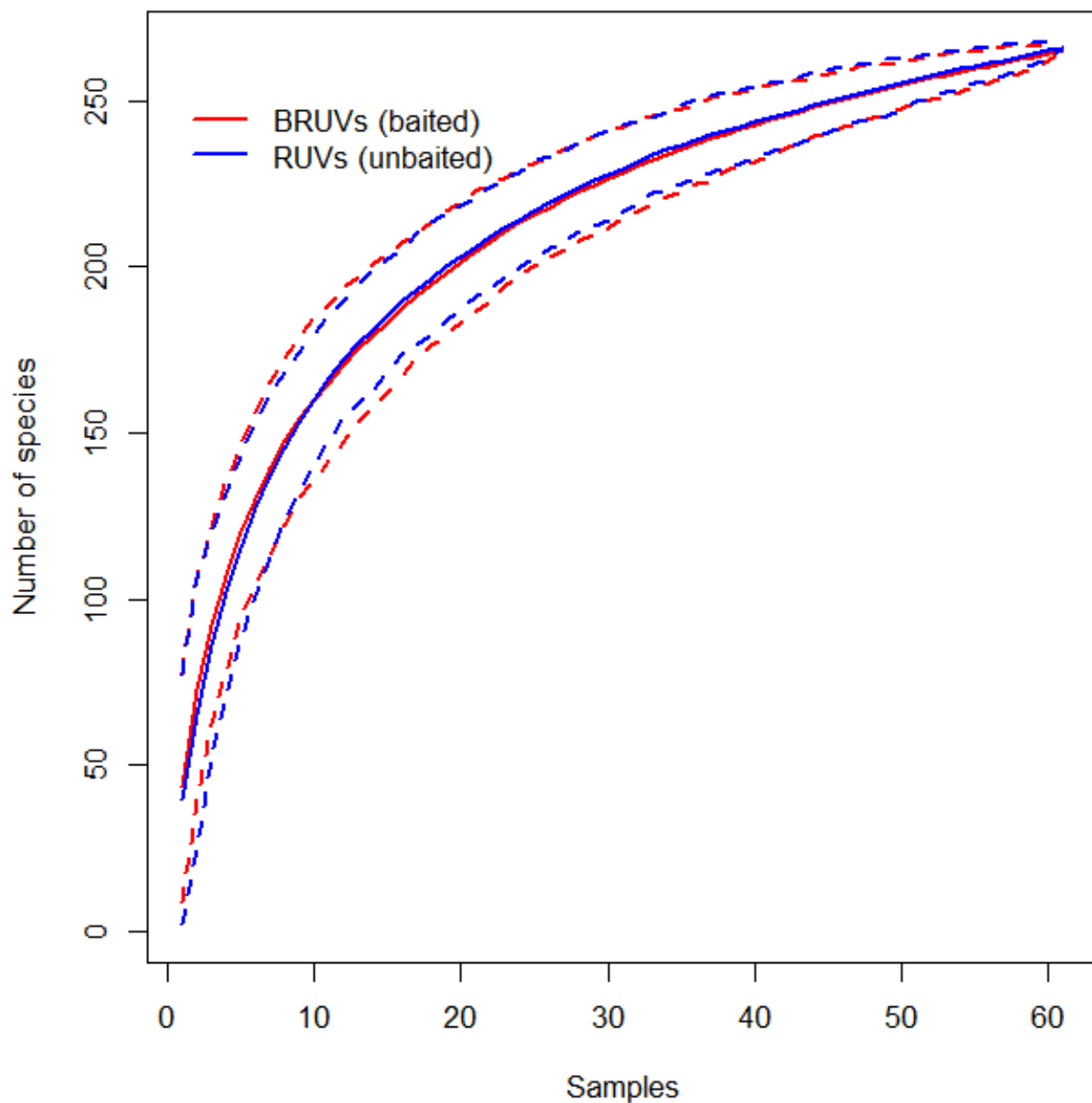


Figure 4.7. Species accumulation curves indicating that Baited Remote Underwater Video systems (BRUVs) (red line) and RUVs (blue line), recorded new species at the same rate with an increase in sample size. The dashed line indicates standard error.

4.4.7 Species level assemblage structure

Fish assemblage structure, based on abundance data, was significantly different between samples (Permutational ANOVA, pseudo- $F = 3.18$, $p < 0.001$), and significantly altered by

bait treatment (sequential PERMANOVA pseudo-F = 2.65, $\text{Pr}(> F) < 0.001$) (See Table 4.4 for the significance of covariates from sequential PERMANOVA test).

Table 4.4. Sequential PERMANOVA of species level fish assemblage structure (MaxN data) recorded using Baited Remote Underwater Video systems (BRUVs) and RUVs at paired sampling sites on the seaward reefs at Aldabra between 0 and 55 m depth.

Covariates	Degrees freedom	Sum of Squares	Pseudo-F	Pr(>F)
Sample area	1	1.005	1.67	0.0102*
Percent water column	1	0.774	1.2865	0.0836
Temperature	1	1.478	2.4568	0.0006***
Wave energy	1	3.114	5.1758	0.0002***
Depth	1	3.52	5.8507	0.0002***
Treatment	1	1.596	2.6524	0.0002***
Residual	113	67.982		

Significance levels: $< 0.001 = \text{***}$; $< 0.01 = \text{**}$; $< 0.05 = *$

The overlap of Principal Coordinates Ordination (PCO) sample group location (grouped by bait treatment) in unconstrained ordination space indicated similarities in the fish assemblage structure across bait treatments. Bait treatment did not have a strong relationship, nor significant goodness of fit (ENVFIT, $r^2 = 0.016$, $\text{Pr}(> r) > 0.05$, based 4 999 permutations) with the PCO points (Figure 4.8). Fitting normalised predictor variables indicated that depth, wave energy, and water temperature had strong and significant relationship ($\text{Pr}(> r) < 0.001$) with the spread of PCO points (Figure 4.8).

The mean ($\pm$ SE) distances of samples from the centroids were 0.81 ± 0.018 for baited, and 0.79 ± 0.019 from unbaited samples (Figure 4.8). The dispersion of variance of sample distance to centroid was not significantly different across bait treatments (Permutational Multivariate Dispersion test (BETADISPER), $F = 0.56$, $\text{Pr}(> F) > 0.05$). The significance of the PERMANOVA and non-significance of dispersion of variance, suggests that there may be a difference in the location of PCO points across treatments, which may be visible in constrained ordination analysis. Put differently, it suggests that there were many similarities in the fish assemblage structure across bait treatments (many ubiquitous species in both sets of assemblages), but that there were a few consistent differences caused by a combination of species composition and abundance differences for particular species.

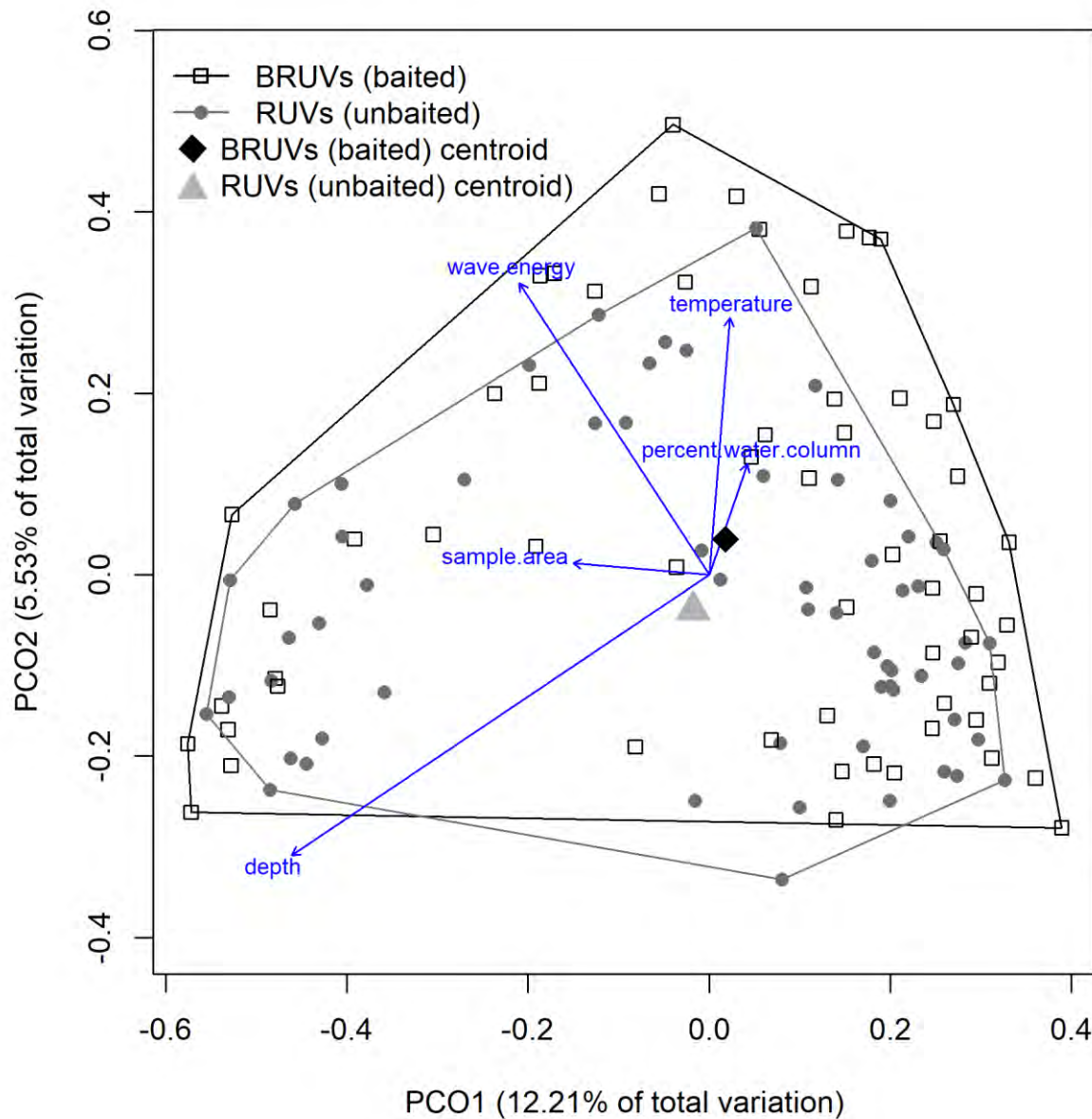


Figure 4.8. Principal Coordinate Ordination showing the differences between species-level fish assemblages recorded at paired sampling sites, using BRUVS (baited) and RUVs (unbaited). Lengths of arrows show the strength of predictor variable correlation to data, and the distance between centroids of distribution of points indicate the level of separation between treatments.

Grouping of fish assemblages became evident in the spatial separation of samples according to bait treatment in the CAP ordination plot (Figure 4.9). Treatment, depth and wave energy were determined to be significant covariates from comparisons of multiple constrained Canonical Analysis of Principal coordinates (CAP) (ORDISTEP Differences in Akaike Information Criterion [AIC] values $\text{Pr}(>F) < 0.01$). CAP analysis confirmed that fish assemblages were significantly different among samples (ANOVA, $F = 4.42$, $p < 0.001$) and across bait treatments (ANOVA, $F = 2.86$, $p < 0.001$). Significance for other covariates is

presented in Table 4.5. Fewer individuals of *Thalassoma hebraicum*, *Lutjanus bohar* and *Thalassoma amblycephalum*, but more *Cirrhilabrus exquisitus*, were recorded in RUVs than BRUVs (Figure 4.9). These species contributed the most to differences observed between baited and unbaited treatments.

Table 4.5. ANOVA of Canonical Analysis of Principal coordinates (CAP) of the species level fish assemblage showing the significance of predictor variables when added sequentially to the model (from top to bottom as listed) and significance determined using 4 999 permutations.

	Degrees freedom	Sum of Squares	F	Pr(>F)
Wave energy	1	2.63	4.37	2e-04 ***
Depth	1	5.25	8.73	2e-04 ***
Treatment	1	1.724	2.8621	4e-04 ***
Residual	116	69.853		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Fish assemblage structure was significantly different between treatments after removing the effect of depth and wave energy in the CAP model (ANOVA of Partial CAP, $F = 2.86$, $p < 0.001$). Cross-validation using predictive assignment of samples to BRUVs or RUVs based on fish assemblage composition was accurate (86.7 % correct, $m = 6$), and had similar accuracy in unbaited (88 %) and baited (85 %) treatments. Relatively high accuracy indicates that the fish assemblage structure was distinct across treatments.

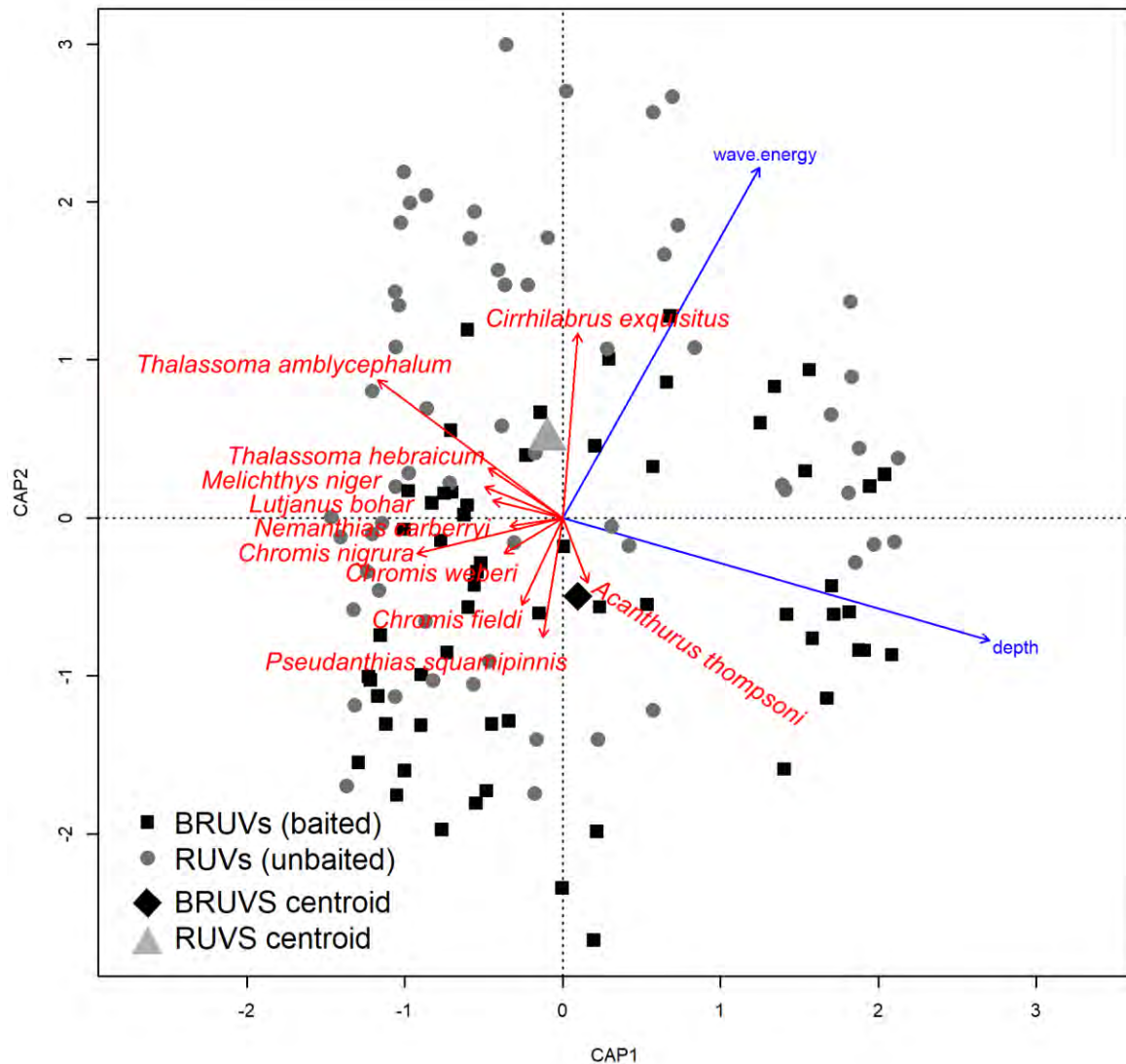


Figure 4.9. Canonical Analysis of Principal coordinates (CAP) plot BRUV and RUV samples according to treatment, constrained by bait treatment, depth, and wave energy. The centroids of baited and unbaited samples show the mean difference between samples by bait treatment in ordination space. The length of the dark blue arrow lines indicates the correlative strength of the change in covariates to change in sample differences. The lengths of the red lines indicate the species and direction in which the most significant change in fish assemblage occurs.

4.4.8 Trophic guilds

4.4.8.1 Species richness, diversity, and abundance within trophic guilds

The mean number of species (N_{sp}) of generalist carnivores and piscivores were significantly greater in baited treatments (permutational ANOVA sequential test $\Pr(>F) < 0.05$), while the numbers of species of herbivores and corallivores were significantly greater in unbaited than baited treatments (permutational ANOVA sequential test $\Pr(>F) < 0.05$) (Figure 4.10a).

Mean relative abundances (MaxN) of generalist carnivores, piscivores and zooplanktivores, were significantly greater in baited treatments (permutational ANOVA sequential test for each guild, $\text{Pr}(> F) < 0.05$), while herbivores were significantly more abundant in unbaited treatments (permutational ANOVA sequential test $\text{Pr}(> F) < 0.05$) (Figure 4.10b).

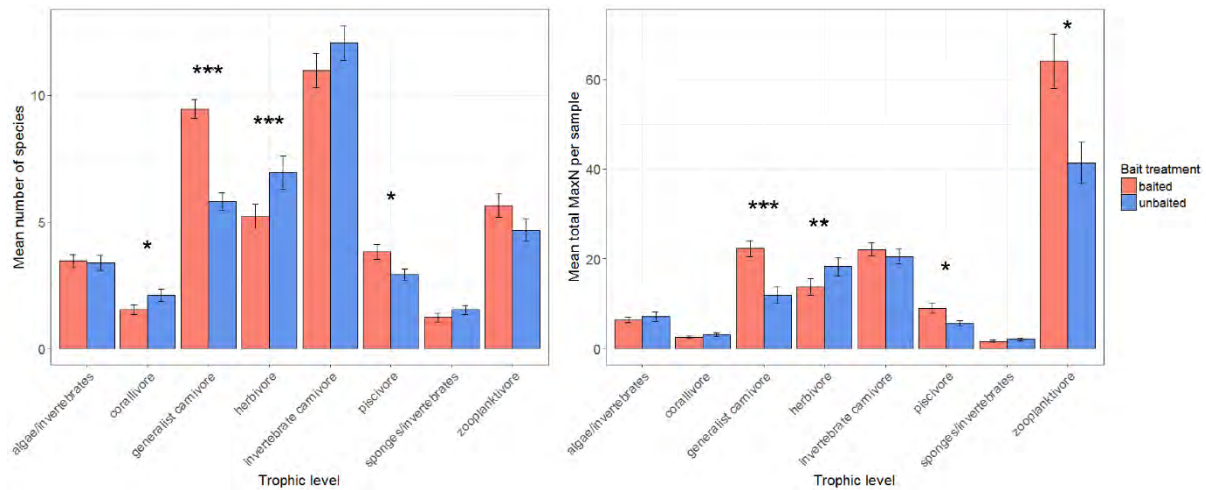


Figure 4.10. Means of the total a) numbers of fish species and b) abundances per sample, for each trophic feeding guild across baited (BRUVs) ($n = 61$) and unbaited (RUVs) treatments ($n = 61$). Significant differences of univariate permutational ANOVA p -values: *** < 0.001 , ** < 0.01 , * < 0.05 .

In total, more species of generalist carnivore were recorded in baited treatments than unbaited treatments, while more species of algal/invertebrate-eaters were observed in unbaited treatments (Table 4.6). Mean Shannon-Wiener diversity for generalist carnivores was significantly greater in baited treatments than unbaited treatments (pairwise Wilcoxon $p < 0.001$) (Table 4.6). The beta-diversity scores across bait treatments were not significantly different for any of the trophic guilds (BETADISPER $\text{Pr}(> F) > 0.05$).

Table 4.6. Trophic guild by treatment, total number of species (gamma (γ)), beta (β) diversity, mean $\pm$ standard error of Shannon-Wiener diversity index ($\bar{H} \pm SE$) from 61 BRUVs and 61 RUVs recorded at paired sampling sites.

Trophic guild	Treatment	γ	β	($\bar{H} \pm SE$)
Generalist carnivore	baited	56	4.92	$2.7 \pm 0.1^{***}$
Generalist carnivore	unbaited	51	7.81	$2.1 \pm 0.1^{***}$
Invertebrate carnivore	baited	65	4.84	3.0 ± 0.1
Invertebrate carnivore	unbaited	68	4.57	3.2 ± 0.1
Herbivores	baited	42	5.47	2.1 ± 0.1
Herbivores	unbaited	41	4.04	2.3 ± 0.1
Piscivore	baited	19	3.57	1.5 ± 0.1
Piscivore	unbaited	17	4.25	1.3 ± 0.1
Sponges/invertebrates	baited	9	3.68	0.7 ± 0.1
Sponges/invertebrates	unbaited	10	3.41	0.9 ± 0.1
Corallivore	baited	12	3.98	1.0 ± 0.1
Corallivore	unbaited	13	3.47	1.3 ± 0.1
Zooplanktivores	baited	37	5.01	1.6 ± 0.1
Zooplanktivores	unbaited	37	5.88	1.4 ± 0.1
Algae/invertebrates	baited	25	5.64	1.6 ± 0.1
Algae/invertebrates	unbaited	29	6.29	1.6 ± 0.1

Wilcoxon rank sum test with continuity correction *p*-values for Shannon-Wiener diversity significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

4.4.8.2 Species accumulation curves per trophic guild

Deconstructing the overall species accumulation curve into its trophic components indicated that there were differences in the species accumulation rate among guilds (Figure 4.11). The species accumulation rates were significantly greater in baited treatments within piscivore and generalist carnivore trophic guilds, while being significantly greater in unbaited treatments within corallivore, algal/invertebrates, sponge/invertebrates, and invertebrate carnivore guilds (Figure 4.11).

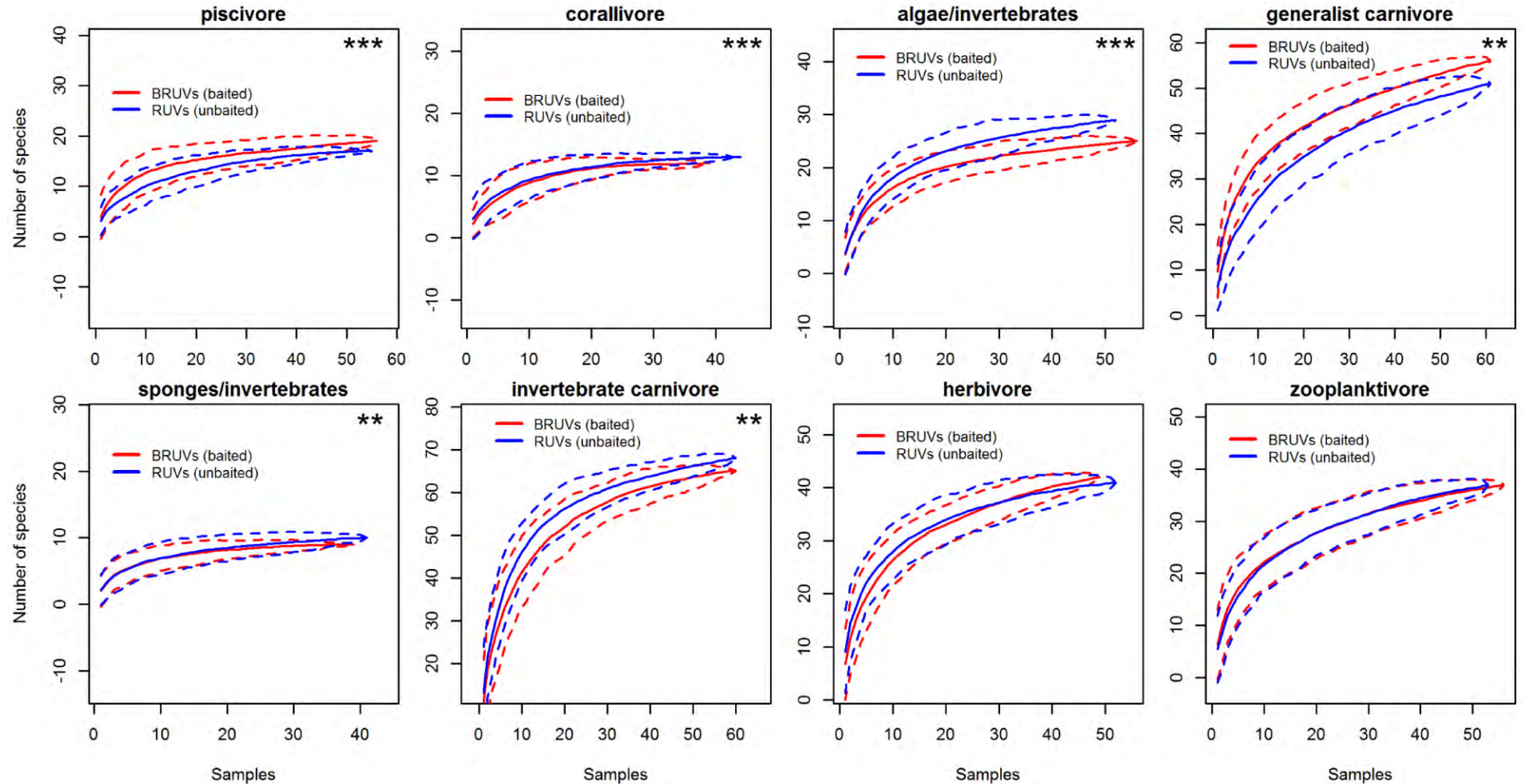


Figure 4.11. Species accumulation curves for each trophic feeding guild recorded at paired sampling sites on the seaward reefs of Aldabra in 0 to 55 m depth. The mean accumulation rate in solid line, and standard error in dashed line, with baited samples in red, and unbaited in blue. Kolmogorov-Smirnoff significance codes: $p < 0.001 = ***$, $p < 0.01 = **$, $p < 0.05 = *$

4.4.8.3 Trophic guild fish assemblage structure

Variation of the trophic guild assemblage structure was significantly different between samples (PERMANOVA overall test, $F = 2.773$, $\text{Pr}(> F) < 0.001$). Bait treatment significantly altered the fish assemblage in terms of its trophic guild structure (PERMANOVA sequential test, $F = 1.83$, $p < 0.05$) (Table 4.7).

Table 4.7. Sequential PERMANOVA test indicating that bait treatment, depth, wave energy had a significant effect on the trophic guild structure of reef fish at paired sampling sites on the seaward reefs of Aldabra.

Terms	Degrees freedom	Sum of squares	F	Pr(>F)
Sample area	1	1.268	1.1177	0.2162
Percent water column	1	1.293	1.1396	0.1862
Temperature	1	1.927	1.6985	0.0326*
Wave energy	1	5.76	5.0767	0.0002***
Depth	1	6.547	5.7711	0.0002***
Treatment	1	2.081	1.8346	0.0152**
Residual	113	128.199		

Significance levels: $< 0.001 = \text{***}$; $< 0.01 = \text{**}$; $< 0.05 = *$

Mean distance from samples to centroids of PCO plots (Figure 4.12) were 1.07 ± 0.02 for baited and 1.09 ± 0.02 for unbaited samples. Dispersion of variance of fish assemblage composition was not significant across treatments at the trophic guild level (PERMUTEST, $F = 0.35$, $p > 0.5$). This suggests that PERMANOVA results were significant because of a difference in the location of samples in the PCO plot. Similarities in assemblage structure were a consequence of many shared species, and differences in abundance of fish in the trophic groups caused significant differences in assemblage structure.

The lines fitted to the ordination graph (Figure 4.12) showed that depth, wave energy and percent water column had significant relationships with the change in fish community (ENVFIT $p < 0.05$). Depth had the strongest relationship of these three variables ($r^2 = 0.37$).

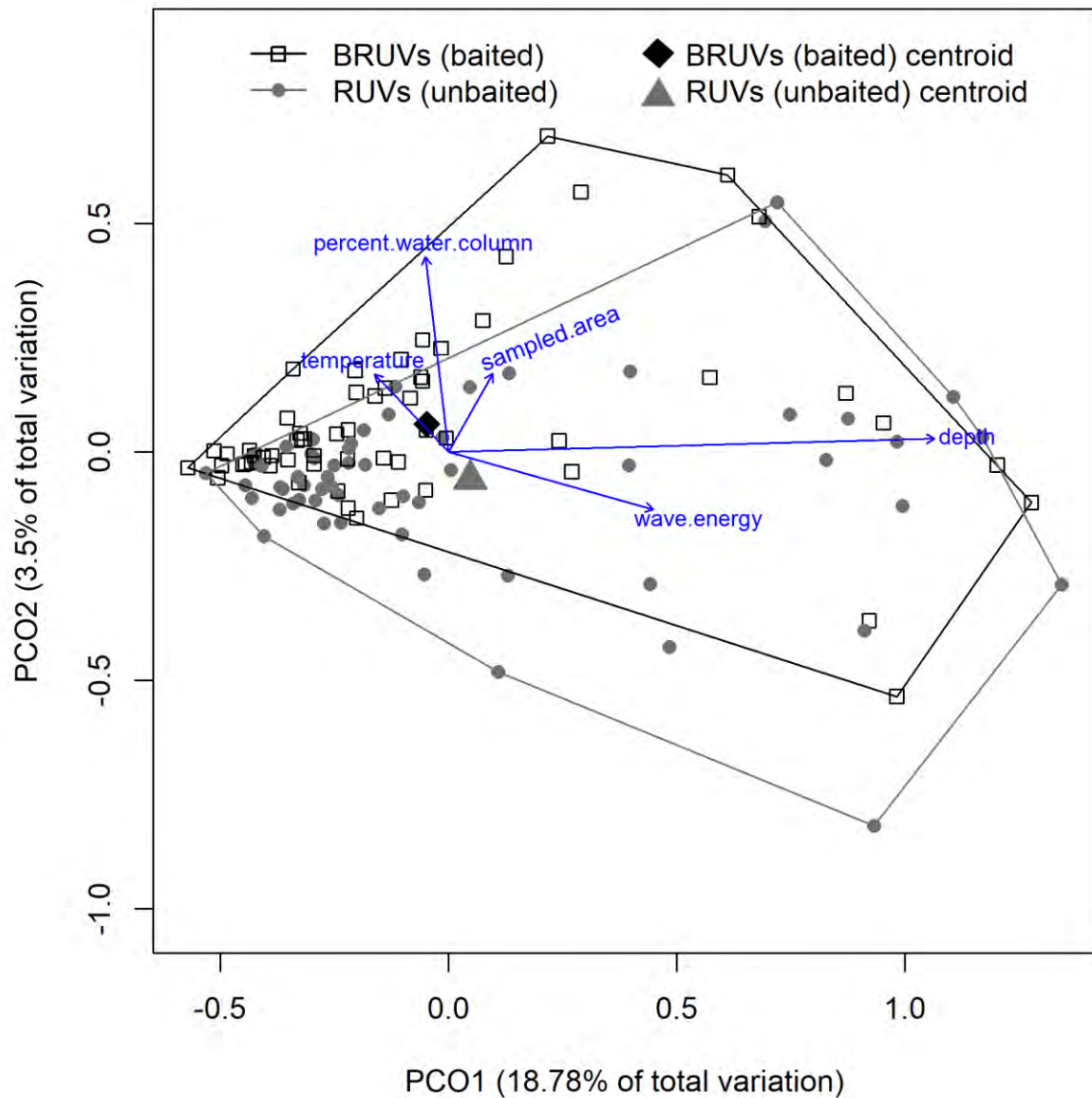


Figure 4.12. Principal Coordinate Ordination showing the similarity of samples representing fish assemblages at the trophic guild between BRUVs (baited) and RUVs (unbaited) based on relative abundance (MaxN) of fish. Length of arrows shows the strength of predictor variable correlation to data, and the distance between centroids of distribution of points indicate the level of separation between treatments.

Clear spatial grouping of samples according to bait treatment indicated a difference in location of samples in the CAP analysis ordination plot (Figure 4.13). Trophic guild assemblages were significantly different from each other in CAP analysis (ANOVA of CAP $F = 4.56$, $\text{Pr}(> F) < 0.001$), and were significantly different across bait treatment (Table 4.8). The increase in the number of zooplanktivores, generalist carnivores, piscivores and a

decrease in the number of herbivores in baited samples contributed most to the differences between trophic guild fish assemblages across bait treatments (Figure 4.13).

Table 4.8. ANOVA of Canonical Analysis of Principal coordinates (CAP) of trophic guild assemblage structure showing the significant effect of bait treatment after accounting for the effects of environmental covariates when added sequentially to the model (from top to bottom as listed).

	Degrees freedom	Sum of squares	F	Pr(>F)
Wave energy	1	2.95	2.5985	0.0014**
Depth	1	10.37	9.1437	0.0002***
Treatment	1	2.19	1.9297	0.0128*
Residual	116	131.6		

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

Fish assemblages at the trophic guild level were significantly different between treatments after removing the effect of depth and wave energy (ANOVA $F = 1.93$, $\text{Pr}(>F) < 0.01$). Cross-validation of correct predictions using CAP discrimination resulted in 74 % correct classification ($p < 0.001$, $m = 5$) of samples to treatment, based on their respective assemblage trophic composition. Accuracy was considerably higher for baited samples (80 %) than unbaited samples (67 %). Distinct location of samples in constrained ordination space and the high level of accuracy with which the type of treatment could be predicted from the assemblage composition indicate distinct, and more consistent, trophic structure around baited samples than unbaited samples.

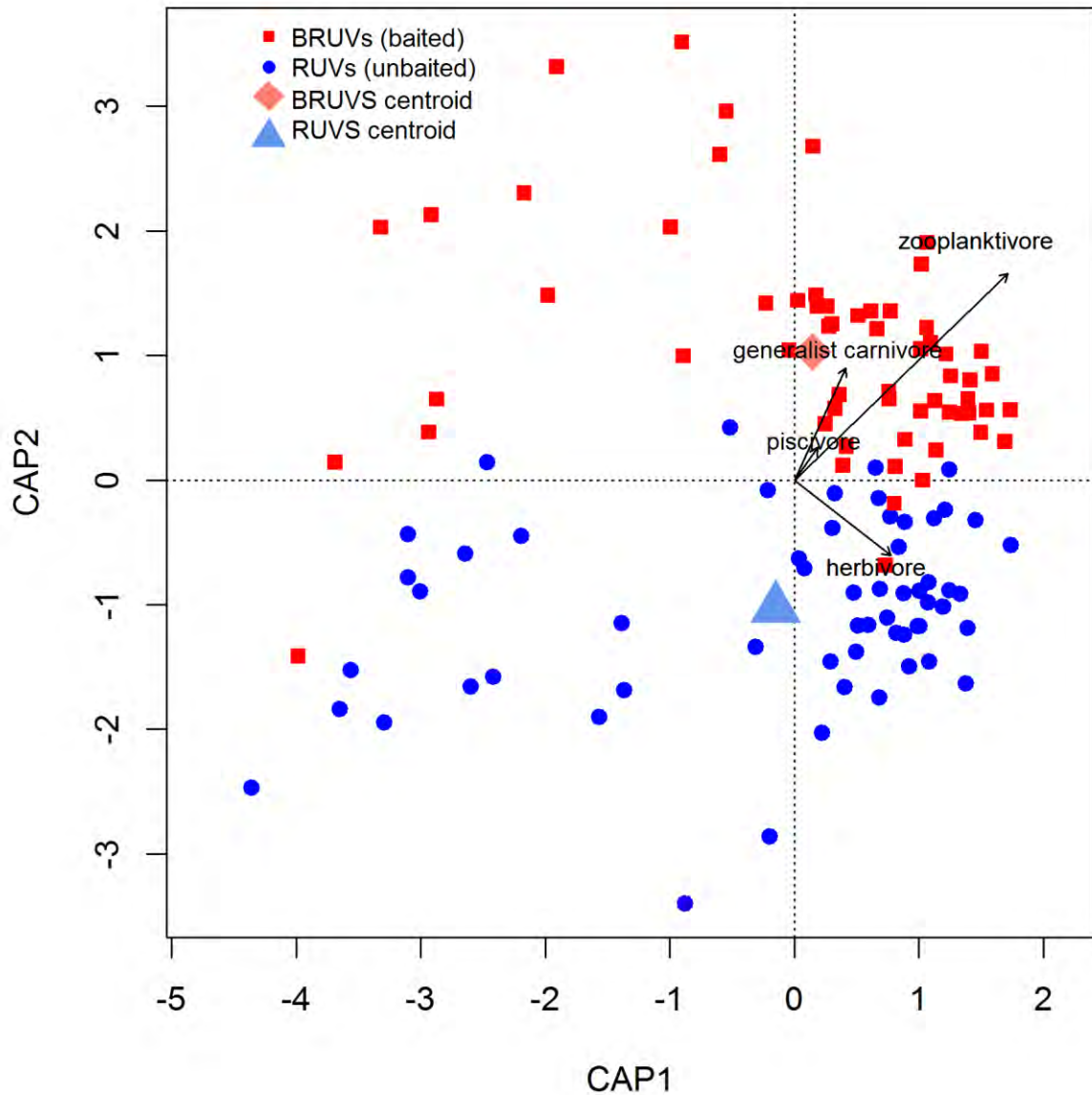


Figure 4.13. Canonical Analysis of Principal coordinates (CAP) plot showing the distribution of samples constrained by treatment, depth, and wave energy. The centroids of baited and unbaited samples show the difference of mean locality in ordination space between the two bait treatments. The length of the black lines indicates the trophic guilds that contributed the most the differences between baited and unbaited treatments.

4.4.8.4 The effect of bait treatment on multi-species fish assemblages within trophic guilds

The species assemblage structure within trophic guilds was significantly different between respective trophic guilds across bait treatments for invertebrate carnivores, generalist carnivores, and zooplanktivores (Sequential PERMANOVA $\text{Pr}(> F) < 0.05$) (Table 4.9).

Table 4.9. Summary table of sequential PERMANOVA results of species assemblage structure within respective trophic guilds between bait treatments.

Trophic guild	Degrees freedom	Sum of squares	F	Pr(>F)
Generalist carnivore	1	3.78	3.41	0.0002***
Invertebrate carnivore	1	1.59	1.81	0.0016**
Zooplanktivores	1	5.95	1.20	0.012*
Herbivore	1	1.96	1.20	0.0384*
Piscivore	1	1.59	1.30	0.0404*
Sponges/invertebrates	1	1.04	1.46	0.081
Corallivore	1	1.02	1.21	0.1418
Algae/invertebrates	1	2.17	0.93	0.814

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Of the five trophic guilds that were significantly different across bait treatment, only generalist carnivores had a clear difference in the locality of samples in the unconstrained PCO ordination plot (Figure 4.14). The dispersion of variance was not significantly different between samples for generalist carnivores, suggesting that significant differences observed in PERMANOVA were due to the difference in location of samples. The difference in dispersion of variance across bait treatments was not significantly different in any of the trophic guilds, apart from sponge/invertivores, where results were marginally significant (PERMUTEST, $\text{Pr}(>F) < 0.05$). As sponge/invertivores were not significantly different between treatments, the dispersion results do not indicate true differences in assemblage structure.

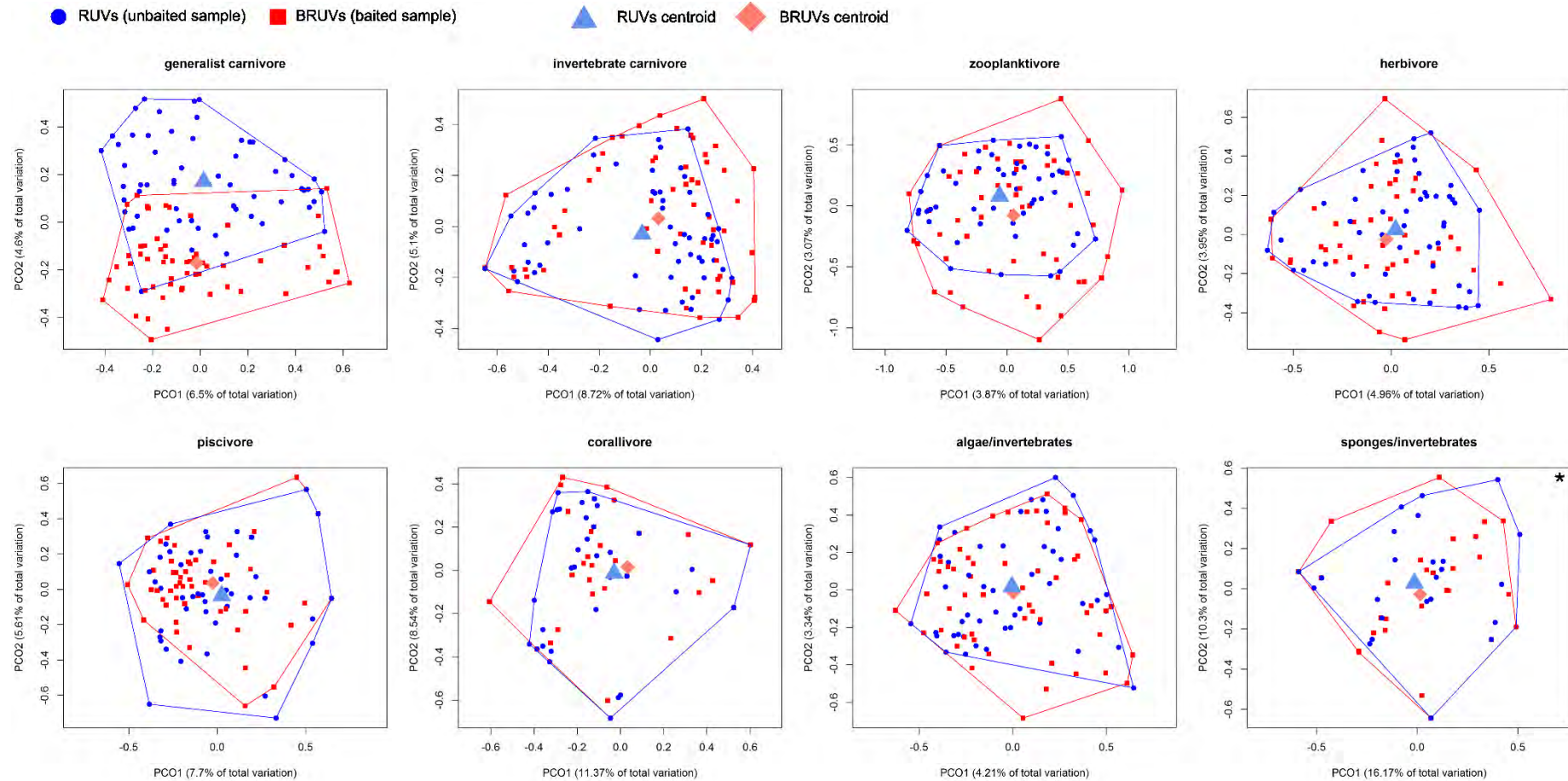


Figure 4.14. Principal Coordinate Ordination of abundance (MaxN) data within respective trophic guilds. Generalist carnivores had the least overlap of samples in ordination space. Distribution of dispersion of variance significant codes: $Pr(F) < 0.05 = *$.

Fish assemblages were significantly different across treatments, including generalist carnivores, invertebrate carnivores, zooplanktivores, herbivores and piscivores (ANOVAs of $CAP_{\text{treatment}} \Pr(>F) < 0.05$ for respective trophic guilds), (See Figure 4.15 for respective significance values).

There was a clear separation between samples (trophic guild assemblages) in constrained ordination space across bait treatments in most trophic guilds (Figure 4.15). The clear separation of samples across bait treatments showed that fish assemblage structure was significantly altered by the presence of bait within trophic guilds.

An increase in *Lutjanus bohar*, *Lethrinus nebulosus*, *Carcharhinus amblyrhynchos* in baited treatments contributed most to the differences observed in generalist carnivores (Figure 4.15). An increased abundance of *Thalassoma hebraicum* and *T. amblycephalum* in baited treatments contributed the most to differences between invertebrate carnivore, and zooplanktivore fish assemblages, respectively (Figure 4.15). A decrease in the number of *Chlorurus sordidus*, *Acanthurus leucosternon* and *Ctenochaetus striatus* in baited treatments contributed the most to differences in herbivorous fish assemblages across bait treatments (Figure 4.15). Herbivores were dominated by Acanthuridae (58 %) and Scaridae (27%), including *Chlorurus sordidus*, *Scarus psittacus*, *Scarus ghobban*, *Naso brevirostris*, *Acanthurus leucosternon*, *A. tennentii*, and *Ctenochaetus binotatus* which were 2 - 4 times more abundant in unbaited samples than baited samples. *Caranx melampygus* was more abundant in baited treatments and contributed the most to the differences observed in piscivores across bait treatments (Figure 4.15). See Annex ~ Chapter 4 for enlarged figures for more detail.

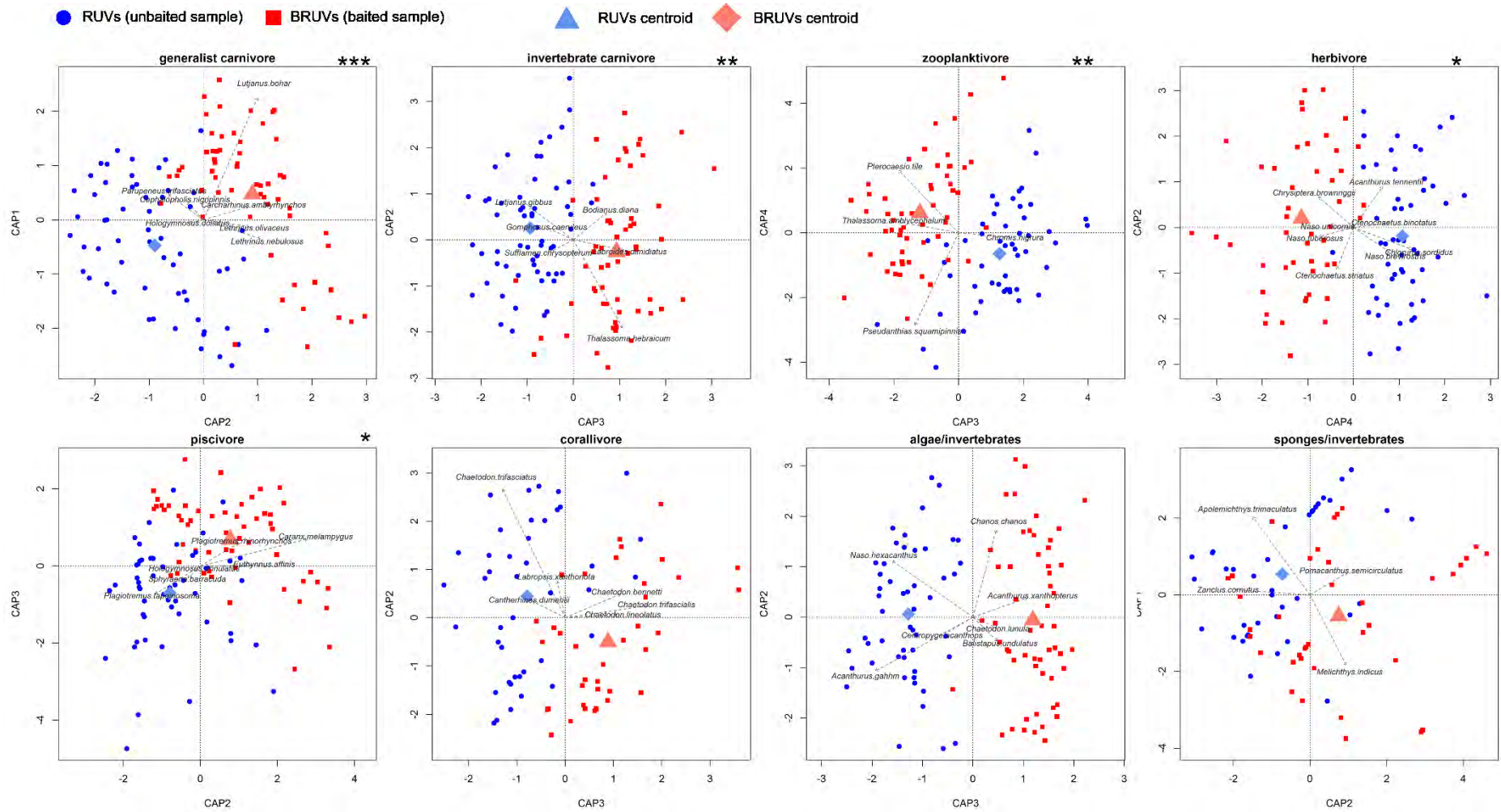


Figure 4.15. Canonical Analysis of Principal coordinates (CAP) plots of abundance-based fish assemblage samples for each trophic guild. The centroid is the mean position within the cloud of points for the respective bait treatments. The length of the arrow shows the relative contribution of species to CAP models. The axis that shows the effect of bait treatment at its maximum is displayed. ANOVA of treatment significance in CAP models: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

Predictive assignment to bait treatment based on fish assemblage structure was significant for generalist carnivores, invertebrate carnivore, zooplanktivores, piscivores, and sponges/invertivores (Table 4.10). The correct prediction was higher in baited treatments for generalist carnivores, and zooplanktivores, but invertebrate carnivores, piscivores, and sponge/invertivores assemblages were more often correctly assigned to unbaited treatments (Table 4.10).

Table 4.10. Cross-validation of Canonical Analysis of Principal coordinates (CAP) model after removing the effect of other significant covariates, showing the percentage correct assignments, and the significance tested using 4999 permutations of the data.

Cross-validation	m	Baited correct prediction %	Unbaited correct prediction %	Significance of percentage	MANOVA (Pr(>F))
Generalist carnivore	3	90	85	0.0002	< 2.2e-16 ***
Invertebrate carnivore	8	78	86	0.0002	4.449e-13 ***
Zooplanktivores	8	75	62	0.0004	6.8e-05 ***
Piscivore	6	58	67	0.013	0.01571 *
Sponges/invertebrates	4	56	72	0.017	0.02644 *
Corallivore	7	55	65	0.06	0.0998
Herbivore	4	46	67	0.14	0.2
Algae/invertebrates	7	60	43	0.3	0.4376

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *; “m” is the number of PCO axis used, and was determined through CAP model optimisation (Kindt and Coe 2005). Note that sponges/invertebrates were not significantly different in overall CAP analysis.

4.4.9 Combined taxonomic-class, trophic guild, and size-class

4.4.9.1 Relative abundance, and number of species, within each of the combined trophic, taxonomic-class-size-classes

Multiple combined taxonomic-class-guild-size groups were significantly different in species richness and abundance between treatments (Figure 4.16). Very large and medium generalist carnivore and invertebrate carnivore elasmobranchs were significantly more species-rich and had higher abundance in baited treatments (Univariate permutational ANOVA Pr(>F) < 0.01).

Large and very large Actinopterygii generalist carnivores, large and medium Actinopterygii piscivores, and large Actinopterygii zooplanktivores were significantly more species-rich and abundant in baited than unbaited treatments (Univariate permutational ANOVA Pr(>F) < 0.05). Small and medium Actinopterygii herbivores were more abundant, and species-rich in unbaited than baited treatments (Univariate permutational ANOVA Pr(>F) < 0.05).

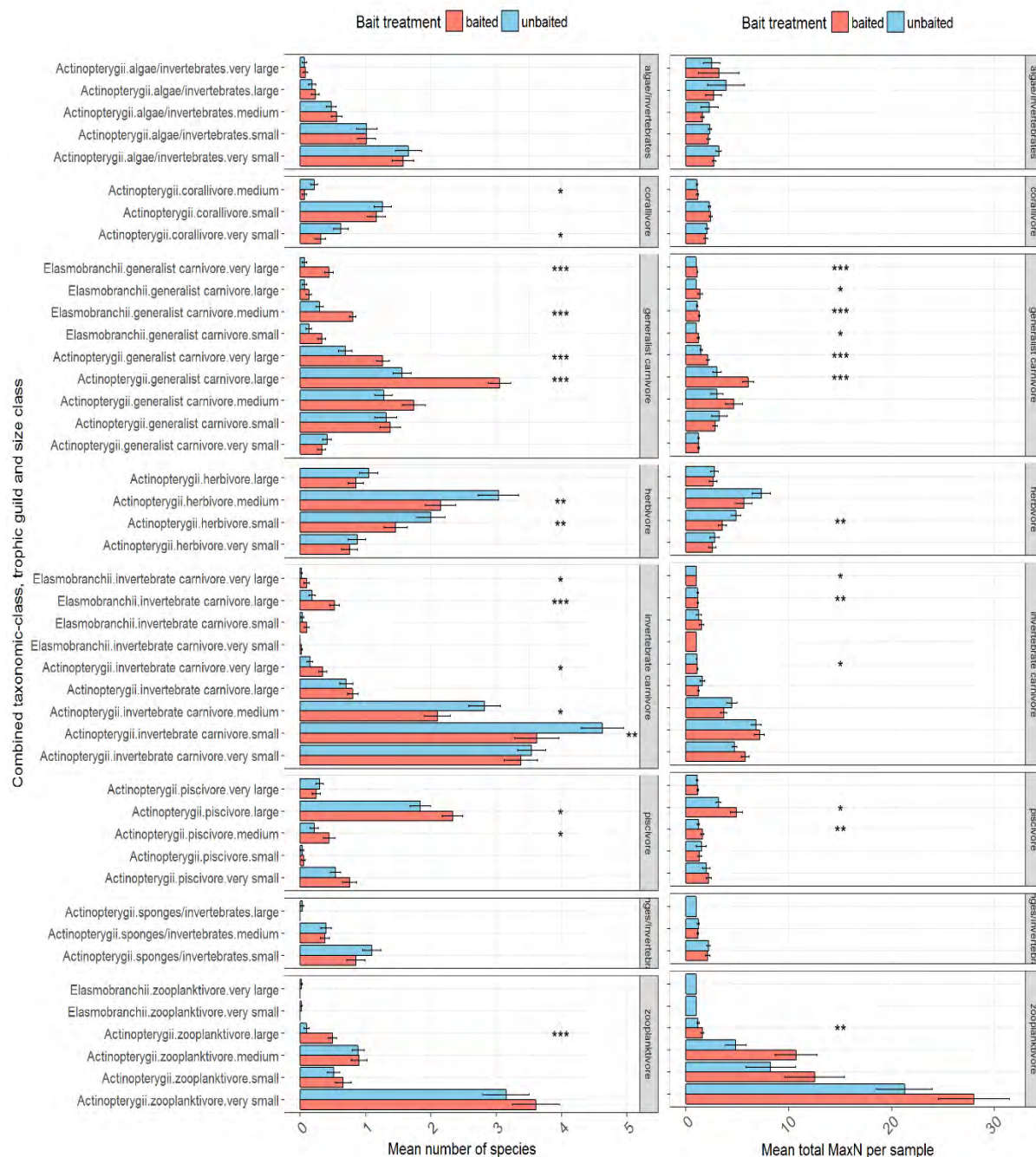


Figure 4.16. The mean number of species and mean relative abundance per sample per bait treatment for each of the combined taxonomic-class-guild-size groups. Error bars indicate standardised error. Univariate permutational ANOVA p -values for significance codes: *** < 0.001 , ** < 0.01 , * < 0.05 .

4.4.9.2 Combined taxonomic-class, trophic guild, and size-class assemblage structure

The structure of combined taxonomic-class-guild-size fish assemblages was significantly different among samples (PERMANOVA overall model, $F = 3.38$, $\text{Pr}(>F) < 0.001$). The differences were significant across bait treatment (Sequential PERMANOVA $F = 3.33$,

$\text{Pr}(> F) < 0.001$) when taking the effect of the other covariates into account prior to calculating the effect of treatment (Significance of covariates in Table 4.11).

Table 4.11. Sequential PERMANOVA of the combined taxonomic-class-guild-size structure of fish assemblages. (Variables displayed in order fit to model).

	Degrees freedom	Sum of Squares	F	Pr(>F)
Percent water column	1	0.86	1.20	0.1602
Sample area	1	0.92	1.28	0.113
Temperature	1	1.73	2.41	0.0024**
Wave energy	1	4.31	5.99	0.0002***
Depth	1	4.30	5.97	0.0002***
Treatment	1	2.8	3.33	0.0004***
Residual	113	95.6		

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

The mean distance of sample localities to the centroid locality in baited treatment was 0.86 ± 0.018 , and 0.87 ± 0.019 in unbaited treatments, in the PCO plot. The dispersion of variance of samples locality was not significantly different across bait treatments (PERMUTEST, $F = 0.057$, $\text{Pr}(> F) > 0.05$). This suggests that PERMANOVA results may be significantly different across treatments as a consequence of the difference in location of PCO points. It also suggests that assemblage structures had many shared species, but that the small the differences in assemblage structure were consistent.

Bait treatment had a weak correlation, but significant goodness of fit (ENVFIT, $r^2 = 0.08$, $\text{Pr}(> r) < 0.001$) of samples in the PCO points around centroids (Figure 4.17). Depth and wave energy had significant correlations with the spread of PCO points in ordination space ($\text{Pr}(> r) < 0.01$, and $\text{Pr}(> r) < 0.001$, respectively) (Figure 4.17).

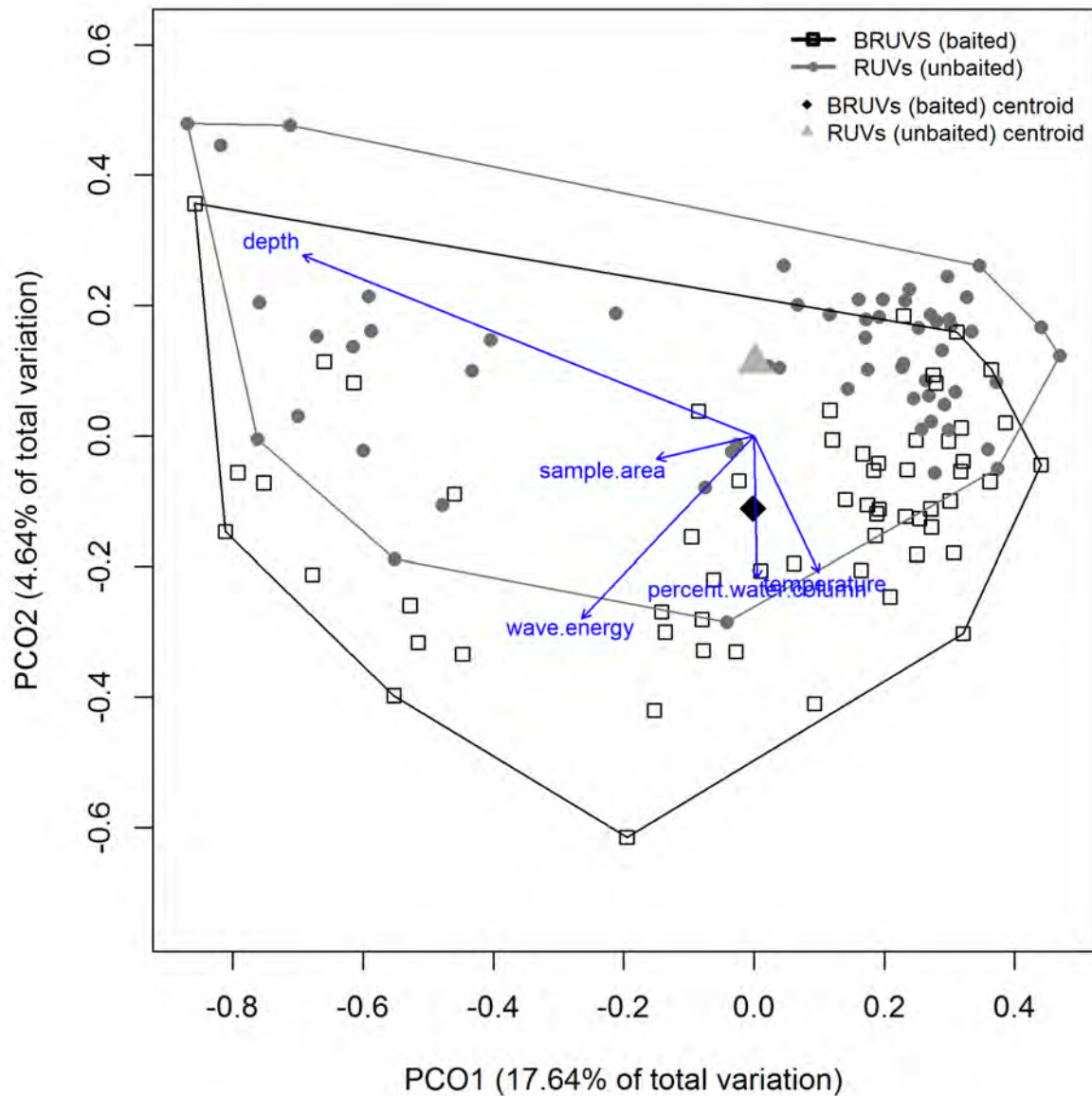


Figure 4.17. Principal Coordinate Ordination showing the grouping of samples according to bait treatment, and the estimated influence of other covariates. Samples represent the structure of fish assemblages at the combined taxonomic-class-guild-size level. Length of arrows shows the strength of respective covariate correlation to data, and the distance between centroids of distribution of points indicate the level of separation between treatments.

Treatment, depth, and wave energy had a significant effect (ANOVA of CAP, $F = 5.66$, $p < 0.001$) on the spread of samples in constrained CAP ordination space (Figure 4.18).

Combined-level fish assemblage structure was significantly altered by the presence of bait in samples (Table 4.12). differences among Actinopterygii groups between bait treatments drove changes in the combined-level fish assemblages Actinopterygii fish: The increase of small and medium zooplanktivores, small invertebrate carnivores, and large generalist

carnivores in baited treatments, and the increase of small herbivores in unbaited treatments contributed the most to the differences of combined taxonomic-class-guild-size assemblage structure across BRUVs and RUVs (Figure 4.18).

Table 4.12. ANOVA of Canonical Analysis of Principal coordinates (CAP) analysis of combined trophic-taxonomic-class-size-class assemblages showing the significance of covariates when added sequentially to the model (from top to bottom as listed).

	Degrees freedom	Sum of squares	F	Pr(>F)
Wave energy	1	2.61	3.61	2.00E-04***
Depth	1	7.06	9.78	2.00E-04***
Treatment	1	2.60	3.60	4.00E-04***
Residual	116	83.72		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Bait treatment was significant in changing the structure of fish assemblages after the effects of wave energy and depth were removed (ANOVA of CAP $F = 3.6$, $p < 0.001$). Predictive assignment of samples to treatment based on fish assemblage structure was accurate (87.5 % correct, $m = 4$) when using the CAP model that accounted for the effects of depth and wave energy. The correct predictive assignment was slightly higher in baited (85 %) than unbaited (90 %) treatments, and the difference was highly significant (MANOVA, approximate $F = 32.5$, $p < 0.001$).

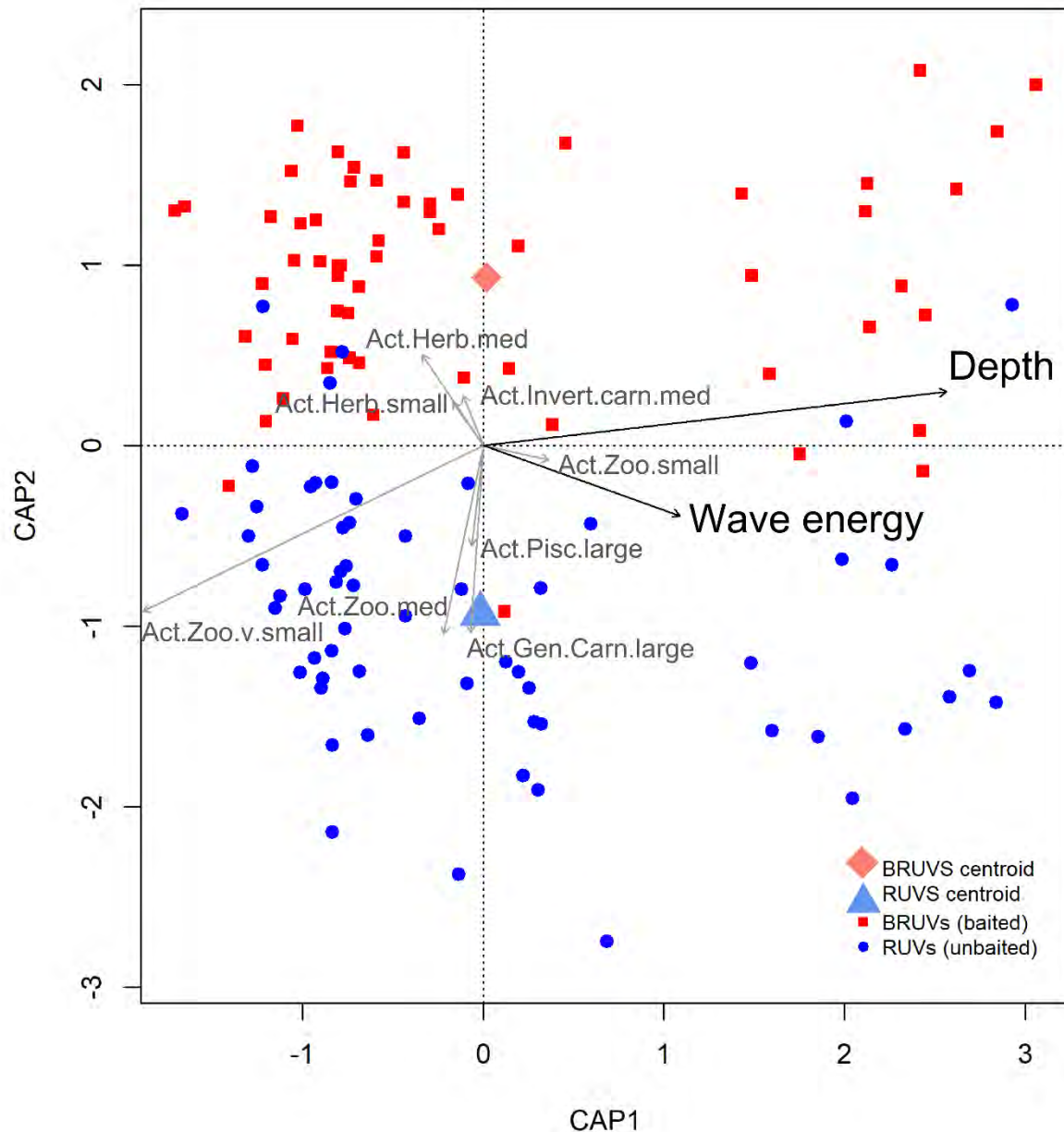


Figure 4.18. Canonical Analysis of Principal coordinates (CAP) plot of combined taxonomic-class-guild-size fish assemblages, constrained by treatment, depth, and wave energy. The centroids show the mean difference between samples by bait treatment in ordination space. The length of the arrow line of depth indicates the strength of the correlation of the covariates (black) and the change in combined category abundance (grey) in structuring the fish assemblage. (Shortened names of combined phylogeny and guild categories were used to fit into the figure where “Act.” represents Actinopterygii, “Zoo.” = zooplanktivore, “Pisc.” = Piscivore, “Gen.Carn.” = General carnivore, “Herb.” = Herbivore, and “med” = medium and “v.small” = very small)

4.4.10 Characteristic species from BRUVs and RUVs

Several characteristic species were identified in SIMPER analysis as significant in discriminating fish assemblages between baited and unbaited treatments, which confirmed species contribution to observed dissimilarity in CAP analysis. Twenty-six species contributed 50 % of the overall differences between baited and unbaited fish assemblages (Table 4.13).

The ratio of the average dissimilarity contribution to the standard deviation thereof indicated that particular species or groups of species were responsible for the observed differences. Very small, to medium Actinopterygii zooplanktivores contribute the most to the between-group separation, comprising the eight of the top ten species that best discriminate between bait treatments. *Thalassoma amblycephalum* was consistently more abundant in baited samples, with a greater average contribution to baited treatments of 10.54 than to unbaited treatments recorded as 3.5. *Chromis nigrura* was consistently more abundant in unbaited samples (RUVs 6.44, BRUVs 5.14) than baited samples. The high abundance of *Lutjanus bohar* was indicative of baited samples (RUVs 1.72, BRUVs 4.62), as were all large elasmobranch generalist macro carnivores, like *Carcharhinus amblyrhynchos* (RUVs 0.34, BRUVs 1.26, percentage contribution < %1), (not shown in table). The high abundance of *Thalassoma hebraicum* (invertebrate carnivore, mostly juveniles observed, but also adults) also discriminated BRUVs from RUVs (RUVs 2.14, BRUVs 4.06). The high abundance of *Chlorurus sordidus*, a medium size herbivore, was indicative of unbaited samples (RUVs 2.16, BRUVs 0.88). *Chaetodon trifasciatus* (RUVs 0.56, BRUVs 0.16), a corallivorous species, was characteristic of unbaited samples, but most other corallivorous species contributed similarly to both treatments.

Table 4.13. SIMPER results for the first 26 species contributing 50 % of the observed dissimilarity. Total average contribution totalled to 85.4 for the 303 species. The ratio between average and standard deviation reflects variation relative to the average contribution per species. Average species contribution to Baited Remote Underwater Video systems (RUVs) and Baited Remote Underwater Video systems (BRUVs) assemblages are indicated. The cumulative sum is the cumulative proportional contribution per species.

Average	Standard Deviation	ratio	Average RUVs	Average BRUVs	Cumulative Sum	Species	Trophic guild	Combined trophic-class-size
0.05	0.07	0.71	3.51	10.54	0.06	<i>Thalassoma amblycephalum</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.04	0.06	0.65	6.70	5.08	0.10	<i>Pseudanthias squamipinnis</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.04	0.05	0.68	6.44	5.15	0.14	<i>Chromis nigrura</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.03	0.06	0.51	3.62	6.59	0.18	<i>Pterocaesio tile</i>	zooplanktivore	Actinopterygii.zooplanktivore.small
0.03	0.05	0.59	2.70	5.80	0.21	<i>Cirrhilabrus exquisitus</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.02	0.05	0.42	2.20	3.49	0.24	<i>Odonus niger</i>	zooplanktivore	Actinopterygii.zooplanktivore.medium
0.02	0.05	0.42	1.98	4.05	0.26	<i>Lepidozygus tapeinosoma</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.02	0.03	0.56	1.51	4.61	0.28	<i>Melichthys niger</i>	zooplanktivore	Actinopterygii.zooplanktivore.medium
0.02	0.03	0.74	1.72	4.62	0.30	<i>Lutjanus bohar</i>	generalist carnivore	Actinopterygii.generalist carnivore.large
0.02	0.03	0.72	2.15	4.07	0.33	<i>Thalassoma hebraicum</i>	invertebrate carnivore	Actinopterygii.invertebrate carnivore.small
0.02	0.03	0.62	2.85	3.25	0.35	<i>Chromis fieldi</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.01	0.03	0.43	1.80	2.64	0.36	<i>Chromis weberi</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.01	0.01	0.78	1.87	2.79	0.37	<i>Caranx melampygus</i>	piscivore	Actinopterygii.piscivore.large
0.01	0.05	0.20	0.90	0.61	0.39	<i>Heteroconger hassi</i>	zooplanktivore	Actinopterygii.zooplanktivore.medium
0.01	0.03	0.28	0.74	2.54	0.40	<i>Nemanthias carberryi</i>	zooplanktivore	Actinopterygii.zooplanktivore.very small
0.01	0.02	0.62	2.16	0.89	0.41	<i>Chlorurus sordidus</i>	herbivore	Actinopterygii.herbivore.medium

Reef fish associations with benthic habitats

0.01	0.03	0.35	1.18	1.56	0.42	<i>Acanthurus thompsoni</i>	zooplanktivore	Actinopterygii.zooplanktivore.small
0.01	0.02	0.43	1.93	1.02	0.43	<i>Naso brevirostris</i>	herbivore	Actinopterygii.herbivore.medium
0.01	0.03	0.32	1.11	1.66	0.44	<i>Caesio varilineata</i>	zooplanktivore	Actinopterygii.zooplanktivore.medium
0.01	0.01	1.12	1.30	2.34	0.45	<i>Labroides dimidiatus</i>	invertebrate carnivore	Actinopterygii.invertebrate carnivore.very small
0.01	0.01	0.81	1.61	1.49	0.46	<i>Parupeneus macronemus</i>	invertebrate carnivore	Actinopterygii.invertebrate carnivore.medium
0.01	0.03	0.28	1.02	1.07	0.47	<i>Siganus sutor</i>	herbivore	Actinopterygii.herbivore.medium
0.01	0.02	0.50	0.97	1.11	0.48	<i>Scarus rubroviolaceus</i>	herbivore	Actinopterygii.herbivore.large
0.01	0.01	0.63	1.36	1.08	0.49	<i>Plagiotremus tapeinosoma</i>	piscivore	Actinopterygii.piscivore.very small
0.01	0.01	0.60	1.18	1.03	0.498	<i>Ctenochaetus striatus</i>	herbivore	Actinopterygii.herbivore.small
0.01	0.02	0.40	0.34	0.80	0.506	<i>Lethrinus nebulosus</i>	generalist carnivore	Actinopterygii.generalist carnivore.large

4.5. DISCUSSION

A significant diversity of 303 species of fish from 51 families was recorded from the seaward reefs of Aldabra Atoll between 0 and 55 m depth. The high overall abundance of fish, presence of large elasmobranch predators and an abundance of herbivores suggested that the key functional components of the reef fish assemblage that drive ecosystem processes on coral reefs were present (McClanahan et al. 2011, 2015; MacNeil et al. 2015; Graham et al. 2017).

Site managers, conservation agencies or planners wishing to monitor fish species diversity and abundance need to understand the relative efficiencies and biases of different survey methods to make informed decisions (Colton and Swearer 2010; Bernard 2012). The reef fish assemblage observed using BRUVS and RUVs differed significantly between the two methods, in terms of species diversity and reef fish assemblage structure, and trophic assemblage structure.

4.5.1 Reef fish assemblage structure

This study demonstrated that the fish assemblage structure was significantly different between the two survey methods tested, namely, baited and unbaited remote underwater video systems (BRUVs and RUVs). Bait significantly altered the observed fish assemblage structure by attracting a greater diversity and abundance of generalist carnivores, piscivores, and zooplanktivores, while recording lower diversity and abundance for herbivores and corallivores. The differences in the fish assemblages recorded between the two methods have important implications for the choice of survey method, and the interpretation of the data collected using BRUVs in other studies. Studies that are only interested in the bait-attracted component of the fish assemblage, such as generalist carnivores or piscivores, which are often targeted by fisheries, may obtain more reliable data and would require fewer samples when using BRUVs rather than RUVs. This is the first BRUVs-versus-RUVs study that suggests that unbaited treatment performs significantly better and required fewer samples when observing the herbivore and corallivore guilds in fish assemblages. The differences in fish assemblage structure between the bait treatments were driven by a few differences in species composition (presence-absence of certain species), and significant differences in relative abundances, at the species, trophic and combined taxonomic-class-guild-size level.

4.5.2 Species richness, diversity and abundance

Overall, significantly more fish were recorded in BRUVs than RUVs, which was consistent with other studies comparing fish abundance across bait treatments in underwater video samples (Watson 2005; Harvey et al. 2007; Watson et al. 2010; Bernard and Götz 2012; Dorman et al. 2012). Consistently recording more fish of a species per sample decreases variability in the data, and consequently increases statistical power (Watson 2005). To achieve the same statistical power using unbaited treatments as in baited treatments, the sample size would have to be increased (Bernard and Götz 2012). Baited Remote Underwater Video systems (BRUVs) were therefore more efficient at sampling overall fish abundance, and this trend appears to be consistent in different ecosystems (tropical and temperate) (Harvey et al. 2007; Bernard and Götz 2012).

The fact that overall species richness was very similar between bait treatments was consistent with the findings of Dorman et al. (2012), but differed from other studies, where more species were recorded in baited samples than unbaited samples. For example, Watson (2005) recorded 33 species in BRUVs, and 23 in RUVs, Bernard and Götz (2012) recorded 48 species in BRUVs compared to 36 in RUVs in the temperate South African waters, and Harvey et al. (2007) also recorded more species in baited treatments than unbaited treatments in tropical and temperate fish assemblages off Australia. The similarity in fish richness and diversity, but differences in the unique species recorded in respective bait treatment samples in my study, suggest that the use of combined baited and unbaited methods will provide more comprehensive species lists.

The 303 species (338 including additional samples collected in Chapter 5) recorded at Aldabra using BRUVs and RUVs in our study was similar to the 332 species recorded as a collective total for the southern Seychelles Islands recorded using SCUBA-based Underwater Visual Census (UVC) (Friedlander et al. 2015b). Earlier UVC surveys at Aldabra recorded fewer species, e.g. 228 fish species in 1973 (Polunin 1984 in Downing et al. 2005a), 244 species (M. D. Spalding, unpublished data collected 1998), and subsequently 211 species (Buckley et al. 2005; Downing et al. 2005a). The greater number of species recorded at Aldabra using BRUVs and RUVs compared to UVC is a testament to the effectiveness of this method to survey reef fish assemblages to establish diversity estimates in tropical marine ecosystems.

The greater abundances, species richness and species accumulation rates of generalist carnivores and piscivores observed in BRUVs compared to RUVs, was consistent previous studies, and is a wide-spread and unsurprising phenomenon (Watson et al. 2005b; Harvey

et al. 2007; Langlois et al. 2010; Bernard and Götz 2012; Dorman et al. 2012). Generalist carnivore assemblage structure was also more distinct in baited than unbaited samples as a consequence of more consistently recording a similar suite of species, which was also found in previous studies (Harvey et al. 2007; Bernard and Götz 2012). Distinct fish assemblages enhance the detection of change, which is important for monitoring the response of fish assemblage structure to human or natural impacts (Harvey et al. 2007; Devictor et al. 2010). Baited Remote Underwater Video systems (BRUVs) being more efficient at sampling generalist carnivores and piscivores therefore ought to be more reliable than RUVs in detecting any changes in this component of the fish assemblage structure (Harvey et al. 2007; Bernard and Götz 2012). The desirable properties of enhanced sampling efficiency and statistical power make this an ideal method to sample the predatory component of the fish assemblage (Bernard 2012; Bernard and Götz 2012). Our study suggested that observations of herbivore and corallivore would benefit to some degree from the same desirable properties by using RUVs instead of BRUVs. This is especially important given the role of herbivores in maintaining resilience on coral reefs through algal grazing (Hughes et al. 2007; McClanahan et al. 2007b; Ledlie et al. 2007; Graham et al. 2013; MacNeil et al. 2015).

4.5.3 Species richness and abundance in trophic guilds

The lower abundance of herbivores and the lower species richness of both herbivores and corallivores in baited treatments (BRUVs), relative to unbaited treatments (RUVs) has not previously been reported for these guilds in other comparisons between BRUVs and RUVs (Watson et al. 2005b; Cappo et al. 2007b; Bernard and Götz 2012). In a study comparing BRUVs with DOVs in Australia, Watson et al. (2010) did not report significantly fewer herbivores in baited compared to unbaited treatments. The authors described the relative abundance of *Coris auricularis*, a known prey species of *Plectropomus leopardus*, as unaffected by the increase of this predator in baited samples. An explanation for fewer herbivores in BRUVs than RUVs at Aldabra but not in the Australian studies (Harvey et al. 2007; Watson et al. 2010), may be a consequence of a higher predator density at Aldabra, which could have caused a greater avoidance response in herbivores than at the Great Barrier Reef Marine Park. The high density of predators may have caused herbivores to move away from the BRUVs at Aldabra. Rasher et al. (2017) have shown that herbivores refrain from feeding in high-risk habitats in the presence of predators. The higher predator density at Aldabra may be a consequence of long-term protection and low levels of exploitation (Ayling and Choat 2008; Pistorius and Taylor 2009). Herbivores from temperate waters are not as species-rich as in the tropics (Floeter et al. 2005), which may cause less

effective detection rates of diversity and abundance of herbivores, which may explain why no significant differences were detected in a study at Tsitsikamma in the temperate Agulhas region (Bernard and Götz 2012; Bernard 2017 personal communication). The reduced abundance of herbivores and reduced number of species of herbivores and corallivores in baited treatments recorded in this study is important, as it suggests that the BRUVs may under-estimate the true abundance and diversity of these groups. This raises the question: *Does the loss in sampling efficiency of herbivore and corallivore assemblages in BRUVs warrant the need to use both methods to obtain comprehensive samples of the fish assemblage?* Given the important ecological function of herbivores in coral reef ecosystems, it may be necessary to incorporate both methods in the sampling design (Ogden and Lobel 1978; Bellwood et al. 2004).

Although previous BRUVs-vs-RUVs studies have not found significant differences in herbivore abundance in baited samples, my findings of reduced herbivores in the presence of bait are supported by fish trap studies (Munro 1974), by some studies using UVC and BRUVs (Colton and Swearer 2010; Andradi-Brown et al. 2016), and by fish behaviour studies reporting reduced herbivore activity in the presence of predators (Rasher et al. 2017). The reasons why the abundance and diversity of prey species from other trophic guilds, e.g. algae/invertivore, remained unchanged between bait treatments remains unclear (Harvey et al. 2007; Bernard and Götz 2012). The lack of change could be because species in these groups have small home ranges and hide in amongst the reef, thus not leaving the baited area despite the increase of predators (Green et al. 2015). Further analysis of species home ranges, behaviour, and their relationships with predatory species, may provide a better understanding of the inconsistency in trophic assemblage response to increased predators.

4.5.4 Predatory species

In addition to the deterrent effect of increased predator abundance on herbivores, the behaviour of predators in the presence of bait may affect herbivore abundance directly. In baited samples, large groupers, often *Epinephelus tukula*, would stay within 50 cm of the baited canister for prolonged periods, and aggressively chase off other fish that approached. Guarding behaviour may have resulted in a lower abundance of fish being observed in BRUVs, as agonistic behaviour in fish has been shown to reduce abundance estimates (Dunlop et al. 2015b). Guarding behaviour was also observed during a fish trap study at Aldabra, which showed how large groupers and sharks were guarding the entrance to fish traps, resulting in very low catch success (unpublished data, SAIAB & SIF; Cowley et al. 2014). Guarding behaviour may deter prey species more than non-prey species because it

has been shown that prey evolve behaviour to avoid predation and reduce feeding in the presence of predators (Pitcher and Turner 1986; Stoks et al. 2003; Rasher et al. 2017). The abundance and behaviour of predators are important to factor into the experimental design when deciding between baited or unbaited methods.

4.5.5 Elasmobranchs

In this study, surprisingly, the total numbers of elasmobranch species were similar between BRUVs and RUVs (14 vs 12). Bernard and Götz (2012) reported 13 cartilaginous species from BRUVs compared to the seven recorded in RUVs. In our study, large adult bull sharks, *Carcharhinus leucas*, and smooth hammerheads sharks, *Sphyrna lewini* were recorded in baited and unbaited samples, in addition to the smaller more common species, e.g. grey reef sharks, *Carcharhinus amblyrhynchos*. Aldabra has a relatively high predator abundance (Friedlander et al. 2015b). The high density of elasmobranch species at Aldabra may have increased the likelihood of species presence being detected in both treatments, resulting in the similarity between the species richness of elasmobranch observed in BRUVs and RUVs.

Although the number of species of elasmobranch was similar between bait treatments, approximately four times as many elasmobranchs were recorded in baited samples. Larger species of shark were particularly more abundant in baited treatments, including a higher relative abundance for *Carcharhinus albimarginatus*, *Negaprion acutidens*, *Nebrius ferrugineus* and *S. lewini*. My findings are consistent with a study in temperate waters of South Africa, which also reported a higher abundance of elasmobranchs in BRUVs than RUVs (Bernard and Götz 2012). Many species of elasmobranch are shy and avoid SCUBA divers, which may result in fewer sharks being detected in SCUBA-based surveys (Cappo et al. 2003; Colton and Swearer 2010). These advantages of baited over unbaited, and remote cameras over SCUBA surveys, make BRUVs particularly well suited to record elasmobranchs. Many sharks are apex predators and act as flagship species providing leverage to implement wider-context conservation plans (Sergio et al. 2008). In some systems, apex predators provide valuable information on fish population structure and act as biodiversity indicators that can be used to inform management decisions (Sergio et al. 2008). Baited Remote Underwater Video systems (BRUVs) was more efficient than RUVs to observe elasmobranch diversity and abundance, and consequently, studies wishing to study elasmobranchs, especially large species, should consider using baited methods.

4.5.6 Species size structure

The collective significantly larger size-structure of species of elasmobranch and Actinopterygii in BRUVs is likely to be a consequence of larger species being preferentially drawn to baited samples (Dunlop et al. 2015b). Consistent with my study, Watson et al. (2010) reported that a significantly greater number of larger-bodied species, including *Gymnothorax* spp, *Lethrinus nebulosus*, *Plectropomus leopardus*, were recorded in stereo-BRUVs in comparison to stereo-DOVs at the Houtman Abrolhos and at Ningaloo Reef. Dunlop (2015b) suggested that increased agonistic behaviour in baited samples may skew observed size frequency to the larger individuals and species. My results suggest that large species of generalist carnivore, piscivore and zooplanktivore are more frequently observed in baited samples, without decreasing the numbers of smaller species in these groups. Baited Remote Underwater Video systems (BRUVs) are therefore particularly useful to inform conservation and site management decisions because larger species are often targeted by fisheries (Graham et al. 2005; Pauly and Watson 2005).

Differences in species-size between BRUVs and RUVs in my study must be interpreted bearing the data limitations in mind. In this study, mono-BRUVs were used. As such, the individual sizes of the fish were not measured, and the size data used here were based on published maximum size attained by the respective species. Measured size of individual fish has been shown to be more useful than species-size when interpreting fish assemblage data in relation to habitat, given that the intra-species size variability may exceed inter-species size variability (Nash et al. 2014). Other studies using mono-BRUVs obtained measured size data by fixing lasers at a set distance apart to the frame, which project a scaled distance onto the fish (Dunlop et al. 2015a but see Coghlan et al 2017 for critique). Synchronised and calibrated stereo-BRUV systems have become a popular and effective method to obtain very accurate size estimates for each individual fish (e.g. Dorman et al. 2012; Harvey et al. 2012b; Zintzen et al. 2012; Heyns-Veale et al. 2016). While species-size used in my study provided a preliminary assessment of the effect of bait on size-spectrum of fish species, measurement of individual fish would allow for more accurate assessment of the effect of bait on the structure of the fish assemblage. Notwithstanding these limitations in methodology, BRUVs appeared to be more useful than RUVs to obtain information about very large fish predatory species at Aldabra, as they were more frequently sampled.

4.5.7 Characteristic species

The overlap in the location of samples in constrained and unconstrained ordination analysis in this study suggests that the fish assemblages across bait treatments shared many

species, but that differences in abundance of a few species were driving the significant differences detected in our analysis. Increased abundances of generalist carnivores, namely *Carcharhinus amblyrhynchos*, *Lutjanus bohar* and *Lethrinus nebulosus*, consistently contributed the most to the differences between baited and unbaited treatments. The latter two species form a large proportion of the subsistence fishery at Aldabra (Pistorius and Taylor 2009). Previous studies have found that BRUVs were more efficient at recording fishery target species (Willis and Babcock 2000; Watson 2005; Colton and Swearer 2010) and therefore supports the notion that BRUVs are useful to monitor fisheries resources (Langlois et al. 2012). The unique species recorded by the respective methods suggested that baited samples were more efficient at recording shy predatory species like large moray eels, *Gymnothorax* spp, and some groupers, e.g. *Epinephelus fuscoguttatus*. On the contrary, the invertebrate carnivore *Digamma oxycheilinus*, which is used an ecological indicator species within its trophic guild in the Indian Ocean (Obura and Grimsditch 2009) was only recorded in unbaited treatments. To obtain detailed information at the ecosystem level, a combination of the two methods should therefore be considered in monitoring programmes.

SIMPER analysis indicated that the differences in fish assemblage structure were highly affected by the increased abundance of smaller zooplanktivores in baited samples. The increased abundance of zooplanktivores in BRUVs in my study was not previously recorded in a study on tropical reefs (Harvey et al. 2007), but the reasons for this inconsistency remain unclear and may require an inter-species comparison between the studies to elucidate causes. The increase zooplanktivores observed in baited treatments may have been caused by an attraction to the bait plume, to scavenge on particles or even attempt to feed directly at the bait canister (personal observation). Some zooplanktivores, e.g. *Melichthys niger*, may have been attracted into the field of view (FOV) by the feeding activity of conspecifics at the system, known as the “sheep effect” (Watson 2005). It is not easy to separate these two attractants in bait-attracted species, as it may be a combination of both effects. The abundance of schooling species was likely to be underestimated because large schools may extend beyond the limited FOV (Cappo et al. 2003), but this limitation provides a conservative estimate that affects both unbaited and baited samples. The increased abundance of zooplanktivores suggests that BRUVs were more effective at sampling the zooplanktivore assemblage structure than RUVs.

4.5.8 Conclusion

This study demonstrated that BRUVs and RUVs each have their own advantages and disadvantages when sampling fish assemblages. Practitioners and researchers are often constrained by resource limitations and may not be able to implement both BRUVs and RUVs surveys (Bernard and Götz 2012). Where resource constraints are limiting, careful consideration of the aims of the data collection programmes is required prior to settling on either of the methods. The differences between our results and those of other studies (Harvey et al. 2007; Colton and Swearer 2010; Dorman et al. 2012; Ghazilou et al. 2016) for different trophic guilds, suggests that pilot studies comparing observed fish assemblage structures between RUVs and BRUVs may be necessary prior to embarking on new research programmes because the effectiveness of the respective methods differ between locations. At Aldabra, BRUVs were better suited to monitor generalist carnivores, piscivores, and zooplanktivores, while RUVs were better at monitoring herbivores and corallivores. Using a combination of the two methods would be ideal at Aldabra for future monitoring, as it would provide more detailed information on predatory and prey species, necessary for fishery and ecosystem management of the site.

4.6. ANNEX ~ CHAPTER 4

The CAP analyses figures (Figure 4.15) are repeated but enlarged to display the results in greater detail. The species which increased the most in the direction relative to the relation to the CAP ordination axis are shown more clearly for each of the respective trophic groups. Note how large bait attracted species such as sharks (*Carcharhinus amblyrhinchos*, *C. melanopterus*), large snappers (*L. bohar*) and smaller species (*Thalassoma hebraicum*) which readily feed on suspended bait particles in the water column characterised BRUVs samples (Figures 4.19 - 4.22). It was clear that different species characterised the respective trophic guilds between the two bait treatments.

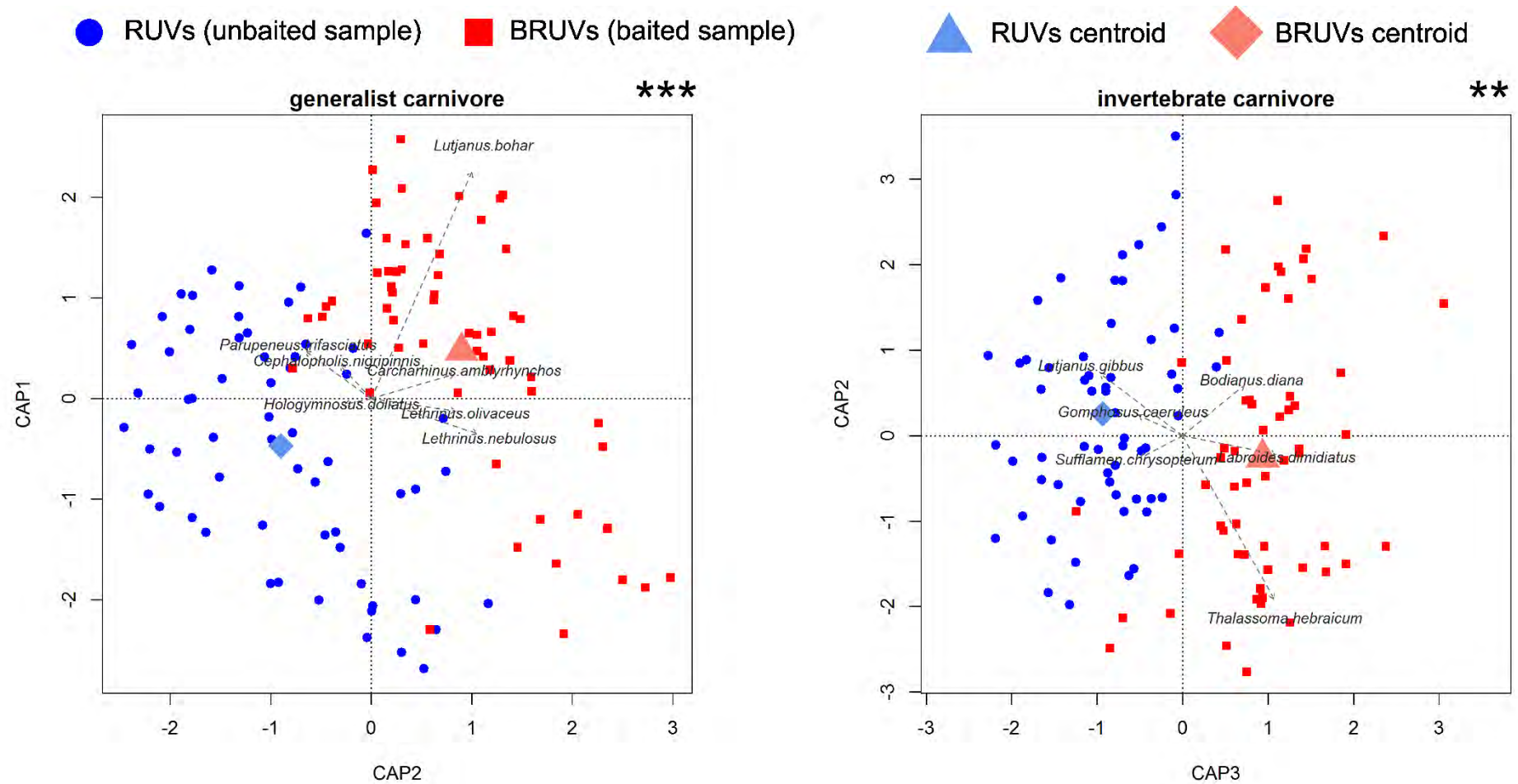


Figure 4.19 Canonical Analysis of Principal coordinates (CAP) plots of abundance based fish assemblage samples for generalist carnivores (left) and invertebrate carnivores (right). The centroid is the mean position within the cloud of points for the respective bait treatments. The length of the arrow shows the relative contribution of species to CAP models. The axis that shows the effect of bait treatment at its maximum is displayed. ANOVA of treatment significance in CAP models: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

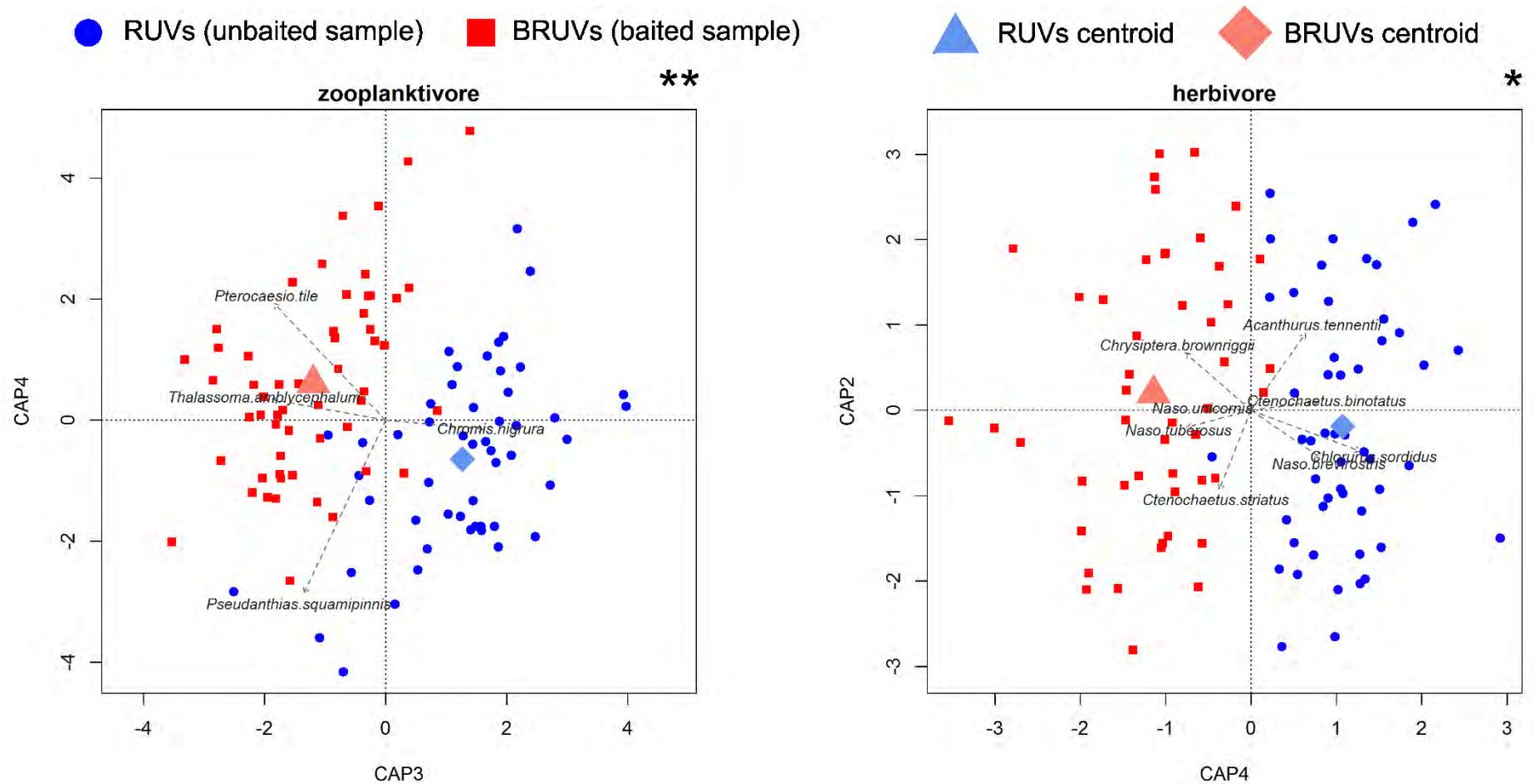


Figure 4.20. Canonical Analysis of Principal coordinates (CAP) plots of abundance-based fish assemblage samples for zooplanktivores (left) and herbivores (right). The centroid is the mean position within the cloud of points for the respective bait treatments. The length of the arrow shows the relative contribution of species to CAP models. The axis that shows the effect of bait treatment at its maximum is displayed. ANOVA of treatment significance in CAP models: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

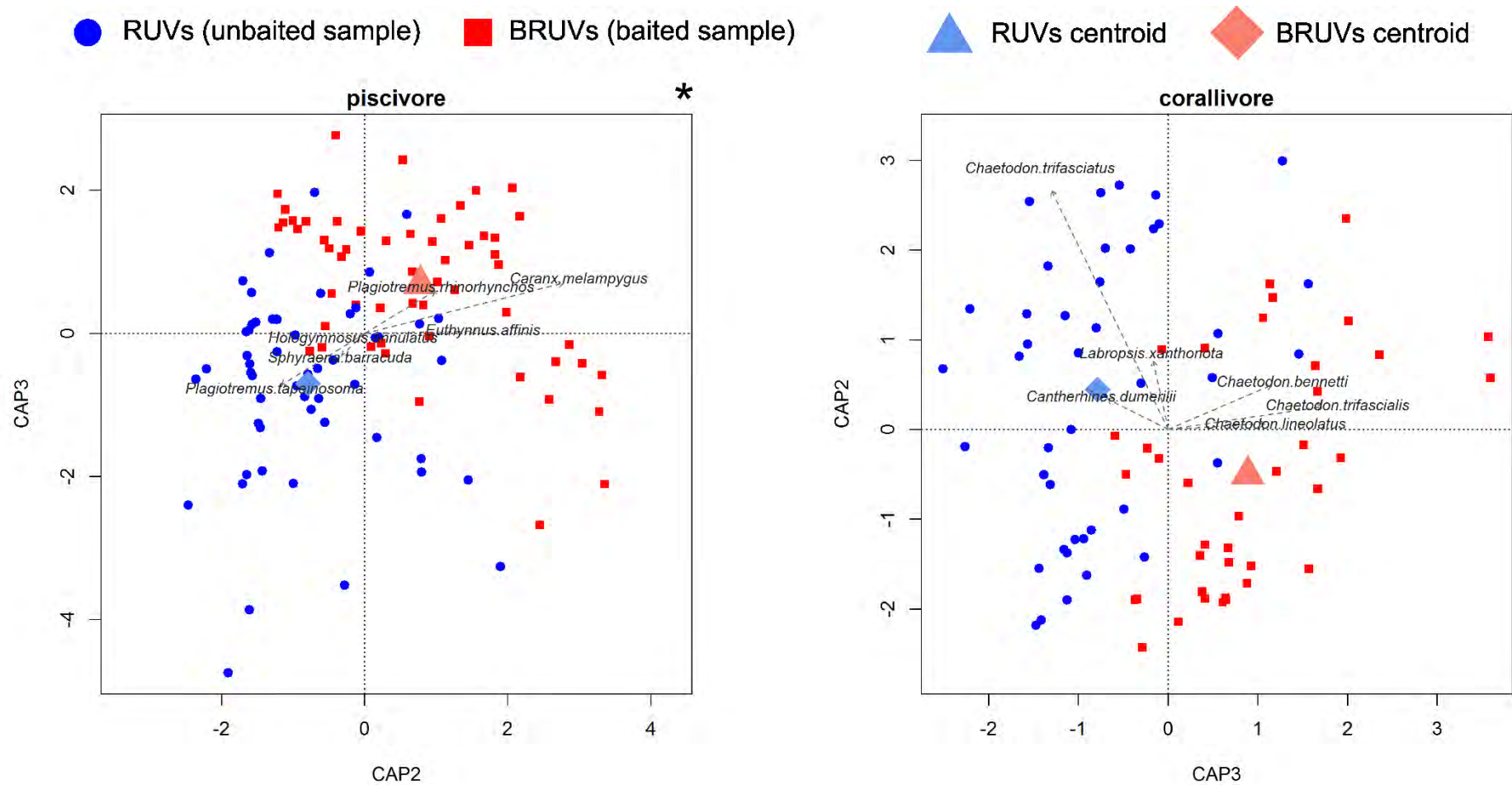


Figure 4.21 Canonical Analysis of Principal coordinates (CAP) plots of abundance based fish assemblage samples for piscivores (left) and corallivores (right). The centroid is the mean position within the cloud of points for the respective bait treatments. The length of the arrow shows the relative contribution of species to CAP models. The axis that shows the effect of bait treatment at its maximum is displayed. ANOVA of treatment significance in CAP models: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

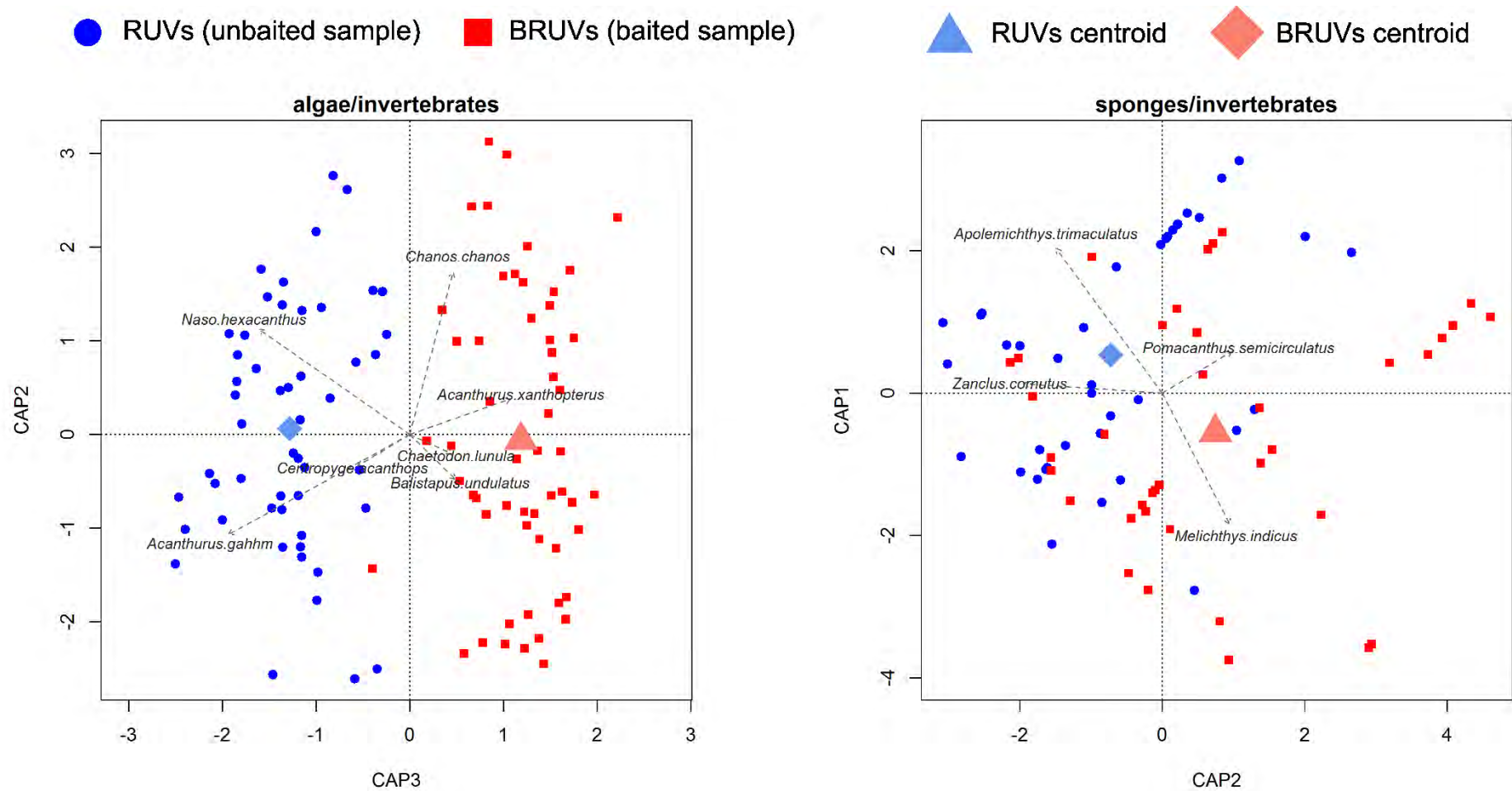


Figure 4.22. Canonical Analysis of Principal coordinates (CAP) plots of abundance-based fish assemblage samples for algae/invertebrate feeders (left) and sponge/invertebrate feeders (right). The centroid is the mean position within the cloud of points for the respective bait treatments. The length of the arrow shows the relative contribution of species to CAP models. The axis that shows the effect of bait treatment at its maximum is displayed. ANOVA of treatment significance in CAP models: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

Chapter 5. Variation in the reef fish assemblage with cyclical change in tide and time of day on a subtidal tropical reef



Potato grouper venturing onto the shallow lagoon reef during a high tide recorded using a Baited Remote Underwater Video system.

5.1. ABSTRACT

The aim of this chapter is to assess the influence of tide and time of day on the reef fish diversity and assemblage structure. Understanding cyclical-temporal changes to reef fish assemblages in response to the tide and time of day is critical to inform reef fish ecology and may have important implications for monitoring programmes. The objective was to compare the structure of reef fish assemblages among early morning, midday and evening on spring high and low tides along the west coast of Aldabra between 0.8 and 49 m depth from 39 samples recorded using Baited Remote Underwater Video systems (BRUVs) and 47 samples of unbaited Remote Underwater Video systems (RUVs). The hypothesis was that tide and time of day altered the observed fish assemblage structures, as fish move between habitats to feed and rest during different stage of the tide and time of day. Shannon-diversity, univariate permutational ANOVA and PERMANOVA were used to assess differences in diversity, abundance and structure of species and trophic level assemblages. The experimental sampling did not allow separating the effects of tide and time of day on the fish assemblage and consequently meaningful conclusions could only be based on the results from three groupings of the data, namely morning-high-tides, midday-low-tides and evening-high-tides. The reef fish assemblage was significantly different between morning-high-tides, midday-low-tide and evening-high-tide for all trophic groups observed using RUVs. Invertebrate carnivores were significantly more abundant during the midday-low-tide than morning-high-tide in RUVs samples. Some of the changes in reef fish assemblage structures observed in RUVs may be explained by fish moving into the lagoon as habitat becomes available with the flooding of the lagoon during high tide, thereby reducing the numbers of fish on the seaward reefs, but further studies are required to support this theory. Neither the species assemblage nor the trophic assemblage structures were significantly altered by tide (water level), or different times of day in BRUVs. The results suggest that the presence of bait eclipsed the effect of cyclical processes like tide and time of day on the reef fish assemblage structure. The use of BRUVs may therefore be robust to standardise reef fish surveys against the influence of tide and time of day. RUVs were sensitive to the natural variation caused by tide and time of day and is therefore a suitable method to study the effects of cyclical environmental parameters on the fish assemblage. The results of this study highlight the ecological effect of tide and time of day on the fish assemblage. It is therefore recommended that temporal variability introduced by cyclical variables is accounted for, particularly with RUVs, when planning surveys and interpreting data that inform management decisions.

5.2. INTRODUCTION

The overarching aim of this chapter is to determine the cyclical temporal changes to a reef fish assemblage as a result of their movement with changes in tide and time of day at a coral reef ecosystem. Knowledge of marine species movements is crucial to inform conservation strategies and ecosystem management, for example establishing Marine Protected Area (MPA) boundaries (CMS 2003; Pittman and McAlpine 2003; Meyer et al. 2007a, 2007b). The spatial distribution of species diversity, the structure of the fish assemblage, and the functional trophic composition within an area may temporarily change as a result of marine species movements (Thompson and Mapstone 2002; e.g. Sheaves 2005). Understanding the change to the fish assemblage arising from cyclic species movements is therefore essential to ensure an accurate interpretation of the observed fish community, and is especially important in designing long-term monitoring programmes (Thompson and Mapstone 2002; Heagney et al. 2007; Krumme 2009).

Marine species movements may occur once during an ontogenetic life cycle, seasonally, over the tidal cycle, or in response to a change in the time of day (diel cycle) (Hobson 1972; Gibson 2003; Krumme 2009). Accurate interpretation of long-term change in composition or structure of an observed fish assemblage requires distinguishing long-term change from the short-term change that arises from species movement in response to variation in seasonal, lunar, tidal and diel cycle patterns (Unsworth et al. 2007; Krumme 2009; Kruse et al. 2016). The short-term movements of species between different habitats at various times of the day or during opposing tidal phases have been shown to alter the fish assemblage structure. Changes of the taxonomic composition and the trophic structure of fish assemblages (Robertson and Howard 1978; Wilson and Sheaves 2001; Unsworth et al. 2007) have been demonstrated to alter ecosystem functioning (Petchey et al. 1999; Bellwood et al. 2003; Green and Bellwood 2009; Chong-Seng et al. 2014). It is therefore important to take the effects of tide and time of day on the fish assemblage into account for sampling design, interpretation of ecological data, and ecosystem management (Pittman and McAlpine 2003; Meyer et al. 2007b).

The rise and the fall of the tide is a crucial process that changes fish distributions by causing short-term movement of marine fish. Marine fish move into the intertidal zone from deeper water as exposed areas become inundated by the rising water level, and leave the intertidal zone with the falling tide (Gibson 2003; Meyer et al. 2007a; Krumme 2009). The rising tide floods the shallow intertidal zone, allowing fish to access and feed on the rich epibenthic fauna and flora in this temporally available habitat (Krumme 2009). The falling tide generates nursery areas by damming water among deeper intertidal back reefs, rock pools,

and mangroves, where juvenile fish shelter from predators (Bennett 1987; Dorenbosch et al. 2005; Adams et al. 2006). The effect of tides is most obvious in the intertidal zone which may be exposed during low tide and inundated during high tide, and less pronounced in subtidal areas that are permanently flooded (Gibson 2003). Changes in tide may therefore alter fish assemblage structure by changing habitat availability.

A change in tide causes a tidal current, i.e. not only vertical raising and lowering of water, but the horizontal flow of water which transports fish between different habitat or islands, known as Selective Tidal Stream Transport (STST) (Gibson 2003; Meyer et al. 2007a; Krumme 2009). Changes in tide therefore exert a horizontal force in addition to the vertical change tide, which may alter fish assemblage structure.

Species also move in response to the cyclical change of diel cycle, with species compositions shifting from diurnal to nocturnal assemblages, and activities changing between resting and feeding behaviours (Hobson 1972; Krumme 2009). The majority of temperate and tropical fish feed during the daytime, while fewer species feed during the night (Hobson 1972; Helfman 1986). The movement of fish between different habitats and the change in behaviour is thought to be driven by exploiting different feeding opportunities while minimising the risk of being predated (Hobson 1972, 1973; Helfman 1986). Species turnover typically occurs during the early morning and early evening twilight when predation risk is highest, and feeding activity is lowest (Hobson 1972; Pitcher and Turner 1986; Gibson 2003; Krumme 2009). The composition of the fish assemblage is therefore likely to change with time of day (Mallet et al. 2016).

The interaction of tide and time of day exerts a strong influence on the short-term migrations of fish and crustaceans in the tropics (Meyer et al. 2007a, 2007b; Krumme 2009). Movement of marine fish with a change in tide and time of day connects feeding and resting sites (Krumme 2009). The vertical migration of fish and fish larvae with the change in the time of day and horizontal movement of fish, fish eggs and fish larvae with tidal currents provides transport mechanisms for completion of ontogenetic fish life cycles (Krumme 2009). The effects of tide and the diel cycle on movement of fish is a well-established phenomenon which occurs globally, with case study examples in Hawaii, Brazil, Tanzania, Indonesia, South Africa, among others, and are therefore likely to affect Aldabra Atoll (Hobson 1972; Unsworth et al. 2007; Félix-Hackradt et al. 2010; Juby 2016; Kruse et al. 2016).

Variation in time of day and tide may be exploited differently by various trophic guilds of fish. Predatory species have been shown to be more active at crepuscular times or under cover of dark, while potential prey species from herbivore and corallivore guilds are typically active

under high visibility to reduce risk of predation (Pitcher and Turner 1986). Tide and time of day may therefore act on species and trophic level fish assemblages.

In order to detect any long-term change in the fish assemblage at Aldabra Atoll, the management authority, Seychelles Islands Foundation (SIF) has initiated a Baited and unbaited Remote Underwater Video system (BRUVs and RUVs) programme (Haupt and Bernard 2015). However, fish distributions observed using BRUVs and RUVs may vary with tide and time of day (Heagney et al. 2007; Birt et al. 2012; Taylor et al. 2013; Myers et al. 2016). Understanding the change in the observed fish assemblage with tide and time of day is therefore necessary to distinguish the short-term movement changes from long-term changes at Aldabra.

Aldabra Atoll experiences a relatively large tidal amplitude, with strong tidal currents, and daylight hours are relatively stable throughout the year, given its geographic position (Stoddart 1968a; Farrow and Brander 1971; Pugh and Rayner 1981). The isolation and long-term protection of Aldabra lend itself to investigating the effects of tide and time of day on the fish assemblage in the absence of anthropogenic pressures (Stoddart 1968a; Downing et al. 2005a). Variation in the reef fish assemblage caused by the tide and time of day at Aldabra is therefore regionally informative as a baseline response of fish to cyclical temporal variability of environmental conditions.

Previous studies at Aldabra investigating the tidal regime, spatiotemporal distribution or hunting behaviour focused on selected species in relation to the tides and tidal environments (Farrow and Brander 1971; Potts 1973, 1981; Pugh and Rayner 1981; Stevens 1984) but none have quantified the effects of tides or time of day on the fish species richness, diversity, abundance or fish assemblage structure.

The rise of the tide causes the shallow outer lagoon reefs (intertidal zone) of Aldabra to flood, temporally making habitat and food resources available (Pugh and Rayner 1981; Stevens 1984). In addition to the change in water level, a tidal current is also generated by the change in tide at Aldabra (Forster 1984). The tidal flushing which generates substantial current velocities inside of the Main channel, measured at 3 m/s during ebb flows, is likely to generate Selective Tidal Stream Transport (STST) near to the lagoon channels (Stoddart et al. 1971; Gibson 2003). Selective tidal stream transport is expected to vary along the coast as a function of distance to channel, and the flow rate from the channels, and further influenced by topography (Stoddart et al. 1971; Forster 1984; Heywood et al. 1990). The change in tide was therefore expected to alter the fish assemblage structure at Aldabra.

Fish assemblage structure at Aldabra may also change in response to a change in time of day, given that it is such a common and widespread phenomenon (e.g. Robertson and Howard 1978; Unsworth et al. 2007; Krumme 2009; Félix-Hackradt et al. 2010; Krumme et al. 2015). While Aldabra's reef fish assemblages have been the subject of numerous studies, few have reported on diel effects on the assemblage. The few studies that have considered the effect of time of day on the fish assemblage have provided some evidence that time of day may affect species composition. For example, catch rates of sharks were slightly higher during night time than during the day at Aldabra, suggesting elevated feeding activity of some elasmobranch species during the night (Stevens 1984). A subsequent study reported on elasmobranch abundance using baited underwater video camera systems (BRUVs) over a 24-hour period at Aldabra, which suggested that there may be a diel-induced difference in elasmobranch species composition but lacked sample replication to provide quantitative measures of shark abundance (Save Our Seas Foundation 2009). Vertical migration of phytoplankton at night has been recorded off the research station at Aldabra (Thalma 2015). The nocturnal species preying on phytoplankton are likely to follow this vertical migration to the surface, suggesting turn-over between diurnal and nocturnal zooplanktivores (Robertson and Howard 1978; Ohlhorst 1982). These indications from previous studies at Aldabra (Potts 1973, 1981, Stevens 1984) and previous studies from a wide range of localities (Unsworth et al. 2007; Krumme 2009; Félix-Hackradt et al. 2010; Krumme et al. 2015) suggest that the fish assemblage will undergo diel changes. Furthermore, the differing feeding opportunities between day and night, and a change in habitat availability may elicit different responses to a change in the time and tide from various trophic feeding groups. The change in response to diel cycles has not yet been recorded for the fish assemblage at Aldabra and required further investigation.

The aim of this chapter is to quantify the cyclical temporal variability of reef fish species richness, abundance, diversity, and differences in species and trophic assemblage structures observed using BRUVs and RUVs in relation to changes in tide and time of day at depths of up to 55 m on the west coast of Aldabra Atoll.

The following hypotheses were tested:

H. 5.1) The tide alters the fish species and trophic assemblage structure, as fish move in response to the vertical change in water level and with selective tidal stream transport.

H. 5.2) The species and trophic assemblage structure changes in response to the combined effect of tide and time of day.

The following objectives were set to:

Obj. 5.1) Establish changes of the species and trophic assemblage, including species richness, diversity, abundance and structure between spring high and spring low tide.

Obj. 5.2) Determine the change to the species and trophic assemblage structure between early morning-high, midday-low, and evening-high spring tides.

This study was restricted to tide and time of day and did not include other important temporal factors, like lunar and seasonal cycles, which have been shown to influence fish assemblages and warrant future investigation (Krumme et al. 2008, 2015). Seasonal effects were not considered in this study due to logistical challenges of sampling in rough seas during the southeast monsoon. The study focussed on fish assemblage structure during spring high and low tide as the effect of the tide would be at its maximum. Resources limited the amount of sampling that could be carried out during this study, and it was expected that the effect of the tide during spring tides would exceed the effect of the lunar cycle. Sampling was limited to daytime between dawn and dusk because seagoing was not permissible after dark. However, this experimental sampling design confounded the effects of tide and time of day that did not allow separating their respective effects on the fish assemblage. Although an attempt was made to disentangle their effects through a variety of data grouping, data formats and different statistical tests, no conclusions could reliably be drawn from their independent effects. Consequently, meaningful conclusions could only be drawn from the data were based on three groupings of the data, namely morning-high-tides, midday-low-tides and evening-high-tides. Data analyses which did not take account of time of day, such as two categories of tide (high tide and low tide), were not able to separate the effects of time of day with tide and consequently the conclusions from these analyses have to be interpreted with care.

This study used BRUVs and RUVs to sample the fish assemblage at Aldabra, because they are consistent with the methodologies used in a long-term monitoring programme at Aldabra, which is intended to assist the Seychelles Island Foundation (SIF) in interpreting data and planning future sampling design. Baited Remote Underwater Video systems sample the fish community using bait to attract fish into the Field of View (FOV). The tidal current disperses the bait plume from BRUVs into the water column and attracts fish into the FOV being recorded by the camera on the BRUVs (Taylor et al. 2013). The presence of bait has been shown to increase the species richness and relative abundance of generalist carnivores, piscivores, and is more effective than RUVs at sampling these species (Harvey et al. 2007). The presence of bait increased the abundance of predators and reduced the number of

herbivores relative to unbaited systems at Aldabra (Chapter 4). Baited sampling was better at sampling generalist carnivores, piscivores, and zooplanktivores, while unbaited was better for sampling herbivores. In order to get a holistic understanding of the effect of tide and time of day on the fish assemblage structure, both methods were used.

5.3. METHODS

5.3.1 Study site

Aldabra Atoll is exposed to large semidiurnal tidal ranges which are larger than expected for oceanic islands, which are often meso or microtidal in the South Western Indian Ocean region (Magori 2009). Aldabra's tidal range is amplified by semidiurnal resonance in the Mozambique channel, because of its geographical position relative to the narrowing between Madagascar and Africa (Pugh 1979). The mean spring tidal range is 2.74 m (Farrow and Brander 1971; Pugh and Rayner 1981). The large (155 km²) and shallow (mean depth 4 m) lagoon of Aldabra Atoll floods and drains with the change of tide, transporting nutrients and fish in and out of the lagoon twice a day (Pugh and Rayner 1981; Granek 2006). Tidal velocities of up to 60 cm/s have been recorded offshore from Aldabra, and increase towards the mouth of the lagoon channels (Stoddart et al. 1971; Heywood et al. 1990, 1996). The large tidal range and the velocity of tidal currents are likely to induce Selective Tidal Stream Transport (STST), which is an important transport mechanism for marine fish (Gibson 2003).

5.3.1.1 Diel patterns at Aldabra

Spring high tides at Aldabra occur around 06:00 AM, and again at 18:00 PM and spring low tides are at approximately 12:00 and 24:00 (SIF. Unpub data). The morning spring high tide therefore approximately overlaps with sunrise which happens at around 06:22 in November, and 06:50 by February (2017). Sunset is at approximately 18:23 in November, and 19:23 by February.

5.3.2 Sampling approach

Baited and unbaited Remote Underwater Video systems (BRUVs and RUVs) were used to collect underwater video data along approximately 18 km of seaward reefs on the west coast of Aldabra Atoll (46.217; -9.369, and 46.253; -9.499, WGS 84 decimal degrees) (Figure 5.1). Samples were collected during the north-west monsoon between 2014-11-09 and 2015-02-07, on the three days around spring tides (the day before, on the day and the day after). The effect of the tide on the fish assemblage was measured during spring tide to ensure that its potential effect is greatest (Neumann 1981; Krumme 2009).

Samples were collected close to the peak tidal states (high and low) on spring tides, during the morning (high), midday (low) and early evening (high). Approximate starting times for sampling were 06:00 AM, 11:00 AM and 12:30 PM, and 17:00 PM (GMT +4), but these were adjusted based on high and low tide times on the day. Note that low tide was sampled

before and after the low tide, but this was not possible for high tides because it was not permissible to be at sea prior to sunrise, or after sunset. Morning-high-tides sampling times included the hour after peak high tide and evening-high-tides were the hour leading up to peak high tide. Morning-high-tides were therefore always outgoing, midday-low-tides included both outgoing and incoming tides, and evening-high-tides were always incoming on tides. The direction of the tide was not included in this study as more sampling was required for meaningful analysis.

Samples were collected at four sampling areas (areas) along the west coast of Aldabra, to restrict the effects of site variability on the fish assemblage. Each sampling area was spread over 3.7 to 7.2 km², and the areas were approximately 3 km apart. Each sampling area ranged from 0.8 to 49 m in depth (at low tide) and was at variable distances from the lagoon mouths. The sampling design was unbalanced across sites because some sampling areas were prohibitively far from the Research Station to reach during early morning or late evenings, as the time at sea was restricted to daylight hours.

All four areas were sampled each day on which sampling took place, such that five samples were collected per site during each single tidal state and time of day, using a single bait treatment per site. = Samples that were collected on the same day had a minimum distance of 300 m between sampling localities to minimise the potential of cross sampling the fish assemblage between simultaneous deployments. After a site was sampled, the boat was moved to the next area, and five replicate samples were collected around the peak of the subsequent tidal state but using the opposite bait treatment from that used at the previous area (See Figure 5.2 for sampling areas and Table 5.1 for tidal phases during sampling events). The use of bait was alternated between areas to avoid a cumulative attraction effect biasing the observed fish assemblage. Some sampling sites were resampled on subsequent dates if a sample failed (e.g. system landed upside down and could not be analysed). Consequently, the spread of samples analysed was not five per sampling area per sampling event (Table 5.1).

Table 5.1. The number of samples collected per sampling event, and time and tide during event. In “Tide phase”, “h” = high and “l” = low. All sampling dates represent tidal states within a day of spring tides.

Sampling date and time	Area name	Time of day group	Sampling tide phase	Daily high tide	Daily low tide	Treatment	Samples (n)
2014-11-09 06:35	West Grand Terre	morning	h	06:05	12:22	unbaited	4
2014-11-09 11:13	Southwest Grand Terre	midday	l	06:05	12:22	baited	4
2014-11-09 13:05	West channels	midday	l	06:05	12:22	unbaited	4
2014-11-09 16:54	Picard	evening	h	06:05	12:22	baited	3
2014-11-10 06:45	West Grand Terre	morning	h	06:38	12:57	baited	4
2014-11-10 11:37	Southwest Grand Terre	midday	l	06:38	12:57	unbaited	4
2014-11-10 13:32	West channels	midday	l	06:38	12:57	baited	5
2014-11-10 16:57	Picard	evening	h	06:38	12:57	unbaited	5
2014-11-24 06:48	Southwest Grand Terre	morning	h	06:07	11:57	baited	4
2014-11-24 10:43	West Grand Terre	midday	l	06:07	11:57	unbaited	5
2014-11-24 12:36	Picard	midday	l	06:07	11:57	baited	5
2014-11-24 16:42	West channels	evening	h	06:07	11:57	unbaited	5
2014-11-25 07:14	West channels	morning	h	06:21	12:44	unbaited	4
2015-01-21 09:32	West Grand Terre	midday	l	17:50	10:45	baited	4
2015-01-21 12:02	Picard	midday	l	17:50	10:45	unbaited	4
2015-01-21 16:41	West channels	evening	h	17:50	10:45	baited	4
2015-01-22 10:48	West Grand Terre	midday	l	18:30	12:24	baited	1
2015-01-22 11:05	Southwest Grand Terre	midday	l	18:30	12:24	unbaited	3
2015-01-22 13:22	West channels	midday	l	18:30	12:24	unbaited	3
2015-01-22 13:59	Picard	midday	l	18:30	12:24	unbaited	2
2015-01-22 16:43	West channels	evening	h	18:30	12:24	unbaited	3
2015-01-22 17:08	Picard	evening	h	18:30	12:24	unbaited	1
2015-02-07 07:12	Southwest Grand Terre	morning	h	06:53	13:05	baited	5

Sampling was repeated during the next suitable spring tides or within a day from spring tides. Each area was revisited at least four times, alternating the bait treatment and tidal state and time of day during which an area was visited to obtain baited and unbaited samples from each area during high or low tides. The logistical constraints of the sampling further away from the Research station meant that not all sites were revisited on all combinations of tide-and-time-of-day.

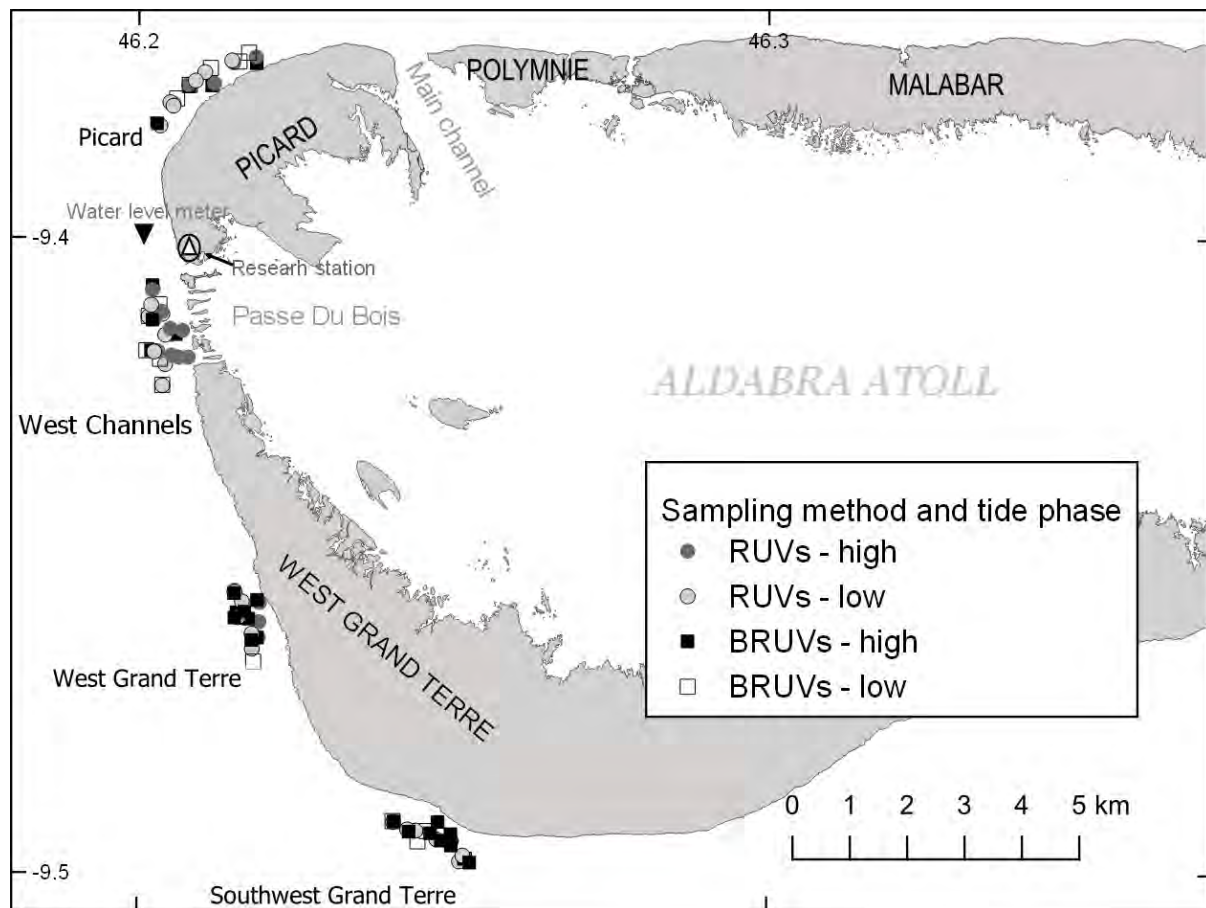


Figure 5.1. Sample localities and the associated tidal phase on the west coast of Aldabra. Samples were collected from four areas using Baited Remote Underwater Video systems (BRUVs) and Remote Underwater Video systems (RUVs)

5.3.3 Sampling method

5.3.3.1 Setup

Five BRUVs and RUVs were used to collect baited and unbaited samples respectively from each sampling site. The tripod frame, video camera and bait attachment of the BRUVs and RUVs were set up in the same way as described in Chapter 4, to obtain video samples of the fish assemblage.

5.3.3.2 Deployment

The BRUVs and RUVs were deployed for just over 60 minutes to ensure 1-hour video data, to conform with commonly used deployment times (Harvey et al. 2007; Cappo et al. 2007b; Bernard and Götz 2012). The five systems were deployed within a sampling area, and only after all five systems were retrieved, would the next area be sampled. A total of 20 samples were collected on each day, using the procedure described in Chapter 4.

5.3.4 Sample processing

Videos were processed in a random sequence to avoid observer learning effects systematically biasing species identification over time. Video imagery was processed using EventMeasure software (www.seagis.com.au). Fish were identified and counted for each species during the video analysis, and the maximum abundance determined using the MaxN method (Cappo et al. 2003). Chapter 4 describes the same procedure in more detail.

5.3.5 Trophic guilds

Fish were assigned to one of eight trophic guilds based on their dietary preference as described in Chapter 4. The eight trophic guilds were herbivore, corallivore, zooplanktivore, piscivore, invertivore carnivore, algae/invertivore, sponges/invertivore and generalist carnivore.

5.3.6 Covariates and predictor variables

Water level (m) above or below mean sea level was recorded every ten minutes by an Onset Hobo 100-Foot Depth Titanium water level data logger, which was deployed on the west coast of Aldabra near to the research station (Figure 5.1). The first and last readings of the six water-level readings taken during each BRUVs or RUVs deployment were discarded, and the average of the remaining four readings was assigned to the sample. Time of day was taken as the mid-point of the video samples (30 minutes after a video sample started). Depth was recorded as meters below sea level measured by echo sounder mounted to the boat (Garmin 520s), when the BRUV or RUV system reached the seabed. Water temperature on the seafloor was recorded using Onset Hobo Pro v2 data loggers every ten minutes during deployment, and average values during respective deployments assigned to each sample (see Chapter 4 for a more detailed description). The percentage water column and visible area (introduced in Chapter 4) were included in the analysis to account for potential bias introduced by differences of visibility and the angle at which the camera was orientated between samples. See Table 5.2 for a list of covariates used in the study, and their units.

5.3.6.1 Depth

The effect of depth on the fish assemblage is important to consider in relation to the tide because the water level may affect the fish assemblage differently at various depths as the shallows become temporally available during high tide for fish to move into and many are then forced to leave during low tide. There may therefore be an interactive effect between depth and time of day, as fish may move between different depths during different times of the day (Robertson and Howard 1978; e.g. Becker et al. 2011).

5.3.6.2 Enhanced tidal stream strength

Selective Tidal Stream Transport (STST) has been shown to cause fish movement, which may result in temporary changes to the observed fish assemblage (Gibson 2003). It was therefore important to account for the variation in tidal stream strength across the distribution of the sampling sites in the analysis. Tidal stream strength at Aldabra is likely to be amplified by the high flow rates near the atoll's lagoon mouths (Stoddart et al. 1971).

A model of the tidal current enhancement, resulting from lagoon flushing, was generated and mapped for the study area, and a value assigned to each BRUV or RUV sample using a spatial join in QGIS (Quantum-GIS-Development-Team 2017). The rate of flow at the lagoon mouth and the distance of the sampling site to lagoon mouth were the only factors used to explain the variability of the tidal stream strength along the west coast of Aldabra. It is likely that the effect of wind and the geostrophic current was similar over this small area, but the effects of topography, depth and habitat rugosity were omitted owing to data limitations. Flow speeds were assumed to be greatest at the mouth of the channels, and to dissipate with increasing distance away from the mouth (Stoddart et al. 1971).

The geographical coordinates of lagoon mouths (midway between the separated land masses) were taken to be the starting point from where maximum values would decrease with increasing distance from the starting point. The proportional drainage volumes of each of the four lagoon channels with respect to the total drainage volume were used to weight the starting point values of the respective channels (Stoddart et al. 1971). Stoddart's (1971) original drainage estimates were used to inform the weighted starting point values. The Main channel on the north-western side of the atoll was estimated to export 60 % of the lagoon waters, with a drainage capacity estimated as approximately 240 million litres of water per tide (Stoddart et al. 1971). The West Channels were assumed to drain 27 %, and Johnny Channel 1 % of the total draining volume (Stoddart et al. 1971). Passe Houareau, in the north-east of the atoll, drains the remaining 11 % but did not affect the study areas (and is therefore not shown in Figure 5.2 below). The drainage volumes of the respective lagoon channels were calculated by multiplying the total lagoon volume by the percent drainage per

channel. Drainage volumes were expressed as kilolitres (kl) and assigned to the starting points in the respective channels.

A two-dimensional surface representing the enhanced flow rates of the tidal stream was mapped, with the weighted starting point values decayed with increasing distance from the starting point. A triweight kernel shape was used to interpolate enhanced tidal stream values over the study area using the HEATMAP plugin in QGIS. Triweight kernel shape gives higher weight to distance closer to the point of origin than other kernel shapes and was deemed appropriate as the enhancing effect near channels rapidly decreases with distance away from channels (Quantum-GIS-Development-Team 2017).

The triweight kernel density estimation, expressed as Equation 5.1, is a unitless probability density estimation (Epanechnikov 1969; Cleveland and Devlin 1988). In the equation below, $K(u)$ is the kernel, and the term (u) is derived from the flow rate and estimated distance of influence from each channel. The distances of influence from the respective channels were estimated from sediment plumes on Quickbird (February and March 2012) and GeoEye satellite imagery (November 2011) over Aldabra. The estimated distances of influence agreed with personal experience and observations of the influence of the current when at sea. The remaining terms are constant within the triweight kernel (Epanechnikov 1969; Cleveland and Devlin 1988). The term ≤ 0 specifies the bandwidth of the equation, which was set to zero or greater to include all sampling stations as these all had a distance greater than 0 from the channels. Units in the weighted map surface (Figure 5.2) take on the inverse of the drainage units (1/kilo-litres [kl]).

$$K(u) = \frac{35}{32}(1 - u^2)^3, |u| \leq 0 \quad (\text{Eqn.5.1})$$

The maximum distances over which the flow from each channel could reach were proportionately scaled relative to the amount of flow at the channel mouth. The distance to which the enhanced tidal flow was effective was scaled to the percentage of the drainage volume from respective channels, which was multiplied by a constant of 100 m. The 100 m constant was used because it resulted in a mapped surface which matched observations: The Main Channel effect decayed to zero at 6 km from the starting point, which is the distance between the Main Channel and Passe Du Bois, from where it is thought that the flow rate of the Main Channel does not further affect flow rate towards the west (personal observation). The enhanced flow rate therefore depreciated to zero after 6 km at Main Channel, after 2.8 km at Passe Du Bois, after 100 m at Johnny Channel, and after 1.1 km at Passe Houareau.

Mapped enhanced flow rate values were associated with BRUVs and RUVs sampling localities based on their spatial overlap and assigned using a spatial join in QGIS. The exact value assigned to the sample represents a scaled proportional enhancement of the tidal stream experienced at various distances from the lagoon channels. Three of the four channels at Aldabra was of consequence in the sample area, two on either side of Polymnie island and Passe du Bois south of Picard island (Figure 5.2).

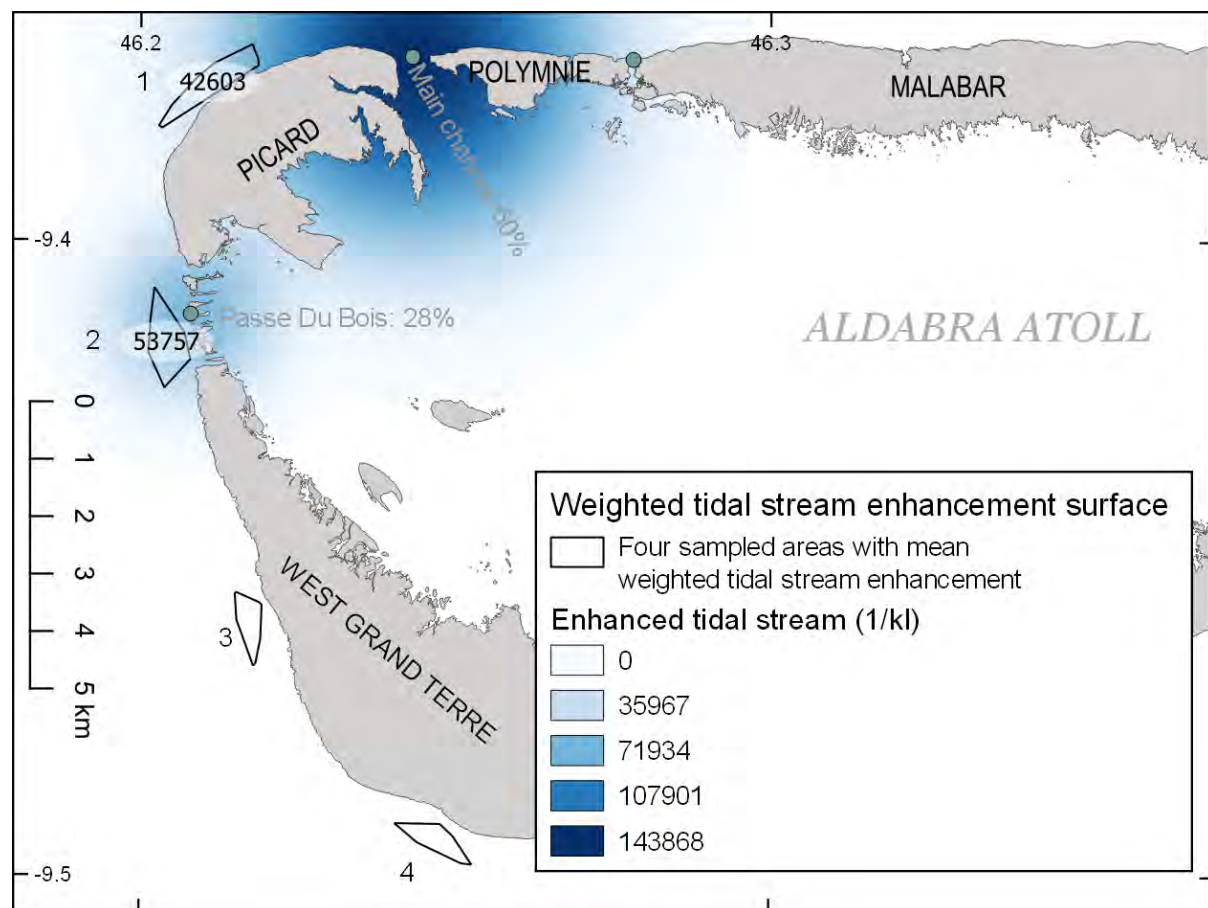


Figure 5.2. Tidal stream enhancement heatmap on the west coast of Aldabra caused by increased water flow near lagoon channels during the tidal cycle, of which the effect decreases with increasing distance away from channels. The mean drainage weighted values for the four sampling areas and the relative drainage from the two channels affecting the sampled area are indicated on the map.

Table 5.2. Table of covariates and units assigned to each sample.

#	Covariates and predictor variables	Unit	Type
1	Visible area	m ²	continuous, covariate
2	Percent water column	%	continuous, covariate
3	Temperature	°C	continuous, covariate
4	Tide	m	continuous, predictor variable
5	Time of day	H, m, s	continuous, predictor variable
6	Depth	m	continuous, predictor variable
7	Enhanced tidal stream	1/kl	continuous, covariate
8	Tide state	High, Low	Two level factor
9	Tide.Time of day	Morning-high-tide, Midday-low-tide, Evening-high-tide	Three level factor

5.3.7 Statistical analysis

All statistical analysis was carried out in R, using the functions in the BASE, STATS, VEGAN packages (Oksanen et al. 2016; R Core Team 2016). All univariate, multivariate and diversity analysis were carried out using the functions in VEGAN (Oksanen et al. 2016). The data from the RUVs and BRUVs were analysed independently from each other, using the methods described below.

5.3.7.1 Environmental data

5.3.7.1.1 Standardising covariates

Continuous covariates were standardised using the DECOSTAND function in VEGAN, prior to analysis as their values were on different scales (Table 5.2) (Oksanen et al. 2016), as described in Chapter 4.

5.3.7.1.2 Outlier assessment

The standardised covariate data were assessed for multivariate outliers using nonmetric multidimensional scaling (NMDS) plots (Minchin 1987; Anderson et al. 2008). The euclidian distance was calculated from standardised environmental covariates and plotted in an NMDS ordination plot. Potential outliers were identified as NMDS points falling outside of the 95 % confidence limits (Anderson et al. 2008).

5.3.7.1.3 Correlations between covariates

Correlation between various environmental covariates can affect multivariate results and was assessed using a correlation test (COR.TEST) and visually assessed using draftsman plots (Best and Roberts 1975; Hollander et al. 2013).

5.3.7.1.4 Comparing covariate sample means

Box and whisker plots (BOXPLOT) were drawn up to visually compare sample means and assess the distribution of the data (Chambers et al. 1983). The data were tested for differences in environmental covariates between tidal states to ensure comparability of data, using a two-sided Wilcoxon rank sum test with continuity correction at the 95 % confidence limit (WILCOX.TEST) as the data had a non-parametric distribution (Hollander et al. 2013).

5.3.7.2 Fish assemblage data

5.3.7.2.1 Species richness, diversity and abundance of fishes

The species richness and relative abundance (MaxN) were totalled for each sample.

Species richness per sample was calculated as the total number of species per sample.

Total relative abundance per sample was calculated by summing the MaxN values of all species per sample. The Shannon-Wiener diversity index was calculated for each sample using the DIVERSITY function in VEGAN, with log base set to two, as described in Chapter 4 (Oksanen et al. 2016).

Univariate permutational ANOVA was used to assess the difference in fish species richness, diversity and abundance between tidal states after accounting for the effects of time of day, depth and other covariates. Univariate permutational ANOVA was used because the data had a non-parametric distribution and were affected by multiple covariates (Anderson et al. 2008; Hollander et al. 2013). The values of species richness, abundance and Shannon-Wiener diversity were left untransformed as recommended for univariate permutational ANOVA (Anderson and Millar 2004; Anderson et al. 2008). The Euclidian distance between sample totals was respectively calculated for each of the three response variables, species richness, relative abundance (MaxN), and the Shannon diversity index. The significance of the effect of tidal state was determined from 4 999 permutations of the data and expressed as Pseudo F ($\text{Pr}(>F)$), using the function ADONIS2 in the VEGAN package in R.

Forward and backward model refinement was carried out to inform the selection of covariates used in univariate permutational ANOVA models and arrive at parsimonious models for the RUVs and BRUVs data sets, respectively. The same process described for model refinement of distance base redundancy models (dbRDA) was followed to determine parsimonious models. Note that in each pair of equations, BRUVs-equations omit wave energy as an explanatory variable, while RUVs-equations include this variable. The difference between the equations for BRUVs and RUVs were a consequence of model selection towards the most parsimonious model that indicated better performance without wave energy in BRUVs-equations. “Species assemblage” in the equations below represent

the untransformed species richness, abundance or diversity, as the response variable in models, expressed as follow:

$$Univariate_{Species(BRUVs)} = \text{adonis2}(\text{Species assemblage} \sim \text{Visible area} + \text{Depth} * \text{Tide.state} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.2})$$

Eqn.5.2 Univariate permutational ANOVA model of species richness, diversity and abundance (repeated for each respectively) from BRUVs samples

$$Univariate_{Species(RUVs)} = \text{adonis2}(\text{Species assemblage} \sim \text{Visible area} + \text{Wave energy} + \text{Depth} * \text{Tide.state} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.3})$$

Eqn.5.3 Univariate permutational ANOVA model of species richness, diversity and abundance (repeated for each respectively) from RUVs samples

5.3.7.2.2 Abundance of fish within trophic groups

Two separate analysis was used to compare the total relative abundance (sum of MaxN) per sample within each trophic guild between, 1) tidal state, and 2) between three categories of combined tidal state and time of day (Table 5.2). The Euclidian distance between samples was calculated from the untransformed total relative abundance per trophic guild per sample.

The selection of covariates used in the analysis was based on the model refinement described below for dbRDA analysis. The equations are expressed as follow, where “i” represent the respective trophic groups:

$$Univariate_{Trophic(i)(BRUVs)} = \text{adonis2}(\text{Trophic assemblage}_i \sim \text{Visible area} + \text{Depth} * \text{Tide state} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.4})$$

Eqn.5.4 Univariate permutational ANOVA model of abundance within each trophic group (respectively) from BRUVs samples

$$Univariate_{Trophic(i)(RUVs)} = \text{adonis2}(\text{Trophic assemblage}_i \sim \text{Visible area} + \text{Wave energy} + \text{Depth} * \text{Tide state} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.5})$$

Eqn.5.5 Univariate permutational ANOVA model of abundance within each trophic group (respectively) from RUVs samples

The equations used to assess the abundance of fish between three categories of tide and time of day are expressed as:

$$Univariate_{Trophic(i)(BRUVs)} = \text{adonis2}(\text{Trophic assemblage}_i \sim \text{Visible area} + \text{Depth} * \text{Tide.Time of day}) \quad (\text{Eqn.5.6})$$

Eqn.5.6 Univariate permutational ANOVA model of abundance within each trophic group (respectively) from BRUVs samples

$$Univariate_{Trophic(i)(RUVs)} = \text{adonis2}(Trophic\ assemblage_i \sim Visible\ area + Wave\ energy + Depth * Tide.Time\ of\ day) \quad (Eqn.5.7)$$

Eqn.5.1 to 5.7 shows the univariate permutational ANOVA model of abundance within each trophic group (respectively) from RUVs samples

Pairwise univariate permutational ANOVA was used as a *post hoc* test for significant difference in mean abundance among pairs of tide-and-time-of-day categories (Arbizu 2017). In pairwise assessments samples are grouped according to tide-and-time-of-day categories, significance was tested using 4 999 permutations of the data, and permutational significance was Holm adjusted to account for the effect of multiple comparisons on significance (Holm 1979).

5.3.7.3 Fish assemblage structure

Fish assemblage structure was represented by relative abundance (MaxN) of fish species per sampling site. Trophic assemblage structure was represented by the number of relative abundances per trophic group per sampling site. Only relative abundance data (i.e. not presence/absence) were used in the analysis because the results from Chapter 4 indicated that presence/absence generally reflected the same patterns as abundance across species and trophic level analysis but conveyed less information about the structure of the assemblage.

5.3.7.3.1 Data transformation and ecological distance resemblance matrix

Two steps were used to reduce the influence of large schools of fish on the data analysis. First, the abundance (MaxN) of schooling fish was capped at 44 which was the mean plus two standard deviations of MaxN from the complete data set. The reason for this was that very large schools of fish had a disproportionate effect on the data analysis even after standard data transformation described below. Secondly, abundance (MaxN) data were $\log_{10}(x+1)$ transformed to reduce the effect of highly abundant species on the analysis. Log base 10 was used during the transformation which equates the loss of a single species (taxon) from the assemblage to there being ten fewer individuals from a single species in the assemblage in a species which was present in the assemblage. The log base of 10 is appropriate for ecological communities with a large range in abundance values (Anderson 2006; Oksanen et al. 2016).

Modified Gower dissimilarity was used to calculate a resemblance matrix from the transformed values. Lingoes transformation was applied to the dissimilarity matrix to avoid negative eigenvalues incorrectly inflating the contribution of axes to the dispersion of points (Legendre and Anderson 1999; Legendre and Legendre 2012).

5.3.7.3.2 Distance based redundancy analysis (dbRDA)

The relationship between the fish assemblage structure, represented by the resemblance matrix, and tide time of day was analysed using distance based redundancy analysis (dbRDA), using the DBRDA function in VEGAN (Legendre and Anderson 1999; McArdle and Anderson 2001; Oksanen et al. 2016). Distance based redundancy analysis (dbRDA), detects linear relationships between dissimilarities in the resemblance matrix caused by non-linear environmental variables (Legendre and Anderson 1999; McArdle and Anderson 2001; Oksanen et al. 2016). Distance based redundancy analysis was appropriate to analyse the Modified Gower resemblance matrix because the method allows analysis of non-Euclidean dissimilarity distances (Legendre and Anderson 1999; McArdle and Anderson 2001; Oksanen et al. 2016).

5.3.7.3.2.1 Model development

The full model including tide and time of day and all the other covariates (Table 5.2, Eqn.5.2) was used as an initial model which was refined towards the most parsimonious model, described below. The interactions between depth and tide and depth and time of day may affect the fish assemblage. These environmental variables are unlikely to covary between samples and were therefore included as two separate two-way interactions in the initial model.

The order of the variables influenced their significance, and consequently, variables were fitted to the model within a specific sequence. The covariates visible area and percent water column were added to the model first because these could bias the results prior to the effect of environmental variables. Tide was fitted after the time of day because it was expected that the effects of the tide would be wider reaching and potentially mask the effect of time of day. (The effects of tide prior to the time of day was also assessed, and the results are provided in the Annex.) Remaining covariates not directly tested in the hypothesis were fitted next to explain variance attributed to environmental variables that could affect result results prior to testing the effect of time of day and tide. The remaining covariates were fit in the order over which there was the least control during the experimental design, the least was fitted first, and the covariate over which there was most control, fitted last. The interaction between depth and time of day, and then depth and tide were fitted last. By fitting the variables for which the hypothesis is being tested in the last position of the sequential-model, the test provided a conservative estimate of the significance of tide and time of day (Anderson et al. 2008).

The full model expressed as Equation 5.8, where “Fish assemblage” represents the transformed Modified Gower dissimilarity matrix of the relative abundance of fish per sample,

and covariates represent the standardised covariates, as described above. Full models were generated for RUVs and BRUVs, independently.

$$\text{Full model} = \text{dbRDA}(\text{Fish assemblage} \sim \text{Visible area} + \text{Percent water column} + \text{Temperature} + \text{Wave energy} + \text{Enhanced tidal stream} + \text{Depth} * \text{Tide} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.8})$$

Eqn.5.8. The full model for distance based Redundancy Analysis (dbRDA).

5.3.7.3.2.2 Model refinement

The dbRDA models were refined towards the most parsimonious models by retaining only tide, time of day, depth and covariates that significantly increased explanatory power or models and did not have excessive collinearity with other predictor variables. Variance inflation factors indicate collinearity between variables that may artificially inflate their explanatory power in the model (Borcard et al. 2011). Variance inflation factors were calculated for all covariates from full models to determine which covariates to remove from the analysis using VIF.CCA (Oksanen et al. 2016). None of the covariates had variance inflation factors that exceeded 10, which is the prescribed value for removal, and therefore all were retained in the model for further refinement (Oksanen et al. 2016).

Parsimonious models were refined from the full models using a stepwise forward and backward model selection procedure, ORDISTEP, in which a permuted pseudo F-values ($\text{Pr}(>F)$) were determined from the deviance defined, here as the residual sum of squares, in dbRDA models (Blanchet et al. 2008; Oksanen et al. 2016).

The process was started using an empty model defining the fish assemblage structure to which the covariates were added, one at a time, and the change in pseudo-F-value evaluated after each addition to determine the gain in model strength by the addition of each covariate. Newly added predictor variables that significantly increased the explanatory power of the model were included in the model. The inclusion of the newly added variable in the model was then re-evaluated by assessing the loss of explanatory power after removing the newly added variable. Predictor variables that caused both a significant increase in explanatory power when included in the model and a significant loss of explanatory power when removed were retained in the new model. This process was repeated by adding the remaining covariates to the new model and repeating the evaluation process. Model refinement concluded when the addition of any remaining variable to the model did not make a significant difference to its explanatory power, and the removal of any variable already included in the model caused a significant reduction in the explanatory power of the model. This process was carried using ORDISTEP (Oksanen et al. 2016) and included all

covariates listed in Table 1, the interaction of depth and time of day, and the interaction of depth and tide.

If the parsimonious models did not already include depth, time of day and tide, the interactions between depth and time of day, and the interaction between depth and water level, they were added to address the research question. The four respective equations used for species and trophic fish assemblages, from BRUVs and RUVs, are expressed below. In the equations, the response variable, “Species assemblage” or “trophic assemblage”, refers to the relevant species or trophic assemblage observed in BRUVs or RUVs, and have undergone the transformation and resemblance matrix calculations described above:

$$dbRDA_{Species(BRUVs)} = dbRDA(\text{Species assemblage} \sim \text{Visible area} + \text{Depth} * \text{Tide} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.9})$$

Eqn.5.9 Distance based redundancy Analysis (dbRDA) model for species observed in BRUVs

$$dbRDA_{Species(RUVs)} = dbRDA(\text{Species assemblage} \sim \text{Visible area} + \text{Wave. energy} + \text{Depth} * \text{Tide} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.10})$$

Eqn.5.10 Distance based redundancy Analysis (dbRDA) model for species observed in RUVs

$$dbRDA_{Trophic(BRUVs)} = dbRDA(\text{Trophic assemblage} \sim \text{Visible area} + \text{Depth} * \text{Tide} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.11})$$

Eqn.5.11 Distance based redundancy Analysis (dbRDA) model for trophic guilds observed in BRUVs

$$dbRDA_{Trophic(RUVs)} = dbRDA(\text{Trophic assemblage} \sim \text{Visible area} + \text{Wave. energy} + \text{Depth} * \text{Tide} + \text{Depth} * \text{Time of day}) \quad (\text{Eqn.5.12})$$

Eqn.5.12 Distance based redundancy Analysis (dbRDA) model for trophic guilds observed in RUVs

5.3.7.3.2.3 Model evaluation

The significance of each term in each dbRDA model was determined in multivariate ANOVA (ANOVA.CCA) using 4 999 permutations of the assemblage data, and significance given by the pseudo-F value, which is the ratio of constrained and unconstrained total inertia (variance) in the model (Oksanen et al. 2016). Terms were assessed sequentially, from first to last.

5.3.7.3.2.4 dbRDA plots

The dispersion of samples was plotted in a multivariate ordination according to dbRDA axis values. The dbRDA axes displayed in the ordination plots were the constrained axes on which tide and time of day explained the largest proportion of differences between the fish assemblages (i.e., axes on which tide and time of day had the greatest proportional

contribution to the Eigenvalues. The covariates of interest were overlaid onto the plot, where the length of the arrow represents the proportionate amount of variance explained, and the direction of the arrow indicates the direction in ordination space in which the covariate changes at the fastest rate.

5.3.7.3.2.5 dbRDA Bubble plots

The eight species and trophic guilds that respectively contributed the greatest proportion of the variance between samples were displayed in a bubble plot in dbRDA ordination space to depict abundance-based trends that contributed to the observed grouping of samples. The size of bubbles represents the relative abundance (MaxN) of species or trophic guilds, in baited or unbaited treatments, respectively. Vectors (directional-line) were overlaid, where the length of the vector indicates the relative contribution of the species or trophic guild to the variance between samples, and the direction of the vector indicates the direction in ordination space in which the species or trophic group most rapidly increases.

5.4. RESULTS

5.4.1 Environmental and other covariates

In total, 86 samples were collected from the west coast of Aldabra to examine the effects of tide and time of day on the fish assemblage, with 39 samples from BRUVs and 47 samples from RUVs Table 5.3. Removing the outliers did not significantly affect results and all samples were kept in the analysis to ensure a sufficiently large sample size.

5.4.1.1 BRUVs environmental variables

The water level during high tide in BRUVs ranged between 3.02 m and 3.58 m, and between 0.48 m and 0.7 m during low tide. The water level was significantly (Wilcox $W = 380$, $p < 0.001$) greater during high tides than low tides (2.73 m [the difference between means]), and therefore suitable to compare the assemblages between tides.

Baited remote underwater video systems (BRUVs) were deployed as early as 06:45 AM and sampling was concluded by 08:37 AM at the latest. Midday low tides were sampled from 09:30 AM at the earliest and the latest sample concluded by 15:30 PM. Sampling during evening high tides started by 16:40 PM at the earliest and were concluded by 18:12 PM at the latest.

Overall, the BRUVs samples covered a depth range of 0.8 to 49 m, and water temperature varied between 26.6 and 28.5 °C. Temperature decreased with increasing depth ($\rho = -0.21$), but the correlation between them was not significant (Spearman rank correlation coefficient $S = 11\,898$, $p > 0.05$). Exposure to wave energy affecting the sampling sites ranged between 4 342 J/m³ at sheltered sites along the west coast to 8 733 J/m³ at the more exposed south-west corner of the atoll. The enhanced tidal stream ranged between 0 and 7330106 kl⁻¹ and was negatively correlated with wave exposure ($\rho = -0.59$, Spearman rank correlation coefficient $S = 15774$, $p < 0.001$). The correlation was due to both wave exposure and enhanced tidal stream varying in strength along the coast, with the most sheltered areas being closest to the sites with the highest enhanced tidal current. There was also a significant positive correlation ($\rho = 0.81$, Spearman rank correlation coefficient $S = 1816.7$, $p < 0.001$) between enhanced tidal stream and time of day, which reflected the sampling pattern concluding closer to the Research station and lagoon channels where the enhanced tidal stream was strongest. The visible area ranged between 6.7 m² and 146 m² and was positively correlated with depth ($\rho = 0.52$, Spearman rank correlation coefficient $S = 4774$, $p < 0.001$). The negative correlation between depth and the visible area could be explained by

higher structural complexity in shallow water habitats that may contribute to obscuring the FOV in the camera. The percentage water ranged between 8 and 79 %.

Multivariate variance inflation factor (VIF) were all below 2, and therefore the risk of artificial inflation of covariate significance in multivariate was too low to be considered a problem.

None of the covariates was significantly different between tidal states in the baited samples set (Two-sided Wilcoxon rank sum test with continuity correction [Wilcoxon hereafter], $p > 0.05$) for percent water column, depth, sample area, wave energy, enhanced tidal stream, or (water) temperature (Figure 5.3).

5.4.1.2 RUVs environmental variables

The water level during high tides ranged between value 2.9 and 3.61 m, while water level ranged between 0.48 and 0.7 m during low tide in RUVs. Water levels were significantly greater (by 2.67 m) during high tide than low tide in unbaited samples (Wilcoxon $W = 360$, $p < 0.001$) and was therefore suitable to measure the influence of water level on fish assemblages.

Unbaited sampling during morning started as early as 06:35 AM and concluded by 08:30 AM at the latest. Midday low tides were sampled from 10:40 AM at the earliest and the latest sample conclude by 15:04 PM. Sampling during evening high tides started by 16:40 PM at the earliest and concluded by 18:22 PM at the latest.

On average, RUVs samples covered a depth range from 1.5 m to 46.7 m, with a water temperature varying between 26.8 and 28.2 °C. There was a weak negative correlation ($\rho = -0.27$) between temperature and depth, but the relationship was not significant (Spearman rank correlation coefficient $S = 21\,983$, $p > 0.05$). Exposure to wave energy affecting the sampling sites ranged between 3 731 J/m³ at sheltered sites along the west coast to 8 742 J/m³ at the more exposed south-west corner of the atoll. Tidal stream varied between 0 and 7303212 kl⁻¹ and had a significant (Spearman rank correlation coefficient $S = 24\,638$, $p < 0.01$) negative correlation with wave exposure ($\rho = -0.42$). The percent water column ranged between 8 % and 76 %, and the visible area ranged between 6.6 and 146 m², and both were significantly correlated with depth ($\rho = -0.3$, Spearman rank correlation coefficient $S = 22\,641.5$, $p < 0.05$; $\rho = 0.61$, Spearman rank correlation coefficient $S = 6\,790.5$, $p < 0.001$).

The multivariate variance inflation factors (VIF) were all below 3, and the conflation of variance did not affect the analysis.

A number of the environmental variables were significantly different between tidal states in the RUVs dataset (Figure 5.3). The mean depth was significantly greater (by 7.6 m on average) during low-tide sampling in the unbaited sample set (Wilcox, $W = 159$, $p\text{-value} < 0.01$, but the difference in temperature was not significant between tidal states. The visible area was not significantly different between high and low tide in RUVs or in BRUVs, but the percent water column was significantly greater (8.4 %) in the high tide than low tide in unbaited data (Wilcox $W = 378$, $p < 0.05$). The exposure to wave energy was significantly greater ($1\,083\text{ J/m}^3$) at the samples collected during the low tide than high tide in RUVs, but not in BRUVs (Wilcox, $W = 130$, $p < 0.01$). The tidal stream was significantly greater ($1\,982\,391\text{ kl}^{-1}$) at localities samples during the low tide, compared to the high tide (Wilcox, $W = 393$, $p < 0.05$).

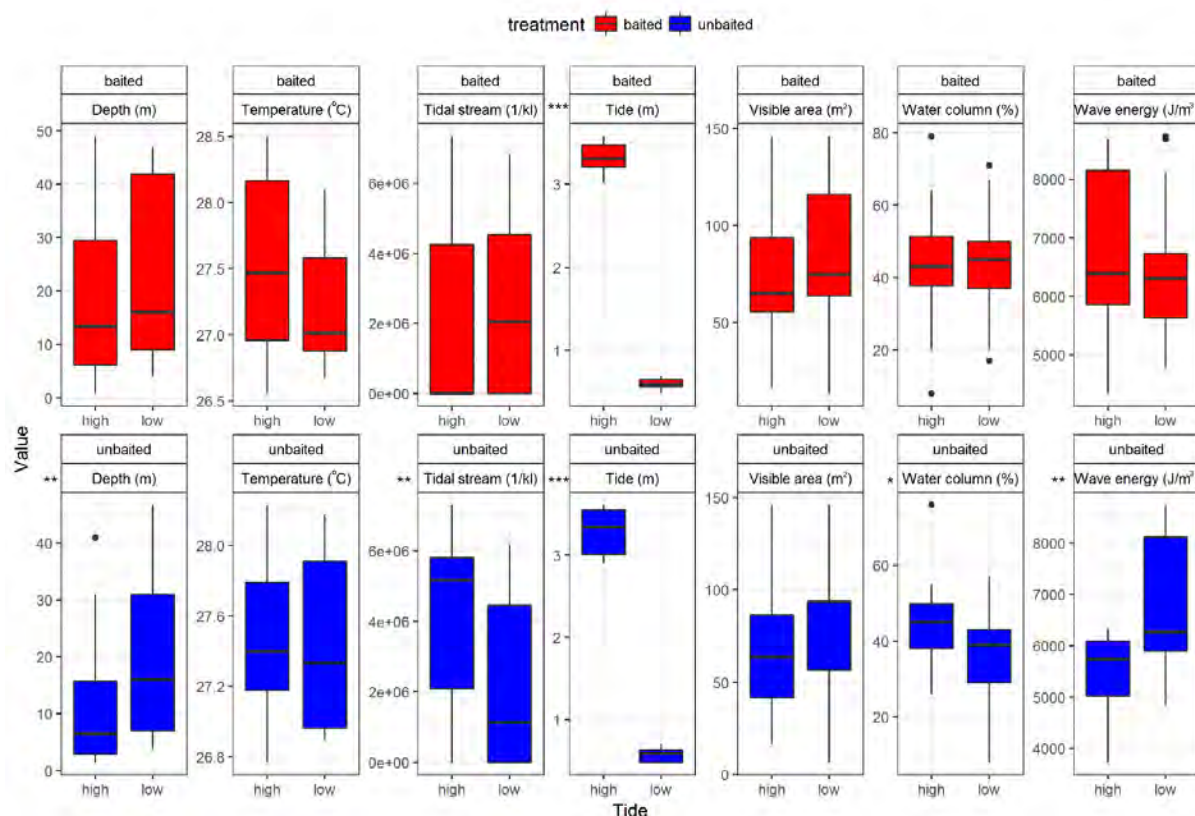


Figure 5.3. Boxplots of environmental variables recorded at the BRUVs and RUVs sampling sites on the west coast of Aldabra. The boxplots show the mean and interquartile range in the box and outlying values as dots. Significant differences between variables between high and low tide (per bait treatment) are indicated: Wilcox significance levels $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$; $= 0.05$.

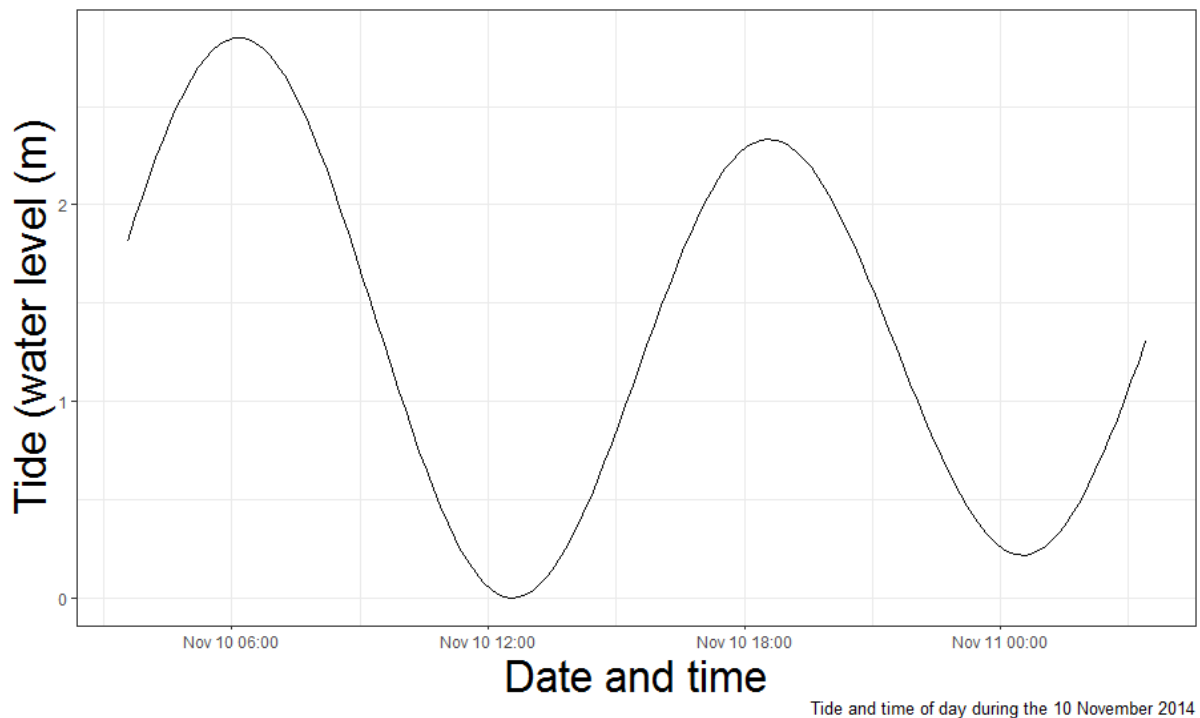


Figure 5.4. Typical tidal (water level) values over the course of a day during a spring tide at Aldabra Atoll. The plot shows the midday low tides and morning and evening high tides. Water level data are from a fixed water level meter at 15 m depth on the west coast of Aldabra Atoll, and readings have been adjusted to mean sea level.

5.4.2 Effects of tide

5.4.2.1 Species richness, diversity and abundance

A total of 274 species was recorded in this chapter. Significantly more species of fish were recorded during low tide than high tide in BRUVs and RUVs (univariate permutational ANOVA, BRUVs: $F = 3.59$, $\text{Pr}(> F) < 0.05$; RUVs: $F = 3.98$, $\text{Pr}(> F) < 0.05$) (Table 5.3, Table 5.8 and Table 5.9 in the Annex), after accounting for the effects of time of day, depth and other covariates. The mean abundance of fish per sample was significantly (univariate permutational ANOVA $F = 4.41$, $\text{Pr}(< F) < 0.05$) greater during low tide than high tide (Table 5.3 and Annex Table 5.10) in BRUVs. The greater abundance of fish during low tide than high tide in RUVs was marginally significant (univariate permutational ANOVA $F = 3.32$, $\text{Pr}(> F) = 0.061$) (Table 5.3 and Annex Table 5.11). The substantial difference in abundance in RUVs (Table 5.3) was explained by the effect of depth and time of day on the fish assemblage (Annex Table 5.11).

Shannon diversity index was not significantly different between low and high tide in BRUVs (Univariate permutational ANOVA $F = 0.095$, $\text{Pr}(> F) > 0.05$) or in RUVs ($F = 3.88$, $\text{Pr}(> F) =$

0.5), after taking time of day, depth and other covariates into account (Table 5.3 and Annex Table 5.12 and 5.13 for statistical significance values of other covariates).

Table 5.3. Summary of the number of samples, species richness, diversity and abundance of species and fish families recorded during high and low tide in baited and unbaited treatments. (MaxN = Relative abundance, Nsp = Number of species).

Bait treatment	Baited		Unbaited	
	High	Low	High	Low
Number of samples	20	19	22	25
Total number of families	37	40	37	40
Total number of species	195	214	184	208
Number of unique species per tide	28	47	28	52
Mean total Nsp/sample	33.2 ± 5.1	44.2 ± 5.2	27.8±4.5	39.7±4.8
Total MaxN	2 670	4 569	2 269	4 224
Mean total MaxN/sample	133.5 ± 32.9	240.5 ± 46.4	103.1 ± 22.8	169 ± 32
Mean Shannon diversity/sample	3.69 ± 0.2	3.66 ± 0.24	3.42 ± 0.23	3.63 ± 0.17

More unique species were recorded during low tides than high tides (Table 5.3). Generalist carnivore and piscivore species, notably *Aprion virescens*, *Plectropomus punctatus*, *Epinephelus fuscoguttatus* and *Gracila albomarginata*, were recorded during low tide but not high tide in BRUVs. Two species of shark, *Negaprion acutidens* and *Carcharhinus albimarginatus*, were recorded (up to four times) in low tide RUV samples but not during high tide (Annex Table 5.14). All species of shark recorded in BRUVs during the low tide were also recorded during the high tide. *Nemateleotris magnifica* was recorded eight times in RUVS during low tide, and not during high tide.

5.4.2.2 Abundance of fish within trophic guilds between tidal states

In baited treatments, zooplanktivores were significantly more abundant during low tide than high tide (Univariate sequential permutational ANOVA $F = 4.93$, $p < 0.05$) after accounting for differences in depth, time of day (and other covariates – see Annex Table 5.15). The seemingly greater abundance of generalist carnivores during low tide compared to high tide was explained by depth (Univariate sequential permutational ANOVA $F = 4.17$, $p < 0.043$) and not by tide (Figure 5.5a). Invertebrate carnivores, sponge/invertebrate feeders and zooplanktivores were significantly more abundant during low than high tide in unbaited treatments after accounting for differences in depth and time of day (and other covariates – see methods) (Figure 5.5b and Annex Table 5.16 – 5.18).

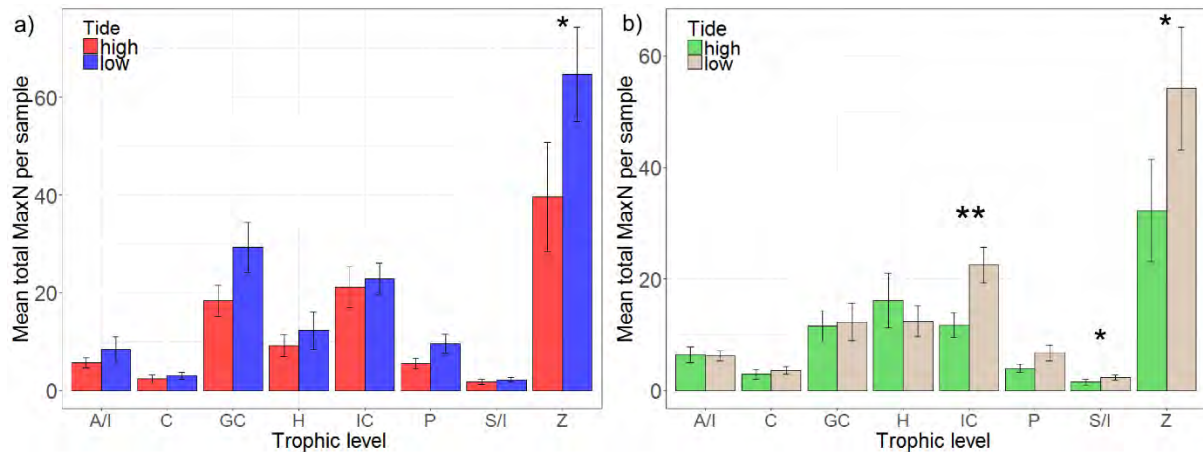


Figure 5.5. Mean total abundance (MaxN) per sample within the respective trophic guilds during high and low tide, for a) baited samples, and b) unbaited samples. Algae/invertebrates (A/I), corallivore (C), generalist carnivore (GC), invertebrate carnivore (IC), piscivore (P), sponge/invertebrates (S/I), zooplanktivore (Z). Univariate PERMANOVA Significance levels tide: < 0.001 = ***; < 0.01 = **; < 0.05 = *.

5.4.3 Effects of tide and time of day on the fish assemblage structure

5.4.3.1 Abundance of fish within trophic guilds

The differences between the mean abundances of fish within the respective trophic guilds (Figure 5.6a) that were explained by the tide and time of day categories were not statistically significant (Univariate sequential permutational ANOVA, $p > 0.05$) in BRUVs.

However, for RUVs, the difference in mean abundance of fish within respective trophic guilds was significantly different between the three tide-and-time-of-day categories for seven of the eight trophic guilds (Univariate sequential permutational ANOVA, $p < 0.05$) (Figure 5.6b). Post-hoc pairwise analysis indicated that invertebrate carnivores were significantly fewer during early morning high tides than midday low tides in RUVs (Pairwise univariate permutational ANOVA Holm adjusted p -value < 0.01). The far lower abundance of zooplanktivores during early morning high tides relative to midday low tides was not statistically significant (Pairwise univariate permutational ANOVA Holm adjusted p -value = 0.07) in RUVs. See Annex **Table 5.19** – Annex Table 5.33 for Univariate permutational ANOVA and post-hoc pairwise PERMANOVA results for each trophic group which had significant results.

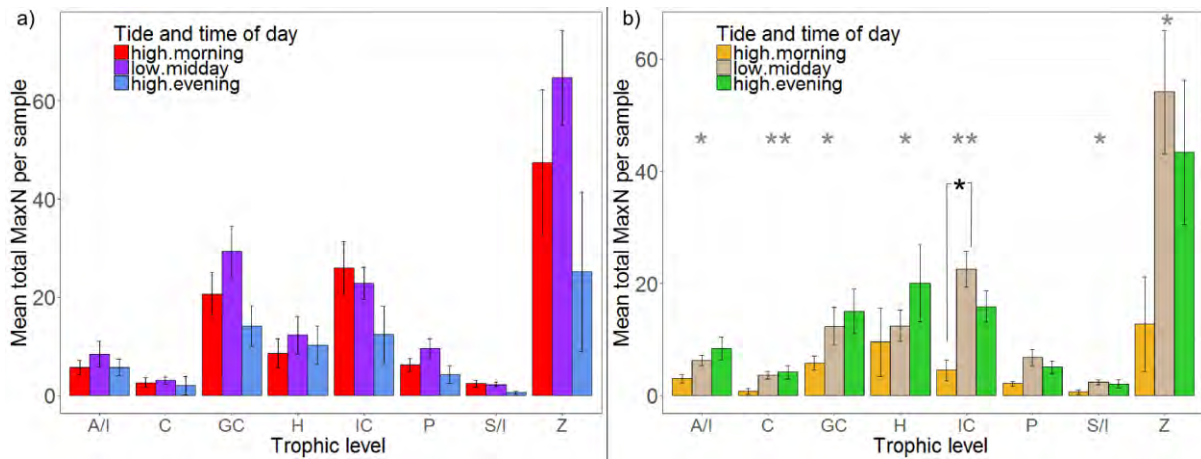


Figure 5.6. Means of total relative abundance (MaxN) per sample within the respective trophic guilds during four times of day, for a) baited samples, and b) unbaited samples. Algae/invertebrates (A/I), corallivore (C), generalist carnivore (GC), invertebrate carnivore (IC), piscivore (P), sponge/invertebrates (S/I), zooplanktivore (Z). Univariate PERMANOVA across all three categories (grey), Pairwise Univariate PERMANOVA between pairs of categories (black with lines) Significance levels tide: < 0.001 = ***; < 0.01 = **; < 0.05 = *; = 0.05.

5.4.3.2 Effects of tide and time of day: Baited species assemblage structure

The results from the distance based redundancy analysis (dbRDA) of the BRUVs data showed that depth explained the largest proportion of variation in the observed fish assemblage structure (Table 5.4). Time of day and tide did not significantly alter the structure of fish assemblages, but the effect of the interaction of depth and time of day on the assemblage was marginally non-significant (Table 5.4). Tide still did not significantly affect the fish assemblage structure in BRUVs when the tide was accounted for in dbRDA models prior to the time of day (Annex Table 5.35).

Table 5.4. Permutational ANOVA of distance based redundancy analysis (dbRDA) of baited remote underwater video systems (BRUVs) data showing the significance of the effects of explanatory variables on the fish assemblage structure.

Covariate	Degrees freedom	Sum of Squares	F	Pr(>F)
Visible area	1	1.0165	1.8018	0.019*
Depth	1	0.7312	1.2961	0.0016**
Time of day	1	0.8204	1.4542	0.1194
Tide	1	0.8385	1.4863	0.0648
Depth:Time of day	1	0.8045	1.426	0.0548
Depth:Tide	32	18.0525	1.8018	0.08
Residual	1	1.0165		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

The grouping of points in the dbRDA plot of the BRUVs data indicated that the observed fish assemblage structure was similar during the same tide and time of day (Figure 5.7).

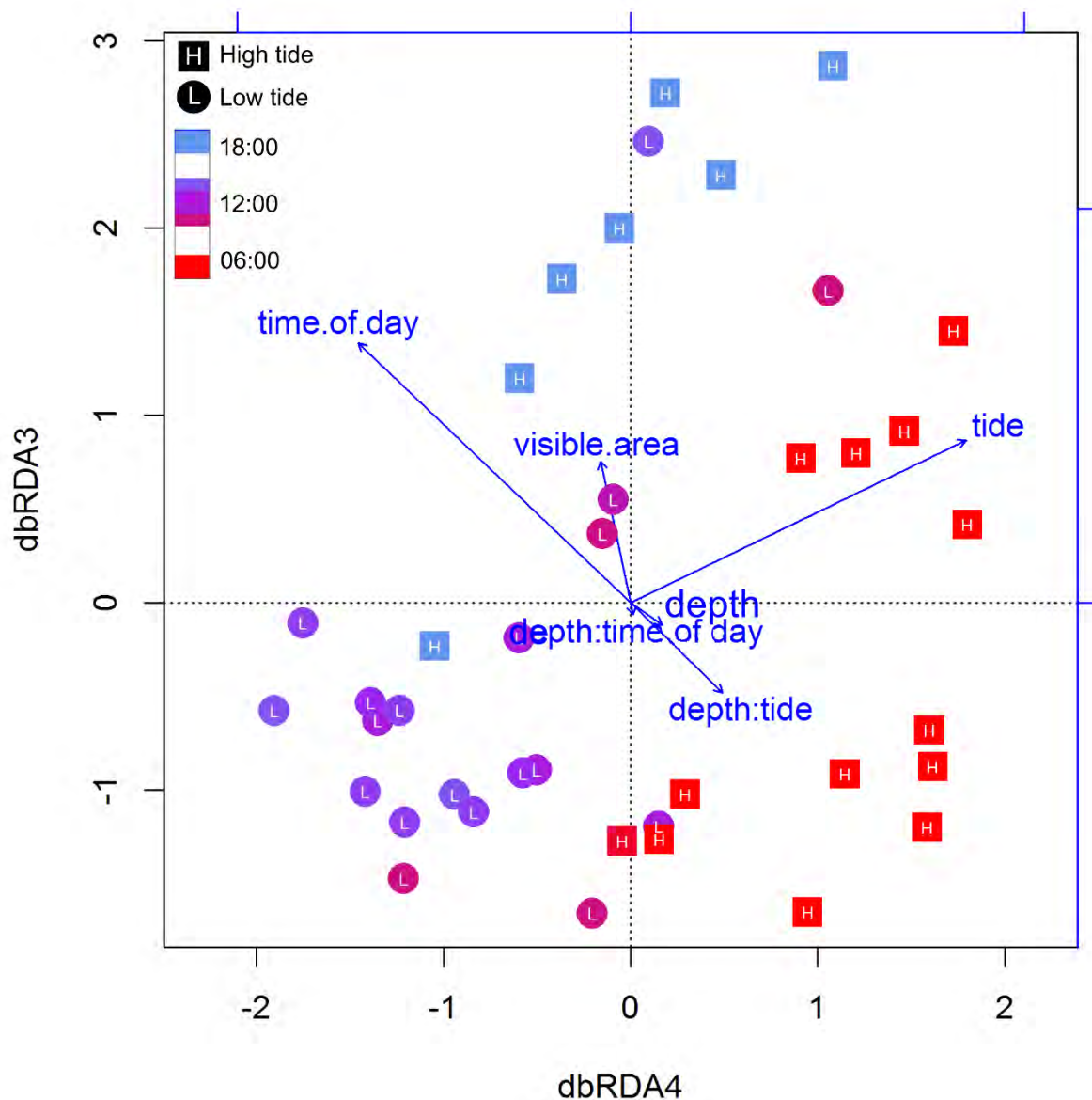


Figure 5.7. Constrained ordination plot of distance based Redundancy Analysis (dbRDA) from Baited Remote Underwater Video systems (BRUVs), showing the grouping according to tide and time of day. The x-axis shows maximum dissimilarity for the tide, and the y-axis shows maximum dissimilarity over time of day.

The eight species that contributed the most to differences in assemblage structure in relation to tide and time of day are shown in Figure 5.8. *Lepidozygus tapeinosmoa*, *Halichoeres hortulans*, *Labroides bicolor*, *Thalassoma amblycephalum* and *Odonus niger* were more abundant during the low tides than high tides. *Melichthys niger* was more abundant from the early morning and midday than during the early evening. *Bodianus bilunulatus* and

Parupeneus macronemus were more abundant during early morning high tides than midday low tides or evening high tides (Figure 5.8).

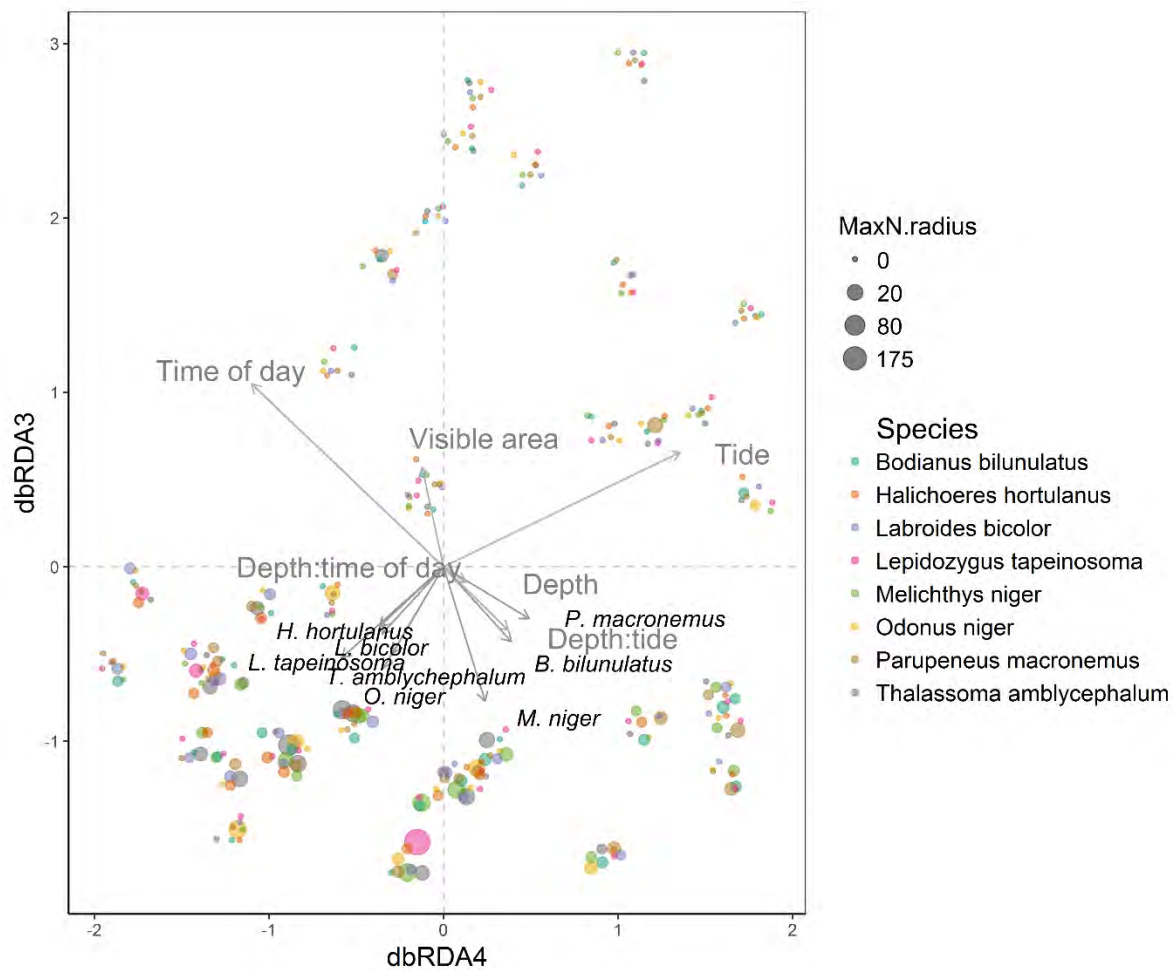


Figure 5.8. The relative abundance (MaxN) of the eight species which increased most rapidly with the direction in which tide and time of day change in the ordination plot. Length of arrows represents the direction in ordination space in which the covariates and species were increasing most rapidly. Bubble size (MaxN.radius) indicates the relative abundances of the eight species of fish

5.4.3.3 Effects of tide and time of day: Unbaited species assemblage structure

Results from dbRDA analysis of the RUVs data indicated that time of day and depth significantly altered the fish assemblage structure (Table 5.5). Depth was the most important variable structuring unbaited fish assemblages (Table 5.5). The tide did not have a significant effect on fish assemblage structure, nor did the interaction of depth with water level, or depth with the time of day (Table 5.5). The visible area in the field of view also significantly explained differences in observed fish assemblage structure among the samples (Table 5.5). The effect of the tide was statistically significant ($\text{Pr}(>F) = 0.428$) on the fish

assemblage structure when incorporating it into the dbRDA model prior to the time of day (Annex Table 5.36).

Table 5.5. Permutational ANOVA of dbRDA of reef fish assemblage structure recorded using remote underwater video systems (RUVs) on the west coast of Aldabra.

	Degrees freedom	Sum of Squares	F	Pr(>F)
Visible area	1	1.0204	1.8494	0.0216*
Wave energy	1	0.6901	1.2508	0.1594
Depth	1	1.736	3.1464	0.0002***
Time of day	1	1.4243	2.5814	0.0028**
Tide	1	0.8388	1.5203	0.064
Depth:Time of day	1	0.3628	0.6576	0.9462
Depth:Tide	1	0.6687	1.212	0.195
Residual	39	21.5182		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

The spatial grouping of points in the dbRDA plot indicated that in the unbaited samples, the fish assemblage structure was more similar to assemblages recorded during the same tide and time of day, than to assemblages that were recorded during different tides and time of day in unbaited samples (Figure 5.9).

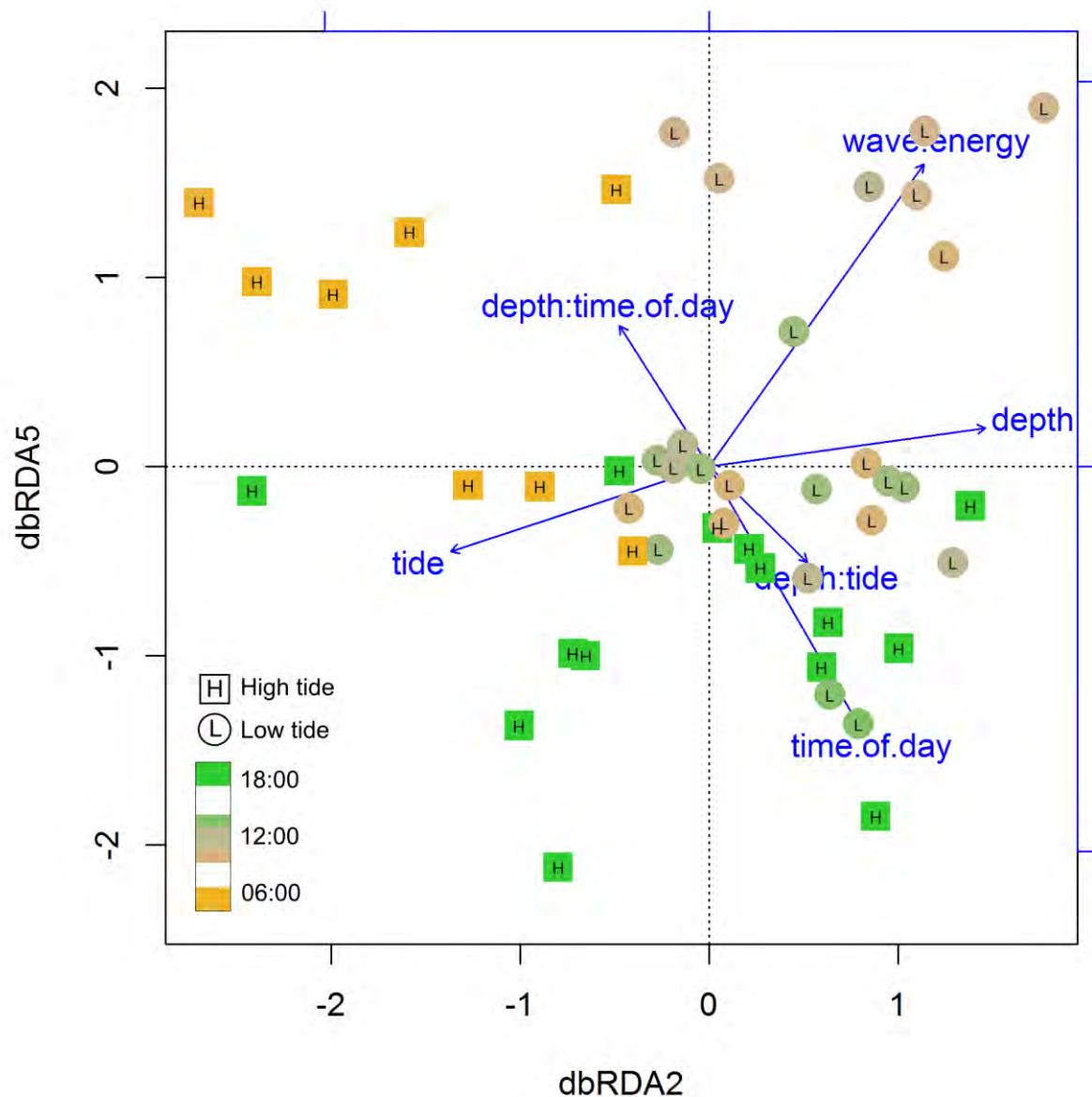


Figure 5.9. Constrained ordination plot of distance based Redundancy Analysis (dbRDA) results of variation in the fish assemblage structure observed using Remote Underwater Video systems (RUVs) data. The x-axis shows maximum dissimilarity of assemblages according to the tide, and the y-axis shows maximum dissimilarity according to the time of day. The vectors (lines with arrows) indicate the relative contribution to and the direction in which covariates change along the displayed ordination axes.

Pseudanthias squamipinnis and *Odonus niger* were more abundant during midday low tides than morning or evening high tides (Figure 5.10). *Acanthurus triostegus* and *Chrysiptera brownriggii* were more abundant during morning high tides than midday low tides or evening high tides (Figure 5.10).

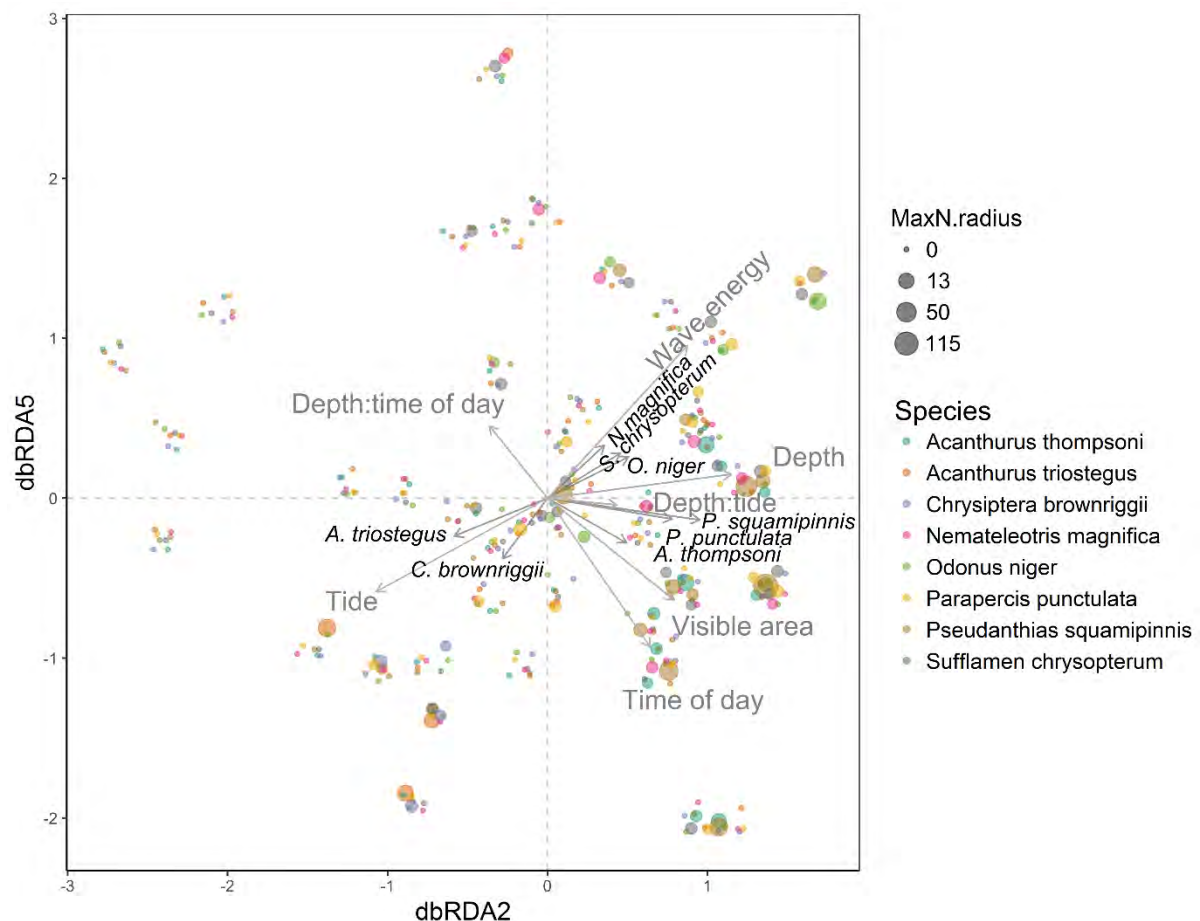


Figure 5.10. The relative abundance (MaxN) of eight species indicated by bubble size in a constrained ordination plot of distance based Redundancy Analysis (dbRDA) of RUVs data. The size of each point is scaled relative to the raw abundance of the species in each sample. Vectors represent the relative contribution to differences in the assemblage structure of the covariates and eight species. Length of arrows represents the direction in ordination space in which a covariate or species was most rapidly increasing.

5.4.3.4 Effects of tide and time of day: Baited trophic assemblage structure

The trophic assemblage structure was not significantly altered by tide or time of day. Neither the interaction between depth and time of day nor the interaction between depth and tide significantly altered the fish assemblage structure (Table 5.6). There was no change in the effect of tide or time of day irrespective of which variable was considered first in the dbRDA sequence (Annex Table 5.37).

Table 5.6. Permutational ANOVA of dbRDA of trophic assemblage from RUVs data showing the significance ($\text{Pr}(> F)$) of explanatory variables.

	Degrees freedom	Sum of Squares	F	$\text{Pr}(> F)$
Visible area	1	1.0017	1.3285	0.191
Depth	1	0.6898	0.9148	0.3916
Time of day	1	0.4831	0.6408	0.785
Tide	1	1.5536	2.0606	0.052
Depth:Time of day	1	0.8137	1.0792	0.2928
Depth:Tide	1	0.5427	0.7198	0.6362
Residual	32	24.1268		

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

The dispersion of ordination points from the dbRDA grouped according to the tide, indicating similarity between trophic assemblages observed during the same tidal state and time of day, but their effects were not statistically significantly different (Figure 5.11 and Table 5.6), although the effect of tide was only marginally non-significant.

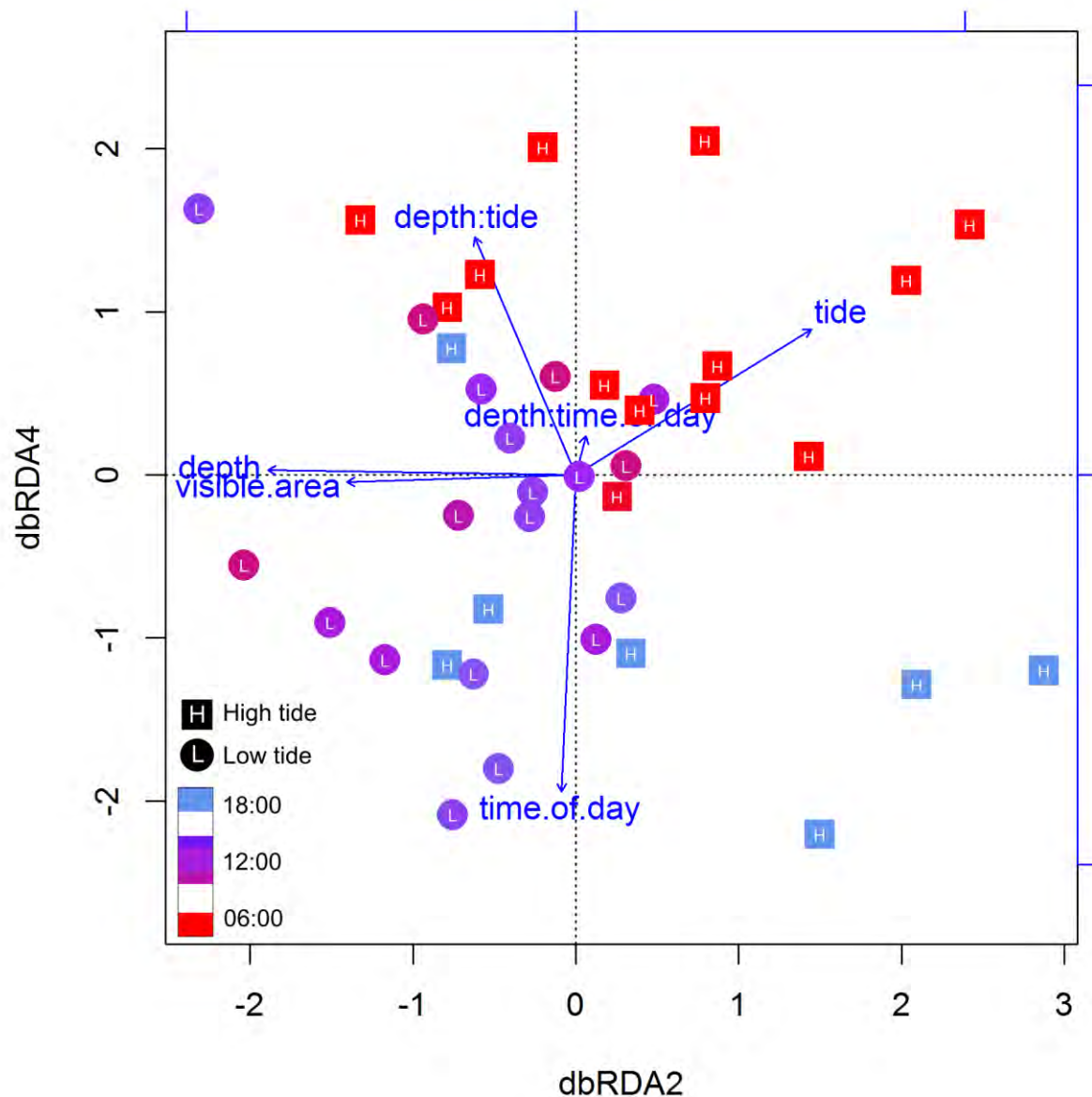


Figure 5.11. Ordination plot of trophic assemblage structure from distance based redundancy analysis (dbRDA) of BRUVs data. The x-axis shows maximum dissimilarity for the tide, and the y-axis shows maximum dissimilarity for the time of day. The vectors (lines with arrows) indicate the relative contribution to and the direction in which covariates change along the displayed ordination axes.

Zooplanktivores and invertebrate carnivores increased most rapidly in the direction of midday low samples in ordination space (Figure 5.12) and were consistent with earlier results from this study which indicated a greater abundance of these trophic guilds during midday low tides (Figure 5.6). Herbivores were most abundant during midday low tide samples. The direction in which herbivores were changing in ordination space in Figure 5.12

appears to be influenced by time of day and tide.

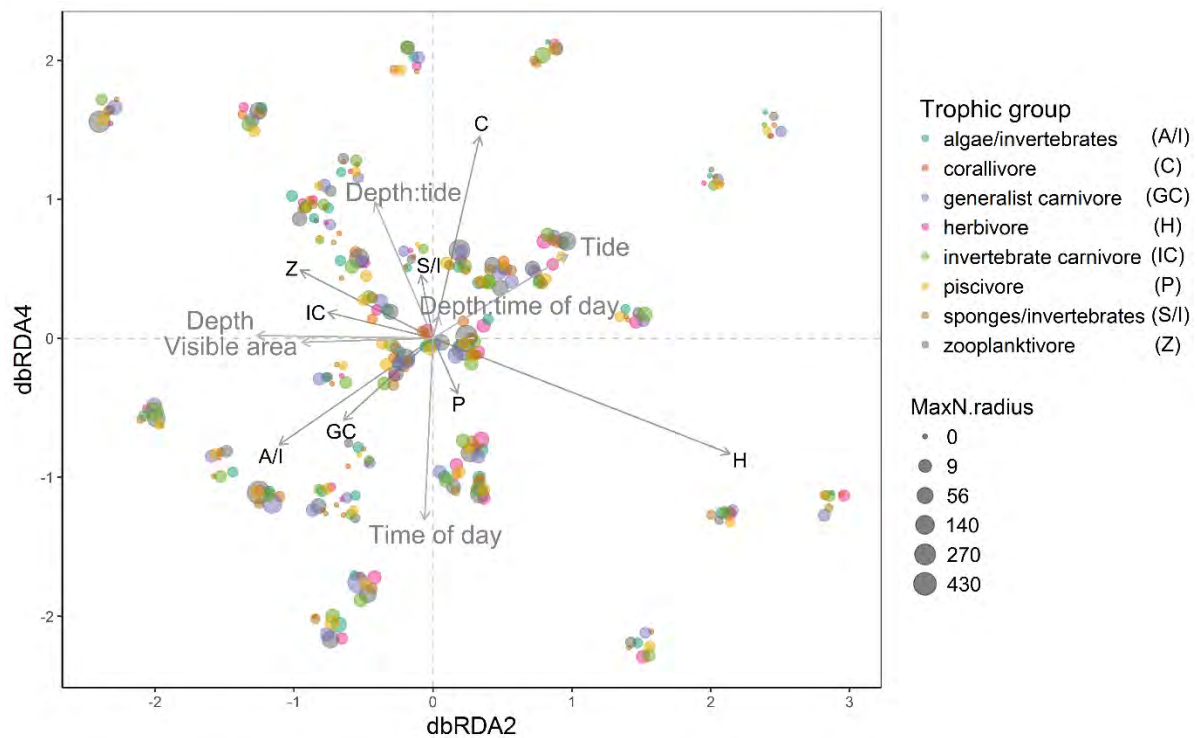


Figure 5.12. The relative abundance (MaxN) of the trophic guilds in baited treatments, represented by the size of points. The locality of points corresponds to approximate site locality in distance based Redundancy Analysis (dbRDA) ordination space. Length of arrows represents the direction in ordination space in which a covariate or trophic group was most rapidly increasing.

5.4.3.5 Effects of tide and time of day: Unbaited trophic assemblage structure

The results from the dbRDA of the RUVs data indicated that time of day and depth caused significant differences in the observed trophic assemblage structure (Table 5.7). The tide, the interaction of depth with the tide, and the interaction of depth with the time of day did not significantly change the structure of trophic level fish assemblages in unbaited samples. The effect of time of day remained significant even when the tide was considered prior to the time of day in the dbRDA analysis (Annex Table 5.38).

Table 5.7. Permutational ANOVA of distance based redundancy analysis (dbRDA) showing the significance of time of day and tide in explaining the observed variation in the unbaited trophic assemblage structure after accounting for sequentially loaded covariates.

	Degrees freedom	Sum of Squares	F	Pr(>F)
Visible area	1	1.157	1.28	0.189
Wave energy	1	1.025	1.1343	0.2612
Depth	1	3.778	4.1796	0.0018**
Time of day	1	3.416	3.7788	0.0032**
Tide	1	1.382	1.529	0.1206

Depth:Time of day	1	0.636	0.7036	0.685
Depth:Tide	1	0.65	0.7191	0.6668
Residual	39	35.251		

*Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = **

The dispersion of points in the dbRDA plot indicated the effect of time of day on the assemblage structure. Trophic assemblages were most similar in their structure to assemblages sampled during similar times of day (Figure 5.13). The dispersion of the points in relation to the directional line indicating an increase in tide (water level) was evident, but differences were not statistically significant (Figure 5.13 and Table 5.7).

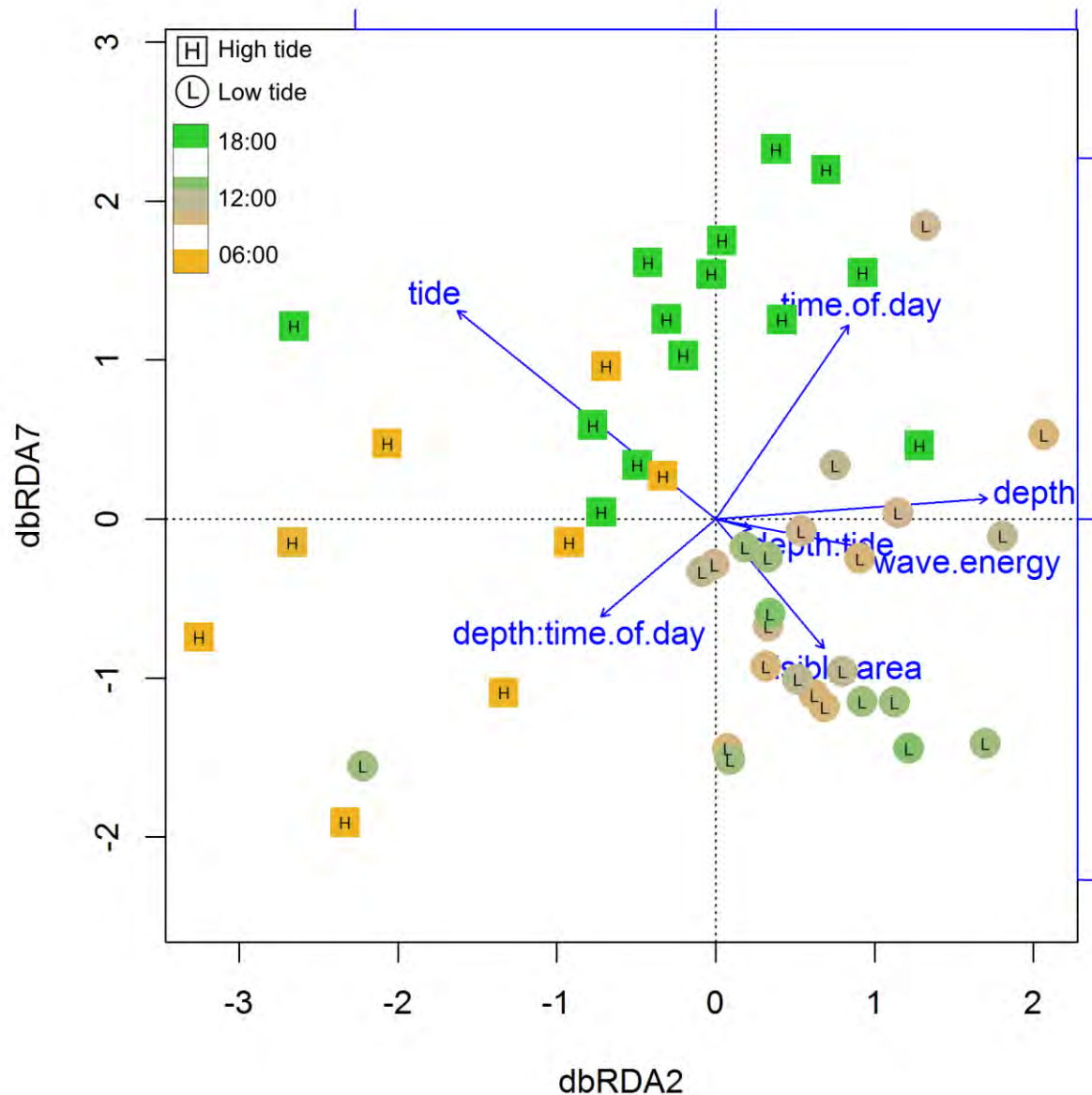


Figure 5.13. Ordination plot of unbaited trophic assemblages based on distance based redundancy analysis (dbRDA), showing the grouping according to tide and time of day. The x-axis shows maximum dissimilarity in assemblage structure owing to the tide, and the y-axis shows maximum dissimilarity owing time of day. The vector lines indicate the relative contribution to the difference in the assemblage structure and the direction in ordination space in which the covariates change.

Zooplanktivores and invertebrate carnivores increased most rapidly in the direction of midday low tides, while herbivores increased most rapidly in the direction of evening high tides in ordination space (Figure 5.13). The directional increase of these three trophic guilds in relation to the time of day and tide were consistent with the results showing the difference in abundance of trophic groups between three categories of tide and time of day (Figure 5.6). Corallivores, algae/invertebrate feeders and sponge/invertebrate feeders increased

most rapidly with an increase in time of day, which was consistent with times when these trophic guilds were most abundant (Figure 5.6).

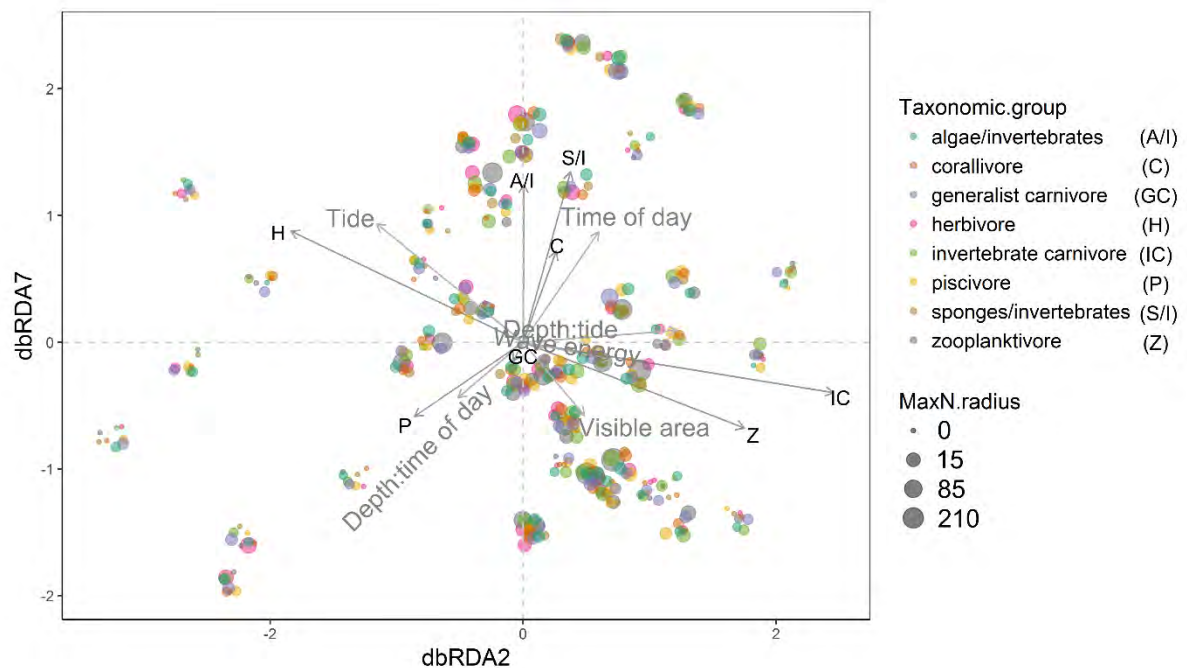


Figure 5.14. The relative abundance (MaxN) of the trophic guilds in unbaited treatments, represented by the size of points in a bubble plot. The locality of points corresponds to approximate site locality in dbRDA ordination space. Length of arrows represents the direction in ordination space in which covariates and trophic guilds were most rapidly increasing.

5.5. DISCUSSION

The results of this study provide an understanding of the change of the fish assemblage in response to a cyclical change in tide and time of day which has important implications for standardising experimental design, accurate interpretation of data on fish assemblages, and to identify important habitat to inform site management (Gibson 2003; Krumme 2009; Bijoux et al. 2013). In this study, it was shown that tide, time of day and depth influenced species richness, abundance and species and trophic assemblage structure observed using BRUVs and RUVs, but the two methods were affected differently making the respective methods suitable for different purposes.

The sampling design used in this study did not allow separating the effects of tide and time of day because all low tide samples were collected at approximately midday as a result of the cyclical nature of tides limiting spring low tides to the middle of the day during daytime. The lack of nighttime-low tide samples precluded the ability to investigate the effects of time of day and consequently only the results from the three combinations of tide and times of day were used to draw conclusions from. The assessment of the effect of the two categories of tide on the fish assemblage (without accounting for the effects of time of day) is discussed, but should be interpreted with care.

5.5.1 Species richness, diversity and abundance at high and low tide

Significantly more fish and a greater species richness were recorded during low tide than during high tide in RUVs and BRUVs. Previous studies have indicated that the movement of fish between habitat, including mangrove, seagrass and coral reefs, during tidal and diel cycles allows fish to access different habitats and maximise foraging while minimising the risk of predation, and this has been suggested as a contributing factor in differences of species richness and assemblage structure (Gibson 2003; Unsworth et al. 2007; Appeldoorn et al. 2009; Krumme et al. 2015; Kruse et al. 2016).

The greater abundance and species richness observed in RUVs and BRUVs during low tide may have been caused by an influx of fish that use Aldabra's large shallow inner atoll lagoon (155 km²) and the outer lagoon reef flats (19 km²) during high tide, and then move out and onto the forereef slope and reef apron during low tide to avoid becoming stranded (Price 1971; Stoddart et al. 1971; Stevens 1984). To test this hypothesis the fish assemblages in the shallow lagoon requires further investigation during spring high and low tides. Another explanation for the greater abundance and species richness during (midday) low tides than high tides could be attributed to a change in fish activity over the course of the day. Remote

Underwater Video systems (RUVs) and BRUVs that were deployed during the early morning (deployment time range 06:30 – 07:39) and early evening (deployment time range 17:00 – 18:40) recorded fish assemblages during the diurnal and “quiet” twilight hours when fish change over from daytime to night-time assemblages. The full complement of diurnal fish may not yet have emerged during the transition between diurnal and the “quiet” twilight hours, when fish are moving between different habitats for feeding and sheltering (Hobson 1972, 1973; Helfman 1986; Rickel and Genin 2005). At the same time, midday low tides were sampled between 09:30 and 14:30 when diurnal fish are actively feeding (Hobson 1972, 1973; Helfman 1986; Rickel and Genin 2005). The combination of species entering the reef slopes and reef apron around the low tide and more diurnal species being present and abundant during the middle of the day may therefore drives the differences in assemblage structure observed.

Depth was the most important covariate explaining fish assemblage structure in BRUVs and RUVs, and was consistent with previous studies that have shown the importance of depth as a critical explanatory variable of fish assemblage structure (Bell 1983; Roberts and Ormond 1987; Friedlander and Parrish 1998; Brokovich et al. 2008). Depth explained more of the variation in fish assemblage structure than tide or time of day. The lack of a significant interaction between depth and tide or depth and time of day indicated that the effects of tide and time of day did not affect the fish assemblage differently across the depth range sampled in this study.

5.5.2 Assemblage structure in three categories of tide and time of day

The distance based redundancy analysis (dbRDA) results indicated that the effect of tide on the fish assemblage structure was not significant in RUVs or BRUVs. However, in RUVs, the effects of tide on the species and trophic assemblage structure estimated by permutational ANOVA of dbRDA model were marginally significant and were statistically significant when the effects of time of day were ignored or the effect of the tide was considered before accounting for time of day. This suggests that the effects of tide may alter the fish assemblage structure in RUVs, but that their effects overlap and time of day may mask the effect of the tide. The significant effect of time of day, which remained significant after accounting for the effect of tide suggests that time has a greater effect on the fish assemblage than tide in unbaited RUVs. Sampling only during spring tide does make it difficult to separate their respective effects, as peak high tides overlap with twilight hours in the morning and evening (Krumme 2009). The effect of tide may therefore be masked by the change in fish activity and behaviour during twilight hours. The overlap in the effect of tide

and time of day during spring tides may be disentangled by sampling across the tidal range of the lunar cycle and requires further investigation (Galzin 1987; Kruse et al. 2016).

Time of day significantly altered species and trophic assemblage structure in RUVs in this study and this was consistent with previous studies using RUVs and other unbaited methods that were carried out in a variety of habitats including coral reef, seagrass, mangrove and sandy shore habitats, including temperate and tropical reefs (Lee et al. 2014; Castellanos-Galindo and Krumme 2015; Krumme et al. 2015; Kruse et al. 2016; Mallet et al. 2016; Myers et al. 2016). The results from my study provide evidence that RUVS were sensitive to the effects of time of day on the fish assemblage when sampling from twilight in the morning throughout the day to twilight in the evening. The results imply that RUVs require standardisation according to the time of day, or an avoidance of sampling fish assemblages during the overlap of twilight and diurnal hours.

Neither the effect of tide or time of day had a significant effect on the species and trophic assemblage structure observed in BRUVs. The non-significant effect of tide and time of day on the assemble structure was consistent with the results of a previous study in an estuarine system sampled using BRUVs (Taylor et al. 2013). The results were not consistent with a study using BRUVs which found that diurnal temperate reef fish assemblages changed with time of day even when not sampling during crepuscular hours (08h00 – 16h00) (Birt et al. 2012). The presence of bait has been shown to influence the fish assemblage structure by increasing the abundance and diversity of generalist carnivores and invertebrate carnivores in previous studies (Watson 2005; Harvey et al. 2007; Dorman et al. 2012) and reducing the abundance and diversity of herbivores and corallivores (Chapter 4). The results of my study suggest that the presence of bait interferes with the cyclical effects of tide and time of day on the fish assemblage. Bait alters the natural fish assemblage by attracting or discouraging fish species from the baited area (Burrows et al. 1994) and consequently hinders the detection of temporal differences in the fish assemblage when using BRUVs (Birt et al. 2012; Myers et al. 2016). BRUVs were therefore robust against the effects of tide and time of day on the fish assemblage structure – a conclusion that is supported by a previous study that indicated that BRUVs do not require standardization to a particular time of day, as hourly temporal variation of the fish assemblage was relatively homogenous (Myers et al. 2016). This suggests that one area could be sampled in the morning and another in the afternoon, and comparisons between these sites will be valid. Remote Underwater Video systems (RUVs) on the other hand will require samples to be recorded on the same tides and times of day to make valid comparisons among fish assemblages.

5.5.3 Trophic assemblage structure response to tide and time of day

The significant effect of time of day on the trophic assemblage structure was supported by the second analysis in this study, which indicated significant differences in abundance within trophic guilds between three categories of tide and time of day observed in RUVs (but not in BRUVs).

Univariate PERMANOVA results found a significantly greater abundance of zooplanktivores during midday (low tide) compared to the morning or evening (high tide). The latest time point sampled in my study terminated during twilight hours (18:40), and therefore prior to the evening rise of zooplankton and the emergence of nocturnal zooplanktivores which typically peaks 2-hours after sunset time (Ohlhorst 1982; Rickel and Genin 2005; Thalma 2015). The greater abundance of zooplanktivores observed in my study during midday relative to morning and evening, may have been caused by morning and evening sampling times overlapping with the onset or conclusion of the quiet period when the transition between nocturnal and diurnal species take place (Hobson 1973; Helfman 1986; Rickel and Genin 2005). For example, the greater abundance of a diurnal zooplanktivore, *Pseudanthias squamipinnis*, during the midday compared to the morning or evening was consistent with the results from a previous study that showed peak activity of this species during daytime hours with marked lower activity during twilight hours (Rickel and Genin 2005).

While tide and time of day had a significant effect on the abundance of most trophic guilds in RUVs, the tide only had a significant effect on the abundance of invertebrate carnivores, sponge/invertebrate feeders and zooplanktivores, after accounting for the effect of time of day. The greater abundance of invertebrate carnivores observed during low tides than high tides may be caused by an influx of invertebrate carnivores, e.g. *Sufflamen chrysopterum*, from the lagoon reef onto the forereef slope and reef apron during spring low tide in RUVs. The lagoon and outer lagoon reef are dominated by sand, seagrass and macro-algal communities, which are rich in benthic invertebrates (Price 1971; Taylor 1971; Hamylton et al. 2012b) and therefore offer suitable feeding opportunities to invertebrate carnivores (among others) during high tide. Following the favourable feeding conditions made available by the high tide, fish are forced to leave the sandy lagoon and outer lagoon reef flats as much of the lagoon runs dry during spring low tide (Price 1971; Stoddart et al. 1971; Stevens 1984). If invertebrate carnivores do make use of this resource, it may explain the significant effect of tides on their abundance. To test this hypothesis, the trophic assemblage in Aldabra's lagoon and reef flats require further investigation.

The reasons for concurrent peak abundance during evening high tide of algae/invertebrate feeders, corallivores, herbivores, and generalist carnivores are not fully understood. The greater abundance of potential prey (algae/invertebrate feeders, corallivores and herbivores) species may drive an increase in generalist carnivores with increased feeding opportunities (Anderson 2001b). Piscivores however, unlike generalist carnivores, did not increase during evening high tides when prey availability was greater. The lack of an increase in piscivores during evening high tides when taxonomic richness of prey was greatest was consistent with a previous study that found no temporal relationship between piscivore abundance and taxonomic richness in samples (Mallet et al. 2016). It is also unclear why algae/invertebrate feeders, herbivore and corallivore abundances were greatest during the evening high tide when predation risk is greatest (Helfman 1986). Species richness of herbivore/detritivores were also higher in a previous study assessing diurnal temporal variation of fish assemblages using RUVs (Mallet et al. 2016). A decrease in food availability with continuous grazing throughout the day could result in a wider search effort in herbivores, and lead to an increase in the observed abundance, but this theory is not supported by previous studies that found that herbivores display a wider search effort during the morning in search of particular algal types prior to depletion (Tricas 1989; Reyes-Bonilla and Calderon-Aguilera 1999; Khait et al. 2013). Easy detection of predatory species during clear-water conditions with the incoming evening high tide may facilitate greater feeding activity in potential prey guilds, and easier observation in RUVs, but there was no evidence for a correlation between the visibility (used to calculate visible area) and time of day. Previous studies have indicated that interspecies variability in response to tide and diel exist within trophic guilds. For example, different predatory species were more abundant in a mangrove creek during high while others were more common during low tide, and others still were more abundant during the evening high tides (Harborne et al. 2016).

5.5.4 Future direction and study limitations

In my study, time of day was limited to daylight hours and data were collected only around spring high and low tide during the northwest monsoon months. The fish assemblages at Aldabra are likely to undergo further temporal changes in assemblage structure during night time, and over the lunar cycle, and with a change in the seasonal monsoons, as has been reported in previous studies (Helfman 1986; Ribeiro et al. 2006; Meyer et al. 2007a, 2007b; Krumme et al. 2008; Mallet et al. 2016; Myers et al. 2016; Viehman and Zydlewski 2017). Not including temporal fluctuations when assessing fish community may underestimate the actual diversity and complexity of fish assemblages, and miss site management opportunities for more appropriate site management (Carpentieri et al. 2005; Harvey et al.

2012a). Sampling across the tide range is required to address the crucial limitation of my study which precluded meaningful conclusions to be drawn on the independent effects of tide and time of day. Further sampling should be carried out across the tidal cycle, particularly during nighttime on a spring tide, to disentangle the effects of tide and time of day. The effects of seasonal, lunar and nocturnal variation of the fish assemblage could be investigated near to the safe and calm conditions in the lee of Aldabra, which would provide a more holistic understanding of the temporal variation in the of the fish assemblage.

The second component of the tide, the enhanced tidal current caused by the additional flow of water did not significantly alter the fish assemblage structure on any of the taxonomic levels, in both RUVs and BRUVS, and consequently was removed from the analysis. The lack of consistency with previous studies (Heagney et al. 2007; Meyer et al. 2007a; Taylor et al. 2013), which indicated a significant effect of Selective Tidal Stream Transport (STST), may be because the simplified enhanced tidal stream model did not sufficiently capture the differences in the STST. The simplified model used to predict enhanced tidal stream in this study did not take into account the effect of friction by topography and structural complexity on the resulting tidal current and may consequently have been too inaccurate to produce a reliable estimate of the difference in current experienced at sampling sites. Collecting *in situ* current speed data during sampling may therefore be used to improve our understanding of the effect of current speed, and variability of tidally induced stream flows on the observed fish assemblage (Heagney et al. 2007).

The effect of tide may vary with depth and future research should consider a comparison of the changes observed between different depths. Furthermore, an understanding the composition of fish on the inner and outer lagoon reefs will be informative to better understand the role of fish movement between the lagoon reefs and the outer reefs with tide.

During spring tide at Aldabra, much of the shallow lagoon reef runs dry, leaving behind unsampled shallow-water habitat, including rock pools, seagrass blowouts and subtidal depressions. Species remaining in such habitats during spring low tides require further investigation to better understand the effect of the tide, and the role that these habitats must play as refuge or nurseries for fish at Aldabra. Innovative approaches like using flat-bottom boats or kayaks might be able to access parts of the shallow lagoon reef and need to be explored, as access to these habitats was not possible using the outboard vessels at Aldabra.

Studies investigating the effect of tidal and diel cycles on fish movement have suggested a phylogenetic signal in fish families, with vagile fish showing the greatest response to a

change in tide and time of day (Castellanos-Galindo and Krumme 2015; Kruse et al. 2016). A species-by-species analysis of mobility and home range size in response to changes in tide and time of day may improve our understanding of the behavioural traits that underpins natural changes in assemblage structure and need to be considered when planning surveys, and interpreting survey data (e.g. Meyer et al. 2007a, 2007b).

5.5.5 Conclusion

In this study, it was shown that time of day and tide governed the fish assemblage structure, species richness and abundance, but it was only detected when using RUVs. In contrast, the insensitivity of BRUVs to the effects of tide and time of day provides an insight into drivers of the differences between observed fish assemblages sampled using RUVs and BRUVs (as found in Chapter 4). The significant effects of time of day or tidal phase on the fish assemblage structure observed using RUVs provides evidence that this method is more appropriate than BRUVs to detect short-term cyclical changes caused by tide and time of day, making it RUVs a more suitable sampling method to study fish assemblages in relation to oceanographic variables. The insensitivity of BRUVs sampling method to variations in the fish assemblages caused by time and tide suggests that the method is robust to assess fish assemblage structure without the need to standardise surveys according to these short-term cyclical changes, but with the caveat that the observed fish are a bait-influenced representation of the fish assemblage that may be insensitive to the effects of oceanographic conditions and may under-sample certain trophic groups (as identified in chapter 4).

5.6. ANNEX ~ CHAPTER 5

Table 5.8. Univariate permutational ANOVA of species richness (Nsp) obtained from BRUVs between tidal states, after accounting for time of day, depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.12509	1.3546	0.2558
Depth	1	0.06109	0.6615	0.4848
Time of day	1	0.04579	0.4959	0.5502
Tide	1	0.33142	3.5891	0.0452*
Depth:Time of day	1	0.33778	3.6579	0.0462*
Depth:Tide	1	0.16908	1.831	0.1732
Residual	32	2.95492		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.9. Univariate permutational ANOVA of species richness (Nsp) from RUVs data between tidal states, after accounting for time of day, depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.1584	1.9187	0.1574
Wave energy	1	0.2032	2.462	0.109
Depth	1	0.7327	8.8782	0.0022**
Time of day	1	0.9706	11.7599	0.0008***
Tide	1	0.3288	3.9834	0.0376*
Depth:Time of day	1	0.0261	0.3166	0.6584
Depth:Tide	1	0.0516	0.6252	0.4824
Residual	39	3.2188		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.10. Univariate permutational ANOVA of relative abundance (MaxN) obtained from BRUVs between tidal states, after accounting for time of day, depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.09755	1.3698	0.2428
Depth	1	0.01665	0.2338	0.7372
Time of day	1	0.00162	0.0227	0.9782
Tide	1	0.31408	4.4103	0.0348*
Depth:Time of day	1	0.17082	2.3987	0.1148
Depth:Tide	1	0.01874	0.2632	0.7104
Residual	32	2.27886		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.11. Univariate permutational ANOVA of relative abundance (MaxN) from RUVs data between tidal states, after accounting for time of day, depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)

Visible area	1	0.09006	1.445	0.2218
Wave energy	1	0.05742	0.9214	0.3528
Depth	1	0.52506	8.4249	0.0028**
Time of day	1	0.50936	8.1729	0.0044**
Tide	1	0.20694	3.3204	0.061
Depth:Time of day	1	0.00392	0.0629	0.916
Depth:Tide	1	0.02179	0.3497	0.6392
Residual	39	2.43058		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.12. Univariate permutational ANOVA of Shannon-Wiener diversity index obtained from BRUVs between tidal states, after accounting for time of day, depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.095	0.1102	0.7408
Depth	1	1.8076	2.0954	0.1558
Time of day	1	0.3159	0.3661	0.551
Tide	1	0.0082	0.0095	0.9186
Depth:Time of day	1	3.8691	4.4852	0.0462 *
Depth:Tide	1	0.5016	0.5815	0.4564
Residual	32	27.6047		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.13. Univariate permutational ANOVA of Shannon-Wiener diversity index obtained from RUVs between tidal states, after accounting for time of day, depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	3.1064	4.5562	0.036
Wave energy	1	1.3077	1.918	0.182
Depth	1	1.5454	2.2666	0.1354
Time of day	1	8.256	12.1094	0.0018**
Tide	1	0.8481	1.2439	0.268
Depth:Time of day	1	0.232	0.3404	0.5702
Depth:Tide	1	0.2862	0.4197	0.5374
Residual	39	26.5898		

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

1 **Table 5.14.** Unique species per tide within respective bait treatments.

Species	Frequency	Species	Frequency	Species	Frequency	Species	Frequency
<i>Chrysiptera brownriggii</i>	5	<i>Aprion virescens</i>	6	<i>Chrysiptera brownriggii</i>	4	<i>Nemateleotris magnifica</i>	8
<i>Acanthurus triostegus</i>	4	<i>Plectropomus punctatus</i>	4	<i>Coris aygula</i>	4	<i>Ctenochaetus binotatus</i>	6
<i>Halichoeres nebulosus</i>	4	<i>Epinephelus fuscoguttatus</i>	4	<i>Halichoeres nebulosus</i>	4	<i>Parupeneus pleurostigma</i>	5
<i>Gymnothorax flavimarginatus</i>	3	<i>Gracila albomarginata</i>	3	<i>Rhinecanthus aculeatus</i>	3	<i>Negaprion acutidens</i>	4
<i>Rhinecanthus rectangulus</i>	3	<i>Macropharyngodon bipartitus</i>	3	<i>Rhinecanthus rectangulus</i>	3	<i>Echeneis naucrates</i>	4
<i>Lethrinus obsoletus</i>	2	<i>Ecsenius bicolor</i>	3	<i>Amanses scopas</i>	2	<i>Carcharhinus albimarginatus</i>	3
<i>Rhinecanthus aculeatus</i>	2	<i>Pseudocoris heteroptera</i>	3	<i>Cheilio inermis</i>	2	<i>Lethrinus rubrioperculatus</i>	3
<i>Lutjanus gibbus</i>	2	<i>Lepidozygus tapeinosoma</i>	3	<i>Lethrinus mahsena</i>	2	<i>Pseudocoris heteroptera</i>	3
<i>Ptereleotris evides</i>	1	<i>Nemanthias carberryi</i>	2	<i>Hyporhamphus affinis</i>	1	<i>Epinephelus lanceolatus</i>	3
<i>Epinephelus lanceolatus</i>	1	<i>Anampses lineatus</i>	2	<i>Plectroglyphidodon dickii</i>	1	<i>Aetobatus narinari</i>	3
<i>Caesio xanthonota</i>	1	<i>Bodianus anthioides</i>	2	<i>Lethrinus xanthochilus</i>	1	<i>Dermatolepis striolata</i>	3
<i>Seriola lalandi</i>	1	<i>Halichoeres scapularis</i>	2	<i>Lutjanus gibbus</i>	1	<i>Bodianus anthioides</i>	2
<i>Myripristis botche</i>	1	<i>Dascyllus trimaculatus</i>	2	<i>Chrysiptera glauca</i>	1	<i>Gymnocranius grandoculis</i>	2
<i>Hemigymnus fasciatus</i>	1	<i>Chaetodon trifascialis</i>	2	<i>Plectroglyphidodon imparipennis</i>	1	<i>Scomberoides lysan</i>	2
<i>Hologymnosus annulatus</i>	1	<i>Calotomus carolinus</i>	2	<i>Pomacentrus trichrourus</i>	1	<i>Acanthurus leucocheilus</i>	2
<i>Chromis atripes</i>	1	<i>Gymnocranius grandoculis</i>	2	<i>Stegastes fasciolatus</i>	1	<i>Cephalopholis miniata</i>	2
<i>Chromis opercularis</i>	1	<i>Albula vulpes</i>	1	<i>Heniochus diphreutes</i>	1	<i>Centropyge acanthops</i>	2
<i>Valenciennesa strigata</i>	1	<i>Lethrinus microdon</i>	1	<i>Chanos chanos</i>	1	<i>Halichoeres zeylonicus</i>	2
<i>Novaculichthys taeniourus</i>	1	<i>Caesio lunaris</i>	1	<i>Plectorhinchus plagiodesmus</i>	1	<i>Rhinecanthus cinereus</i>	1
<i>Arothron meleagris</i>	1	<i>Chaetodon mitratus</i>	1	<i>Carcharhinus leucas</i>	1	<i>Caranx lugubris</i>	1
<i>Ostorhinchus angustatus</i>	1	<i>Diagramma centurio</i>	1	<i>Pomacanthus chrysurus</i>	1	<i>Lethrinus variegatus</i>	1
<i>Acanthurus leucocheilus</i>	1	<i>Bodianus opercularis</i>	1	<i>Dasyatis brevicaudata</i>	1	<i>Manta alfredi</i>	1
<i>Gunnelichthys curiosus</i>	1	<i>Halichoeres leucoxanthus</i>	1	<i>Thalassoma purpureum</i>	1	<i>Epinephelus malabaricus</i>	1
<i>Chaetodon lineolatus</i>	1	<i>Paracaesio sordida</i>	1	<i>Ptereleotris zebra</i>	1	<i>Pseudanthias evansi</i>	1
<i>Naso tuberosus</i>	1	<i>Cephalopholis hemistiktos</i>	1	<i>Trachinotus blochii</i>	1	<i>Heniochus acuminatus</i>	1
<i>Cheilio inermis</i>	1	<i>Epinephelus gabriellae</i>	1	<i>Chromis atripes</i>	1	<i>Gnathodentex aureolineatus</i>	1
<i>Thalassoma purpureum</i>	1	<i>Carcharhinus leucas</i>	1	<i>Gymnosarda unicolor</i>	1	<i>Canthigaster tyleri</i>	1
<i>Echidna nebulosa</i>	1	<i>Acanthurus dussumieri</i>	1	<i>Acanthurus lineatus</i>	1	<i>Chaetodon interruptus</i>	1
		<i>Siganus sutor</i>	1			<i>Ostracion cubicus</i>	1
		<i>Plectorhinchus paulayi</i>	1			<i>Caesio xanthonota</i>	1
		<i>Plectorhinchus vittatus</i>	1			<i>Elagatis bipinnulatus</i>	1
		<i>Elagatis bipinnulatus</i>	1			<i>Chaetodon bennetti</i>	1
		<i>Coris cuvieri</i>	1			<i>Plectorhinchus gaterinus</i>	1
		<i>Sphyrna putnamae</i>	1			<i>Thalassoma lunare</i>	1
		<i>Pseudanthias evansi</i>	1			<i>Lutjanus fulvus</i>	1
						<i>Pomacanthus semicirculatus</i>	1
		<i>Scarus psittacus</i>	1				

<i>Synodus variegatus</i>	1	<i>Atherinomorus lacunosus</i>	1
<i>Synodus jaculum</i>	1	<i>Cephalopholis urodeta</i>	1
<i>Mugil cephalus</i>	1	<i>Naso vlamingii</i>	1
<i>Cephalopholis sonnerati</i>	1	<i>Aspidontus dussumieri</i>	1
<i>Naso vlamingii</i>	1	<i>Epinephelus polyphekadion</i>	1
<i>Epinephelus malabaricus</i>	1	<i>Arothron mappa</i>	1
<i>Acanthurus lineatus</i>	1	<i>Gunnelichthys monostigma</i>	1
<i>Naso brachycentron</i>	1	<i>Gunnelichthys curiosus</i>	1
		<i>Oxymonacanthus</i>	
<i>Naso fageni</i>	1	<i>longirostris</i>	1
<i>Lethrinus lentjan</i>	1	<i>Pomacentrus indicus</i>	1
		<i>Epinephelus</i>	
<i>Manta alfredi</i>	1	<i>coeruleopunctatus</i>	1
		<i>Anampses lineatus</i>	1
		<i>Arothron immaculatus</i>	1
		<i>Scarus caudofasciatus</i>	1
		<i>Synodus dermatogenys</i>	1
		<i>Lutjanus rivulatus</i>	1

Statistically significant results of difference in relative abundance of fish between two tidal states from univariate permutational ANOVA within trophic guilds shown in Annex tables 5.15 to 5.18.

Table 5.15. Univariate permutational ANOVA of relative abundance (MaxN) within zooplanktivores between two categories of tidal state in BRUVs.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	65.84643	1.730623	0.1862
Depth	1	3.504098	0.092097	0.7574
Time of day	1	4.328133	0.113755	0.7324
Tide	1	187.7477	4.93452	0.0318*
Depth:Time of day	1	1.025574	0.026955	0.8772
Depth:Tide	1	10.58963	0.278324	0.5918
Residual	32	1217.53	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.16. Univariate permutational ANOVA of relative abundance (MaxN) within invertebrate carnivore guild between two categories of tidal state in unbaited RUVs.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.019361	0.006684	0.936
Wave energy	1	5.816265	2.008067	0.171
Depth	1	0.707716	0.244339	0.6122
Time of day	1	16.78462	5.794896	0.0194**
Tide	1	24.33138	8.400417	0.0054**
Depth:Time of day	1	1.584131	0.546922	0.4586
Depth:Tide	1	0.909009	0.313836	0.575
Residual	39	112.9615	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.17. Univariate permutational ANOVA of relative abundance (MaxN) within sponge/invertebrate feeders between two categories of tidal state in RUVs.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.354876	0.407135	0.5398
Wave energy	1	2.924551	3.355218	0.0744
Depth	1	2.866985	3.289175	0.0744
Time of day	1	3.590822	4.119603	0.0466*
Tide	1	0.542198	0.622042	0.4294
Depth:Time of day	1	0.166032	0.190482	0.6618
Depth:Tide	1	0.004684	0.005374	0.9378

Residual	39	33.99406	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.18. Univariate permutational ANOVA of relative abundance (MaxN) within zooplanktivores between two categories of tidal state in RUVs.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.983509	0.028701	0.8746
Wave energy	1	13.77268	0.401914	0.536
Depth	1	118.0184	3.444009	0.0738
Time of day	1	82.19985	2.398754	0.1394
Tide	1	143.6092	4.190799	0.0412*
Depth:Time of day	1	1.624203	0.047397	0.8246
Depth:Tide	1	16.37455	0.477842	0.4878
Residual	39	1336.441	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Statistically significant results of difference in relative abundance of fish between three categories of time of day and tidal state from univariate permutational ANOVA within trophic guilds shown in Annex tables 5.19 to 5.34. Univariate results table followed by a Pairwise PERMANOVA comparing the differences between pairs of tide and time of day categories, where Univariate results were significant for tide and time of day.

Table 5.19. Univariate permutational ANOVA of relative abundance (MaxN) within trophic groups from BRUVs data between three categories of tide and time of day, after accounting for depth and other covariates. No significant results for the effects of tide and time of day on the fish assemblage in Baited Remote Underwater Video System data, therefore none showed below.

Table 5.20. Univariate permutational ANOVA of relative abundance (MaxN) of algae/invertebrate feeders from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.309947	0.295384	0.5964
Wave energy	1	0.084569	0.080595	0.7868
Depth	1	3.320934	3.164894	0.0898
Tide.Time of day	2	9.119469	4.345487	0.0206*
Depth:Tide.Time of day	2	0.571844	0.272487	0.7592
Residual	39	40.92283	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.21. Pairwise comparison between the three categories of tide and time of day, using univariate permutational ANOVA of relative abundance (MaxN) from RUVs data for algae/invertebrate feeders.

	pairs	F.Model	R2	p.value	p.adjusted	sig
1	high.morning vs low.midday	2.232645	0.067182	0.145	0.29	
2	high.morning vs high.evening	5.3689	0.211633	0.023	0.069	
3	low.midday vs high.evening	1.030271	0.027091	0.331	0.331	

P-adjusted significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.22. Univariate permutational ANOVA of relative abundance (MaxN) of corallivores from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	1.558086	1.538867	0.2234
Wave energy	1	2.178439	2.151567	0.1578
Depth	1	10.20316	10.0773	0.0026**
Tide.Time of day	2	14.07891	6.952622	0.0024**
Depth:Tide.Time of day	2	0.325033	0.160512	0.8682
Residual	39	39.48709	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.23. Pairwise comparison between the three categories of tide and time of day, using univariate permutational ANOVA of relative abundance (MaxN) from RUVs data for corallivores.

	pairs	F.Model	R2	p.value	p.adjusted	sig
1	high.morning vs low.midday	5.820549	0.158079	0.028	0.084	
2	high.morning vs high.evening	5.221878	0.207038	0.04	0.084	
3	low.midday vs high.evening	0.004993	0.000135	0.956	0.956	

P-adjusted significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.24. Univariate permutational ANOVA of relative abundance (MaxN) of generalist carnivores from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.582147	0.202519	0.659
Wave energy	1	0.112249	0.03905	0.8464
Depth	1	7.31724	2.545547	0.122
Tide.Time of day	2	18.5763	3.231195	0.0432*
Depth:Tide.Time of day	2	4.158878	0.723403	0.4166
Residual	39	112.1065	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.25. Pairwise comparison between the three categories of tide and time of day, using univariate permutational ANOVA of relative abundance (MaxN) from RUVs data for generalist carnivores.

	pairs	F.Model	R2	p.value	p.adjusted	sig
1	high.morning vs low.midday	3.987068	0.113958	0.063	0.126	
2	high.morning vs high.evening	4.799187	0.193522	0.04	0.12	
3	low.midday vs high.evening	0.861746	0.02276	0.339	0.339	

P-adjusted significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.26. Univariate permutational ANOVA of relative abundance (MaxN) of herbivores from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	11.12723	2.350811	0.1312
Wave energy	1	0.361818	0.07644	0.788
Depth	1	89.91263	18.99552	4.00E-04
Tide.Time of day	2	43.17354	4.560561	0.017
Depth:Tide.Time of day	2	0.534863	0.056499	0.9508
Residual	39	184.601	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.27. Pairwise comparison between the three categories of tide and time of day, using univariate permutational ANOVA of relative abundance (MaxN) from RUVs data for herbivores.

	pairs	F.Model	R2	p.value	p.adjusted	sig
1	high.morning vs low.midday	2.394513	0.071704	0.148	0.296	
2	high.morning vs high.evening	3.142569	0.135792	0.09	0.27	
3	low.midday vs high.evening	0.318082	0.008524	0.567	0.567	

P-adjusted significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.28. Univariate permutational ANOVA of relative abundance (MaxN) of invertebrate carnivore from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.019361	0.006652	0.9358
Wave energy	1	5.816265	1.998469	0.1744
Depth	1	0.707716	0.243171	0.613
Tide.Time of day	2	42.50948	7.303131	0.0022**
Depth:Tide.Time of day	2	0.557165	0.095721	0.91
Residual	39	113.504	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.29. Pairwise comparison between the three categories of tide and time of day, using univariate permutational ANOVA of relative abundance (MaxN) from RUVs data for invertebrate carnivores.

	pairs	F.Model	R2	p.value	p.adjusted	sig
1	high.morning vs low.midday	21.33627	0.407677	0.002	0.006	**
2	high.morning vs high.evening	4.186735	0.1731	0.044	0.088	
3	low.midday vs high.evening	2.295485	0.058416	0.138	0.138	

P-adjusted significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.30. Univariate permutational ANOVA of relative abundance (MaxN) of piscivores from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.059808	0.036257	0.8504
Wave energy	1	0.286795	0.173861	0.68
Depth	1	4.987583	3.023584	0.0898
Tide.Time of day	2	5.388119	1.633199	0.2042
Depth:Tide.Time of day	2	0.954958	0.289458	0.7528
Residual	39	64.33284	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.31. Univariate permutational ANOVA of relative abundance (MaxN) of sponge/invertebrate feeder from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.354876	0.421379	0.5332
Wave energy	1	2.924551	3.472601	0.07
Depth	1	2.866985	3.404248	0.0698
Tide.Time of day	2	5.402876	3.207678	0.0486*

Depth:Tide.Time of day	2	0.049956	0.029659	0.971
Residual	39	32.84497	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.32. Pairwise comparison between the three categories of tide and time of day, using univariate permutational ANOVA of relative abundance (MaxN) from RUVs data for sponge/invertebrate feeders.

	pairs	F.Model	R2	p.value	p.adjusted	sig
1	high.morning vs low.midday	3.528134	0.102181	0.06	0.177	
2	high.morning vs high.evening	4.08243	0.169519	0.059	0.177	
3	low.midday vs high.evening	0.005498	0.000149	0.943	0.943	

P-adjusted significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.33. Univariate permutational ANOVA of relative abundance (MaxN) of zooplanktivores from RUVs data between three categories of tide and time of day, after accounting for depth and other covariates.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	0.983509	0.029164	0.8732
Wave energy	1	13.77268	0.4084	0.5332
Depth	1	118.0184	3.499585	0.0704
Tide.Time of day	2	254.7761	3.777424	0.0306*
Depth:Tide.Time of day	2	10.25541	0.152051	0.8686
Residual	39	1315.218	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.34. Pairwise comparison between the three categories of tide and time of day, using univariate permutational ANOVA of relative abundance (MaxN) from RUVs data for zooplanktivores.

	pairs	F.Model	R2	p.value	p.adjusted	sig
1	high.morning vs low.midday	7.489688	0.194589	0.017	0.051	
2	high.morning vs high.evening	5.284187	0.208992	0.035	0.07	
3	low.midday vs high.evening	0.154898	0.004169	0.694	0.694	

P-adjusted significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.35. Distance based redundancy Analysis (dbRDA) of BRUVs data of the species assemblage, assessing the effects of tide on the fish assemblage prior to time of day.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	1.016451	1.747579	0.022*
Depth	1	1.333172	2.292116	0.0042**
Tide	1	0.739202	1.270905	0.1458
Time of day	1	0.812319	1.396616	0.0824
Depth:Tide	1	0.501527	0.862273	0.646

Residual	33	19.19392	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.36. Distance based redundancy Analysis (dbRDA) of RUVs data of the species assemblage, assessing the effects of tide on the fish assemblage prior to time of day.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	1.020395	1.849379	0.0216*
Wave energy	1	0.690147	1.250833	0.1594
Depth	1	1.736027	3.146402	2.00E-04***
Tide	1	0.911729	1.652432	0.0428*
Time of day	1	1.351389	2.449277	0.004**
Depth:Tide	1	0.66222	1.200218	0.1946
Depth:Time of day	1	0.369339	0.669396	0.9326
Residual	39	21.51825	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.37. Distance based redundancy Analysis (dbRDA) of BRUVs data of the trophic assemblage, assessing the effects of tide on the fish assemblage prior to time of day.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	1.001671	1.328543	0.1824
Depth	1	0.689762	0.91485	0.4014
Tide	1	1.419926	1.883286	0.0692
Time of day	1	0.61681	0.818092	0.5088
Depth:Tide	1	0.559954	0.742682	0.6168
Depth:Time of day	1	0.796459	1.056364	0.3104
Residual	32	24.12679	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Table 5.38. Distance based redundancy Analysis (dbRDA) of RUVs data of the trophic assemblage, assessing the effects of tide on the fish assemblage prior to time of day.

	Degrees freedom	Sum of squares	F	Pr(>F)
Visible area	1	1.156951	1.279996	0.189
Wave energy	1	1.025299	1.134342	0.2612
Depth	1	3.777804	4.179582	0.0018**
Tide	1	1.592765	1.762159	0.082
Time of day	1	3.204824	3.545664	0.005**
Depth:Tide	1	0.623985	0.690347	0.7216
Depth:Time of day	1	0.661918	0.732314	0.6384
Residual	39	35.25098	NA	NA

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Chapter 6. Change in coral reef fish assemblage structure and species size structure within and across multiple scales of benthic habitat.



Potato groupers near gorgonian fans at a reef on the north coast of Aldabra, credit: Pristine Seas Survey, National Geographic

6.1. ABSTRACT

This chapter aims to assess differences in reef fish assemblage among habitats and determine the changes in species turnover rates within size categories among three scales of habitat at Aldabra's coral reef. Distinct fish assemblages have been shown to associate with specific habitats, but variability in assemblage structure may be further explained by the scale of the habitat (coarseness at which the habitats were defined). Species size has been shown to be a reliable predictor of fish home-range size, therefore changes in the composition of fish assemblages among habitat scales may be related to the size of the species in the assemblage. The objective was to assess the reef fish assemblage structures and species turnover rates between benthic habitats within the same scale and then compare the turnover rates within species-size classes across three scales of habitat at the seaward reefs of Aldabra in 3 to 58 m depth. Three hypotheses were tested 1) that the fish assemblage structures are significantly different among habitats, 2) the rate of species turnover within all fish size-class assemblages is greater between larger scales than finer scales of habitat, 3) smaller species have higher turnover rates at fine-scale habitats than larger species. The reef fish assemblages were sampled at 73 sites using Baited Remote Underwater Video systems (BRUVs) and 69 sites using unbaited Remote Underwater Video systems (RUVs) spread over four geomorphic reef zones, six broad-scale habitats and 12 fine-scale habitats, as defined in Chapter 2. Differences in fish assemblages among habitats were analysed using univariate permutational ANOVA and PERMANOVA and species turnover rates were compared across habitat scales using multivariate permutational dispersion. Assemblage structures were significantly different among habitats within respective scales. However, there were no significant differences in the fish assemblages among the finer-scale benthic habitat categories that belonged to the same broad-scale benthic habitat category. These results suggest that the observed variation in the reef fish assemblage among benthic habitats may be adequately captured at the geomorphic or broad-scale habitat level when using BRUVs or RUVs. Species turnover rates within size-classes of Actinopterygii were significantly different between the three scales of habitat, but not within size-classes of elasmobranchs. These weak habitat associations across the three habitat scales, and the wide-ranging nature of elasmobranchs suggests that management efforts should aim to protect sufficiently large areas such as entire atolls and, potentially, nearby islands to conserve their populations. Conversely, the significant change of Actinopterygii fish turnover rates between habitats and habitat scales suggests that representative and replicated habitats within the atoll should be conserved. The results from this chapter highlights the importance of habitat and the scale at which habitat is defined to explain the differences between reef fish assemblage structures.

6.2. INTRODUCTION

This chapter aims to determine the associations between reef fish assemblages and benthic habitats, and the role that the scale of habitat has on the associations between different size classes of fish at a coral reef. The structure (species composition and abundance) of biological communities underpins ecosystem functioning and influences vulnerability of communities to environmental and anthropogenic pressures (Villéger et al. 2010; Mouillot et al. 2011; Stuart-Smith et al. 2013). Reef fish are a key component of the tropical reef community because the structure of reef fish assemblages directly influences the benthic composition and the functioning of important ecological processes which maintain the reef, like herbivory and predation (Ogden and Lobel 1978; Dulvy et al. 2004a; Graham et al. 2006). The high degree of niche specialisation in tropical reef fish results in a variety of co-occurring species within the various tropical reef habitats (Sale 1977; Connell 1978; Brandl et al. 2015). The reef fish assemblages in the different habitats therefore comprised a variety of these combinations of co-occurring species. The associations of different reef fish assemblages with various habitats provides critical information from which to assess how environmental or anthropogenic disturbances influence benthic habitat composition and ecosystem processes. Understanding the differences in the structures of reef fish assemblages between tropical reef habitats is therefore a fundamental starting point that can inform reef management, such as marine protected areas to manage anthropogenic disturbance (Crowder and Norse 2008).

The associations between reef fish and habitat are often studied at a single scale, despite the fact that multiple scales of habitat exist (Mellin et al. 2009), and that fish use habitat at different scales (e.g. Nash et al. 2013; Sekund and Pittman 2017). The scale of habitat in this study refers to the level of detail at which substrate and benthos are grouped into thematic units. Figure 6.1 illustrates how Aldabra's benthic habitats can be categorised according to three scales: geomorphic reefs zones, broad-scale habitats and fine-scale habitats, as was undertaken in Chapter 2. Geomorphic reef zones, which included the lagoon reef and top of the forereef slope, for example, represent a coarse-scale habitat categorisation considered as part of the photic tropical reef. Within geomorphic reef zones, habitats occur at a finer resolution with variations that occur within the geomorphic reef zones. For example, habitat categories such as Hard coral, Seagrass or Sand were defined as broad-scale benthic habitats that occur at an intermediate scale of habitat in this study. Within these broad-scale habitats, fine-scale benthic habitat categories include a greater amount of detail about the substrate and benthos, some including biotope-level information.

For example, the broadscale habitat 'Hard coral' contains a finer-scale category of massive and submassive forms, *Millepora* and *Rhytisma*.

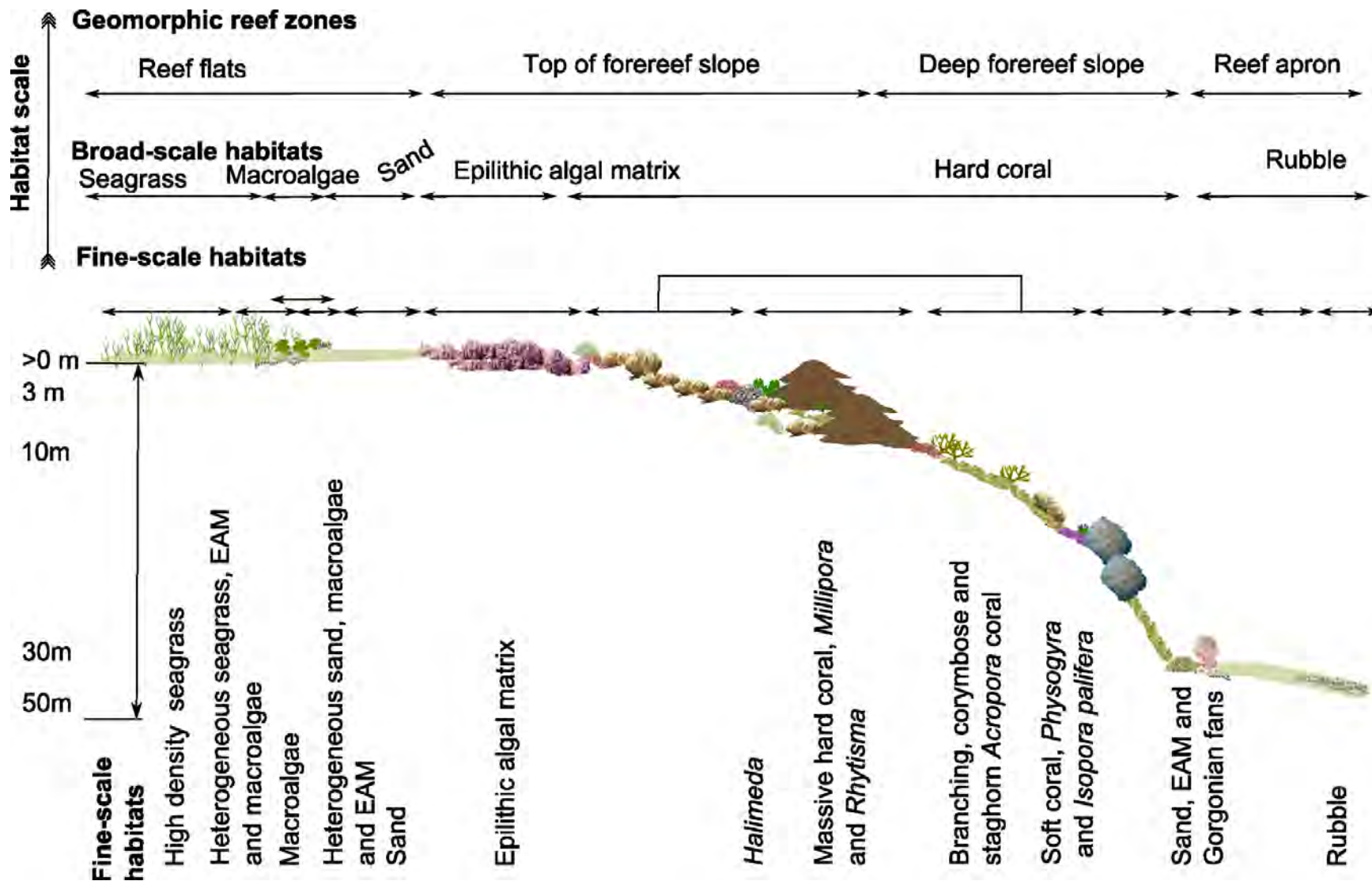


Figure 6.1. Illustration of the Aldabra's benthic habitat categorised according to three scales, namely geomorphic reef zones, broad-scale habitats and fine-scale habitats. The benthic habitat categories of each scale show how the coarser scale habitat comprising multiple finer scale habitats.

The association of fish with this hierarchical scale of habitat categorisation is the function of this chapter. Ecological niche breadth has been shown to relate to geographical range-size (Slatyer et al. 2013), and therefore differing niche requirements may be met in habitats that operate at different scales. Reef fish have varied degree of niche specialisation, from highly specialised to generalist species (Sale 1977; Connell 1978; Brandl et al. 2015). Given that the ecological niche breadth is highly varied among different species it follows that the various species within the reef fish assemblage have different spatial distributions because of specific niche requirements and that there is great variation in home range size. Reef fish home range sizes vary at the scale of meters to tens of kilometres (Green et al. 2015). For example, cryptobenthic reef fish with strong microhabitat associations have home ranges spanning less than 1 m² (Depczynski and Bellwood 2004), while giant trevally (*Caranx ignobilis*) undertake atoll wide migrations up to 29 km (Meyer et al. 2007a). The difference in inter-specific home ranges and the varying degree of niche specialisation of reef fish is expected to cause distinct combinations of species occurring in different habitats, and that the size and complexity of habitat with which different species associate will vary (e.g. McCormick and Makey 1997; Wilson et al. 2008). The fish species for which their niche requirements are met within the scale selected to define a particular benthic habitat may therefore remain within its boundaries, while species for which niche requirements exceed the scale selected to define the benthic habitat may traverse such boundaries as their benthic habitat may be defined by environmental parameters that operate at a broader scale (Sekund and Pittman 2017). The amount of species turnover (change in species composition) between different habitat types is therefore expected to vary across different scales of habitat.

As different fish are likely to associate with habitats of differing scales, it is important to determine the appropriate scale of habitat to use in order to obtain an accurate species habitat requirement, and in turn inform sampling strategies and data analysis (MacNeil et al. 2009; Mellin et al. 2009). The range of scales at which benthic habitat has been recorded to study the association of fish assemblages has been highly variable in previous studies, ranging from broad, such as coral or seagrass, to fine-scale, such as branching *Acropora* coral (e.g. Bellwood and Hughes 2001; Chittaro 2004; Pittman et al. 2004, 2009; Kuffner et al. 2007; MacNeil et al. 2009; Mellin et al. 2009; Kendall and Miller 2010; Sekund and Pittman 2017). In studies of fish and habitat association, where the habitat information was obtained from habitat maps, the information tends to be at a single habitat scale, typically including habitat categories such as, coral reef, macroalgal reef, and seagrass beds, (e.g. Cappo et al. 2007a; e.g. Friedlander et al. 2007; Grober-Dunsmore et al. 2007, 2008; Harvey et al. 2007; Mellin et al. 2007; Purkis et al. 2008; Wedding et al. 2008). Habitat maps provide

habitat information at a relatively coarse scale and cover a large area, which may exceed the home ranges of many fish. Fine-scale benthic habitat information may be collected during underwater visual census (UVC) in order to assess such fine-scale habitat characteristics in relation to the fish assemblage, or specific fish species (e.g. Wilson et al. 2008). During UVC benthic habitat information is often highly detailed but covers only a small area, e.g. 50 m². Given that some fish inhabit micro-niches within the reef, fine-scale habitat information is required to assess their association to habitat, while wide ranging species such as giant trevally *Caranx ignobilis* may be better studied using habitat information at a broader scale, such as that obtained from habitat maps. Sampling designs in previous studies that used Baited Remote Underwater Video systems (BRUVs) or unbaited Remote Underwater Video systems (RUVs) to observe fish assemblages have, like other marine survey methods, often use a general reef descriptor, such as high or low profile reef (e.g. Heyns-Veale et al. 2016), or a general broad-scale habitat categories such as sand, seagrass, coral reef (e.g. Cappelletti et al. 2007a; Harvey et al. 2007, 2012a; Colton and Swearer 2010). Only a few examples that compare the results between broad and fine-scales have been carried out using BRUVs (e.g. Fitzpatrick et al. 2012). There is therefore still a need to understand which components of the fish assemblage associate with fine-scale habitat, and which components associate with the broad-scale habitat.

Differences in reef fish assemblage structure at various scales may be a consequence of how species' functional traits, such as feeding guild, mobility, shape, or size, relate to the scale of benthic habitat and environmental parameters (Kramer and Chapman 1999; Nash et al. 2013). It has been shown that fish home-range size increases with body size (Kramer and Chapman 1999; Woolnough et al. 2009). For example, small damselfish and butterfly fish are confined to short distance movements (<0.1 – 0.5 km), slightly larger fish, like goatfish, surgeonfish and parrotfish, move slightly further (0.5 – 3 km), while even larger fish, like snappers, groupers and Carangids, move between islands several kilometres apart (Meyer et al. 2007a, 2007b; Cowlishaw 2014; Green et al. 2015). Larger fish species need larger home ranges because they have greater dietary requirements, decreased energy cost and faster recovery when swimming long distances (Kramer and Chapman 1999; Kieffer 2000). The scale of the habitat with which fish associate may therefore be related to the size of the fish species, given that ecological niche breadth is related to geographical-range (Slatyer et al. 2013), and that body size is related to home range size (Kramer and Chapman 1999). As such, it may be expected that higher levels of species turnover between habitats will occur in smaller-bodied fish than larger bodied fish, and that the rate of turnover will differ among habitats of different scales.

The benthic habitat maps that were generated from remotely sensed imagery in Chapter 2 provided multiple scales of habitat to test how fish assemblage structure varies between benthic habitats defined at different scales and how fish size influences the associations. Data on reef fish assemblages were obtained using Baited Remote Underwater Video systems (BRUVs) and unbaited Remote Underwater Video systems (RUVs) because the methods were able to sample the fish assemblages in a variety of benthic habitats including depths that are not typically sampled using SCUBA (Fitzpatrick et al. 2012; Whitmarsh et al. 2017). In this study, additional benthic habitat information was obtained directly from the video footage collected by BRUVs and RUVs to improve the fine-scale information from benthic habitat maps. A range of scales of benthic habitat, where the level of thematic detail included 1) geomorphic reef zones, 2) broad-scale benthic habitat categories, and 3) fine-scale benthic habitat categories, were used to test the association between fish assemblages and their habitat.

The aim of this chapter is to establish the associations between reef fish assemblage structures and multiple scales of habitat on the seaward reefs of Aldabra Atoll between 0 and 55 m depth.

The following hypotheses were tested:

H. 6.1) The fish assemblage structure differs between benthic habitats of the same scale.

H. 6.2) If fish assemblages are distinct between fine-scale benthic habitats, and broad-scale benthic habitats include multiple fine-scale benthic habitats within them, then the species turnover will be greater at broader scales of benthic habitat relative to finer scales.

H. 6.3) A change in benthic habitat will result in greater turnover in assemblage structure in small fish than large fish, given that small fish niche requirements may be met in fine-scale benthic habitat while large fish niche requirements may only be met within coarser-scale benthic habitat (Kramer and Chapman 1999; Nash et al. 2014; Brandl et al. 2015; Green et al. 2015).

The objectives of the chapter were:

Obj. 6.1) To establish if the variation in the reef fish assemblage structure was significant between different habitats (within the same scale and repeated for the three different habitat scales used in this study) at the seaward reefs of Aldabra Atoll using Baited Remote Underwater Video systems (BRUVs) and Remote Underwater Video systems (RUVs).

Obj. 6.2) To establish if the amount of change in species turnover within each of the species size-classes differs among habitat scales, including geomorphic reef zones, broad-scale benthic habitat, and fine-scale benthic habitat.

The habitat maps developed in Chapter 2 representing the spatial distribution for geomorphic and broad-scale habitats were assigned to BRUVs and RUVs samples based on their geographical overlap. However, for fine-scale benthic habitats only the habitat categories were retained, and these categories were assigned to BRUVs and RUVs samples using a classification tree analysis of an image captured for each sample.

6.3. METHODS

6.3.1 Study site

The study was carried out on the seaward reefs within the Aldabra Atoll Marine Protected Area (MPA) between 3 and 58 m depth along all sides of the Atoll's coast. Aldabra's MPA represents a near-pristine ecosystem and is a World Heritage Site as its coral reefs and rich fish community represent one of the best-preserved examples in the Indian Ocean (<http://whc.unesco.org/en/list/185>). No exploitative activities other than the fishing for subsistence of the 15 – 25 people on the atoll are carried out within the MPA (0.3 people/km of reef), and research and recreational SCUBA diving activities are restricted to a few selected reefs, with fewer than 100 dives per year conducted by parties ranging from 4 – 8 people (Pistorius and Taylor 2009; Aldabra Management Plan 2016). The direct human activities are thought to have a minimal impact given the large size of the atoll, with a circumference of 85.6 km (Stoddart 1971; Pistorius and Taylor 2009; Friedlander et al. 2015a). The large isolated and protected MPA provides the opportunity to study the relationship between fish assemblages and benthic habitat under minimal human influence (Stoddart 1984; Downing et al. 2005a).

6.3.2 Fish assemblage Sampling approach

Seventy-three samples of the reef fish assemblage were recorded using Baited Remote Underwater Video systems (BRUVs) and 69 using (unbaited) Remote Underwater Video systems (RUVs) at Aldabra between 22 October 2013 and 18 March 2015. Both BRUVs and RUVs were used to ensure a representative sample of species from all trophic feeding guilds, as the diverse groups of fish present were more effectively sampled using both of these methods (Chapter 4). Sampling was carried out during daylight hours in the transitional calm phase between monsoons when winds were lightest. One hundred and forty-two samples were recorded between depths of 3 m and 58 m along each of the four aspects of the Atoll's coastline to ensure fish assemblages from a representative sample of benthic habitats, wave exposures, water temperatures, and fishing effort were recorded. For more details on the BRUVs and RUVs set-up, see Chapter 4.

6.3.3 Video sample processing

The video samples were processed using the MaxN method as described in Chapter 4 to obtain observed fish assemblage composition and abundance estimates for each sample.

6.3.4 Fish size classification

Fish species identified in the analysis were assigned to size-class categories based on their maximum asymptotic size, using the size-class categories that were determined in Chapter 4. Previous studies suggested that maximum asymptotic size of a species is a useful parameter, in the absence of individual size measurements, to assess the relationship of fish body-size to habitat (Jennings et al. 2002; Nash et al. 2014). Maximum asymptotic size data were obtained for each species from www.fishbase.org (Froese and Pauly 2014). The size-class categories were determined by calculating length bins within the density distribution of maximum asymptotic size of the fish identified in this study, using Kernel Density Estimates (KDE). Plots of KDE to inform five size-class categories were respectively compiled for Actinopterygii and Elasmobranchii, given the larger size of elasmobranchs (Figure 6.2).

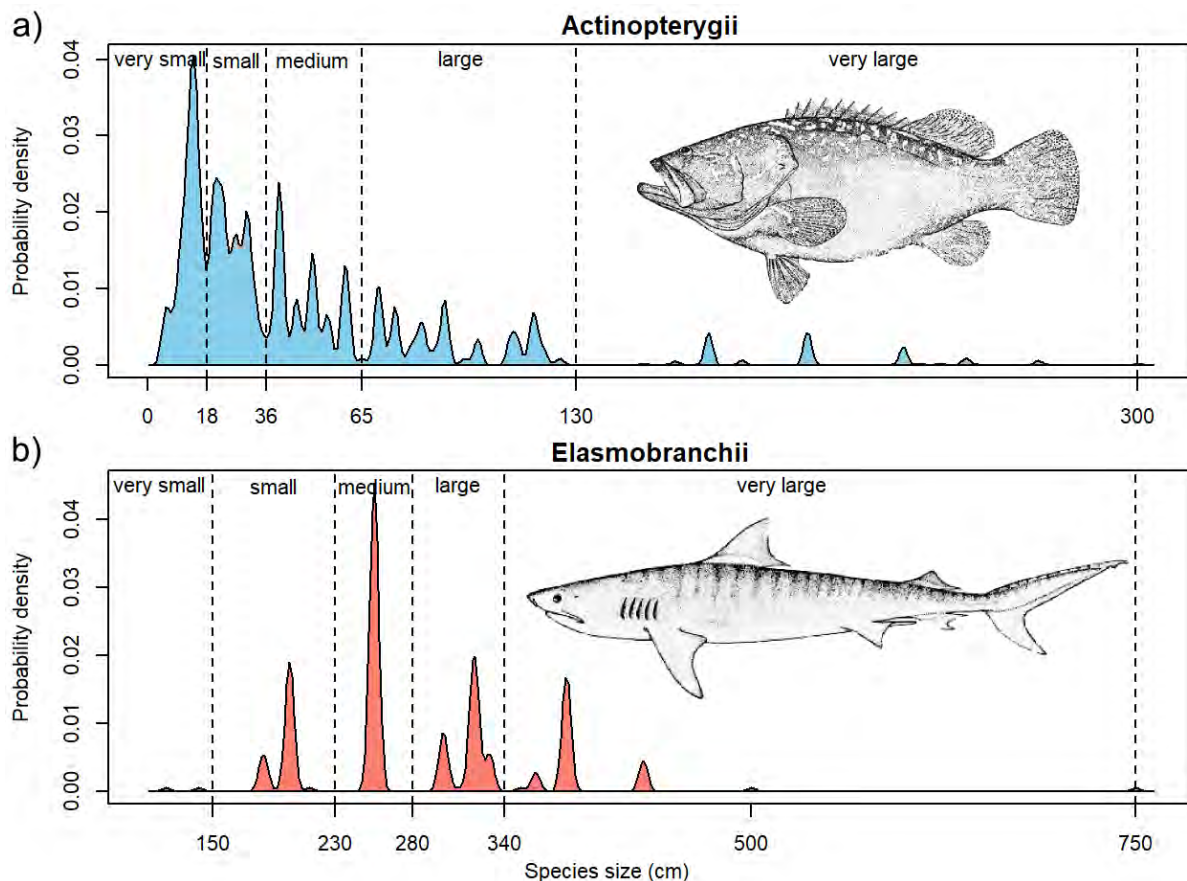


Figure 6.2. All fish in this study were assigned to size-class categories based on kernel density estimates (KDE) from maximum asymptotic fish size data. (Drawings FAO).

6.3.5 Benthic habitat classification

The benthic habitats included in this study, which were classified and mapped in Chapter 2, included three scales (levels of benthic habitat organisation), from coarsest to finest: geomorphic reef zones, broad-scale benthic habitats, and fine-scale benthic habitat. The three scales of benthic habitat differ in the number of habitat categories and level of detail about the benthic composition of each category (Figure 6.1). Chapter 2 describes how the different benthic habitats were derived and mapped for each scale.

6.3.5.1 Geomorphic reef zones

The geomorphic reef zones encircle the Atoll and included the lagoon reef (reef flats), top of the forereef slope, deep forereef slope and reef apron (reef platform) (Table 6.1).

Table 6.1. The four geomorphic reef zones associated with fish assemblage samples on the seaward reefs of Aldabra Atoll in 3 to 58 m depth. Proportional coverage representative of reef to 55 m depth.

Category	Typical depth range	Mean habitat patch area (km ²)	Proportional coverage (%)
Lagoon reef	1 – 3.5 m	0.69	36
Top of forereef slope	3.5 – 9 m	0.78	15
Deep forereef slope	9 – 30 m	0.41	22
Reef apron	30 – 50 m	0.22	27

See Chapter 2 for details

The geomorphic reef zones were associated with BRUVs and RUVs samples using a spatial join (joining of attributes of two spatial data layers based on their spatial overlap) in QGIS (Quantum-GIS-Development-Team 2017), which associated the habitat information with the locality of BRUVs and RUVs deployment based on their geographic coordinates (Quantum-GIS-Development-Team 2017).

6.3.5.2 Broad-scale benthic habitats

Broad-scale benthic habitat categories differed from the geomorphic reef zones by providing information on the substrate and benthos, while the geomorphic reef zones provide more general information on the location along the topography of the reef. The broad-scale habitats were less contiguous than the geomorphic reef zones and were made up of a mosaic of multiple large patches (Table 6.2 and Figure 6.1).

Six categories of broad-scale benthic habitat were recognised (Table 6.2), and were mapped using remotely sensed imagery in Chapter 2, and were similarly assigned to BRUV and RUV samples using a spatial join in QGIS. See Chapter 2 for more details on the composition, proportional coverage of the six broad-scale benthic categories.

Table 6.2. The six broad-scale benthic habitat categories on the seaward reefs at Aldabra which were associated with fish assemblage samples. Proportional coverage representative of reef to 55 m depth.

Broad-scale benthic category name	Detailed description	Mean patch area (m ²)	Proportional coverage (%)
Epilithic algal matrix	Epilithic algal matrix (87 %)	339	10
Hard coral	Hard (43 %) and soft (10 %) coral	4179	17
Rubble	Rubble (37 %)	2051	28
Macroalgae	Macroalgae (42 %)	66	2
Seagrass	Seagrass (73 %)	18568	28
Sand	Sand (89 %)	435	14

(See Chapter 2 for more detail)

6.3.5.3 Fine-scale benthic habitats

The fine-scale benthic habitats were less contiguous than either the geomorphic reef zones or the six broad-scale benthic habitats consisting of a mosaic of far smaller and more numerous patches (Table 6.1-6.3, Figure 6.1 and see Chapter 2 for a detailed account).

At the fine-scale, twelve benthic habitat categories were defined, and included information about the dominant species or growth forms within each benthic community, as well as other characteristic minor co-occurring species (Table 6.3). Fine-scale benthic habitat categories were assigned to sampling sites based on the benthic composition captured by the still frame image taken at the start of BRUVs and RUVs samples. This approach was preferred to a spatial join for assigning fine-scale benthic habitat categories to BRUVs and RUVs samples, given that validation of the reef habitat map had low spatial accuracy for most fine-scale benthic habitat categories.

The benthic habitat in each still frame was analysed by overlaying 24 points in a randomly stratified order within a grid of three rows by four columns onto each image. Each image was processed only once. The benthic type under each point was labelled according to the minor benthic habitat types defined in Chapter 2 using Coral Point Counts with Excel extensions (CPCe) (Kohler and Gill 2006). The percent cover of each benthic type was calculated from the labelled 24-points in the image.

The still frames captured by the BRUVs or RUVs included the relatively small area directly in front of the camera, of which the surface area was highly influenced by visibility, obstacles in front of the camera and the angle in which the camera is orientated in the water column (Bernard and Götz 2012). The visible area and percent water column was described in

Chapter 4 and these were included in all analysis to account for the bias introduced by these variables, as recommended in previous studies (Bernard and Götz 2012; Heyns-Veale et al. 2016), and are described under the *Sample bias* variables section below.

A tree analysis was performed in R using the package TREE (Ripley 2016) to derive cut-off points for the various benthic habitat types to assign BRUVs and RUVs samples to one of the 12 fine-scale benthic habitat categories. The tree was grown by binary recursive partitioning of the minor benthic type composition associated with each of the benthic samples analysed in Chapter 2. The tree was optimised using the cross-validation procedure in the TREE package to identify the number of terminal nodes that result in the lowest residual deviance and misclassification rate. The cross validation process reduces the number of terminal nodes by removing the least important splits from the tree to arrive at a highly parsimonious tree model (Ripley 2016). The number of terminal nodes was set to 15, which was based on the number of nodes resulting in the lowest unexplained deviance value. There were therefore 15 terminal nodes representing one of the 12 fine-scale benthic-habitat categories (Figure 6.3). The accuracy of the pruned tree model had a misclassification rate of 13% (39 / 291 sites) and residual deviance of 0.85 which was deemed acceptable to perform predictive classification of the BRUV and RUV sampling sites.

The sampling sites' benthic composition (derived using CPCe analysis) were fitted to the tree model using the PREDICT.TREE function in the TREE package (Ripley 2016). The fine-scale benthic category was then assigned based on the cut-off values of percentage benthic habitat determined in the dichotomous tree (Figure 6.3).

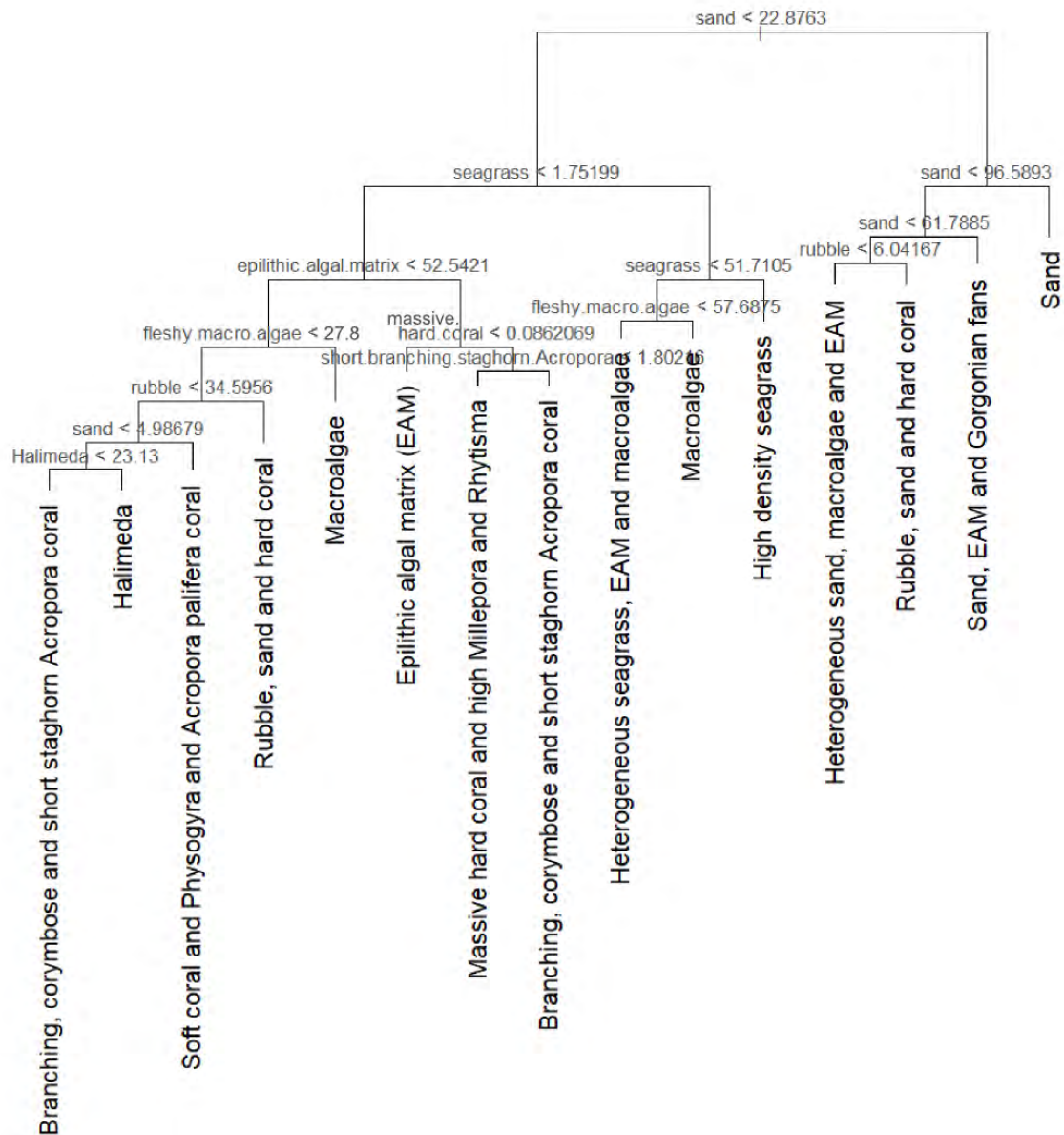


Figure 6.3. Tree analysis showing the cut-off points of percentage substrate coverage of various benthic types in a dichotomous tree, to arrive at the respective 12 fine-scale benthic habitat categories represented by fifteen terminal nodes. The condition at the top of the split points to left if the condition is met.

The twelve fine-scale benthic habitats had a smaller mean habitat patch size and lower proportional coverage per habitat category than broad-scale benthic habitats or geomorphic reef zones (Table 6.3 and Figure 6.1).

Table 6.3. Twelve fine-scale benthic habitat categories and the area occupied on the Aldabra seaward reef in 3 to 58 m depth.

Fine-scale habitat category name	Detailed description	Mean patch area (m ²)	Proportional coverage (%)
Massive hard coral and high <i>Millepora</i> and <i>Rhytisma</i>	Hard coral (19 %) consisting of massive and submassive forms (11 %), (1 %) <i>Millepora</i> and (2 %) <i>Rhytisma</i> .	258	6.6
Rubble	Rubble (58 %), sand (15 %), and (18 %) hard coral.	2075	9.8
Branching, corymbose and short staghorn <i>Acropora</i> coral	Hard coral (36 %), consisting of (5 %) branching, (8.7 %) encrusting, and (2.7 %) corymbose and (3.7 %) short staghorn <i>Acropora</i> .	444	0.5
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> coral	Soft coral (10 %), and sponge (2 %), Hard coral (44 %), consisting of <i>Physogyra lichtensteini</i> (5 %) and <i>Isopora palifera</i> (5 %).	31	28.3
Macroalgae	Fleshy macroalgae (70 %)	56	2.2
<i>Halimeda</i>	<i>Halimeda</i> (41 %)	87	1.0
Heterogeneous seagrass, epilithic algal matrix and macroalgae	Heterogeneous seagrass (20 %), epilithic algal matrix (43 %), and macroalgae (21 %)	61	0.6
Epilithic algal matrix	Epilithic algal matrix (88 %)	463	1.6
High density seagrass	High density seagrass (73 %)	7018	9.2
Sand	Sand (98 %)	407	26.4
Heterogeneous sand, macroalgae and epilithic algal matrix	Heterogeneous sand (40 %), macroalgae (21 %), and epilithic algal matrix (24 %)	42	1.5
Sand, epilithic algal matrix and Gorgonian fans	Sand (78 %), epilithic algal matrix (7 %) and Gorgonian fans (3 %).	201	12.5

6.3.6 Environmental parameters

Variability of environmental parameters within each of the benthic categories was accounted for by including depth, water temperature and wave energy as covariates in models assessing the fish assemblage. Depth (m) was recorded using the echo sounder and GPS (Garmin GPSMAP 520s) mounted to the boat for each sample when the BRUVs or RUVs reached the seabed during deployment. The interaction of depth with the benthic habitat was included as a covariate to test the changing effect of habitat with depth. Water temperature (°C) (temperature hereafter) readings were taken during deployment using temperature data loggers (Onset Hobo Pro V2 Water Temp Pro v2) which were mounted to the BRUVs and RUVs frames. (See Chapter 4 for more details on depth and temperature recordings taken during deployment). Wave energy values were associated with BRUVs and RUVs sampling

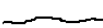
sites using a spatial join (Quantum-GIS-Development-Team 2017) to a modelled wave energy surface. The wave energy around Aldabra was modelled in Chapter 3 where more details about the wave model can be obtained.

6.3.7 Habitat rugosity

Habitat rugosity has been shown to be an important environmental variable influencing reef fish which has been shown to predict species richness, diversity, abundance and biomass (Floeter et al. 2005; Gratwicke and Speight 2005; Nemeth 2005; Friedlander et al. 2007; Wedding et al. 2008; MacNeil et al. 2009; Graham and Nash 2013; Richardson et al. 2017). The high levels of heterogeneity in habitat complexity of coral reefs dictate that there should be high levels of variation of rugosity between sampling sites and within habitat categories defined for this study. Previous studies have shown that habitat complexity (of which rugosity is a component), has largest effects on the fish assemblage at the transect level or within 5 m radius of the sampling site on the forereef slope (Gratwicke and Speight 2005; Kuffner et al. 2007; MacNeil et al. 2009). As such, rugosity was estimated within the visible area in the Field of view (FOV) of each BRUV or RUV sample to control for differences in rugosity between sampling sites and within habitat categories.

A still frame was taken during the beginning of each BRUVs or RUVS video sample to estimate habitat rugosity using a simplified version of the habitat assessment score (HAS) method (Gratwicke and Speight 2005). A habitat rugosity score was derived for each of the samples by assigning an ordered categorical value ranging from one to five which increased with increasing visible height and complexity. The height and complexity profile of the benthic substrate was visually evaluated and compared to the standardised profiles of structure (Table 6.4). The standardised profile which best matched the observed profile in the still frame was used to inform the habitat rugosity score. The forward-facing camera on a BRUVs or RUVs lends itself to the HAS method by allowing easy visual estimations of the habitat rugosity profile against the water column.

Table 6.4. Habitat complexity assessment of still images using the Habitat Assessment Scoring (HAS) system adapted from Gratwicke and Speight (2005).

	HAS Score				
	1	2	3	4	5
Rugosity (visual topographic estimate of each substratum in each quadrat)					

6.3.8 Fishing effort

In addition to environmental parameters, human activities like fishing pressure may alter the fish assemblage structure and thereby the functional traits associated with the reef community, leading to erosion of biodiversity and change ecosystem processes (Villéger et al. 2010; Mouillot et al. 2013). Despite Aldabra being renowned for its remote and isolated reefs with rich fish assemblages, very light levels of subsistence fishing take place along the outer reefs of the atoll under the management authority's supervision, Seychelles Islands Foundation (SIF), to sustain the 15 – 25 staff permanently based on the island (Pistorius and Taylor 2009; Aldabra Management Plan 2016). It is acknowledged that isolated incidents of poaching or previous research fishing may have had an additional impact that was not accounted for in this study due to a lack of spatial data (e.g. Forster 1984; Stevens 1984; Grandcourt 2005). While these isolated incidents of high levels of fishing pressure probably contributed to an altered fish assemblage structure, it was not thought to override the constant pressure, as the affected fish assemblages were likely to redistribute themselves along the atoll.

Even light levels of fishing have been shown to alter fish species assemblage structure, by removing the largest individuals of a population which may lead to trophic cascades (Dulvy et al. 2004b, 2004a). There was a gradient in fishing effort around Aldabra, with the highest levels being near to the sheltered waters of the Research Station, and the lowest levels along the distant windward east coast of Aldabra (Pistorius and Taylor 2009). The effect of fishing was included in the analysis to account for variability of fish assemblage structure which could be caused by the uneven distribution of fishing effort around the Aldabra coastline.

The overall fishing effort was calculated as the total effort per fishing trip between 2005 and 2015 within Aldabra's MPA. Each fishing trip's effort was calculated as total time fished during a fishing trip and multiplied by the number of fishing lines used during each trip. The number of lines used per fishing trip was accounted for by multiplying the time spent fishing with the number of lines used during a trip. The geographic boundaries within which each fishing trip took place was recorded to allow calculation of the fishing effort within an area. The fishing effort per trip per area was summed over the entire period to derive a total fishing effort map. The fishing effort included both pelagic trolling and demersal reef fishing with handlines. The total fishing effort was then associated with the BRUVs and RUVs samples by overlaying the localities of the samples onto the fishing map and using a spatial join in QGIS (Quantum-GIS-Development-Team 2017) to associate fishing effort with samples.

6.3.9 Sample bias variables

The sample area is the unobstructed 2-dimensional wedge shaped planar area calculated using the estimated visibility in front of, and the angle of, the video camera's field of view (FOV). The percent water column in the FOV was calculated as the area above the seabed substrate from a still frame taken at the start of the video, using Vidana software (Hedley 2003). Both sample area and percent water column is described in greater detail in Chapter 4, and see the R script that was used to calculate the sample area (https://github.com/philiphaupt/bruv_area/blob/dev/fov.R).

6.3.10 Statistical analysis

The statistical analysis was carried out in R, using the VEGAN community ecology package for univariate and multivariate analysis of covariates and the fish assemblage (Oksanen et al. 2016; R Core Team 2016). Remote Underwater Video Systems and BRUVs data were treated and analysed independently from each other, to simplify the interpretation of the results.

6.3.10.1 Variables and covariates used in statistical models

The multivariate statistical analysis therefore included the benthic habitat categories respectively from each habitat scales at a time. The number of habitat categories remaining after underrepresented habitats were removed are shown as the number of levels in the factor in column Type in Table 6.5. All other covariates were included in the analysis of hypothesis 1 (described below), other than depth which was not included in models where geomorphic reef zone was included, given that the geomorphic reef zones were highly correlated to depth.

Table 6.5. Variables and covariates used in the analysis of reef fish assemblages in different habitats, showing the units, and type of value.

#	Covariate	Unit	Type
1	Fine-scale benthic habitat		6 level factor
2	Broad-scale benthic habitat		3 level factor
3	Geomorphic zone		4 level factor
4	Rugosity		integer
5	Depth	m	continuous
6	Fishing pressure	lines*hours	continuous
7	Visible area	m ²	continuous
8	Percent water column	%	continuous
9	Temperature	°C	continuous
10	Wave energy exposure	J/m ³	continuous

6.3.10.2 Covariate data analysis

The covariates were assessed for multivariate outliers using a non-metric dimensional scaling (nMDS) analysis. Multivariate outliers outside of the 95 % confidence interval were removed from the dataset as the cumulative effects of outliers can affect multivariate analysis (Anderson et al. 2008).

Correlations between covariates were assessed, as high multi-collinearity ($r > 0.8$) can affect multivariate analysis (Anderson et al. 2008; Bouchard Marmen et al. 2017). Spearman rank correlation tests were used as they do not require the data to have a normal distribution to test for relationships (Zar 1999). Where high multi-collinearity between variables was found, the effect of individual variables on the multi-collinearity was assessed using a leave-one-out approach to determine which variables to remove from the analysis.

Boxplots were generated for environmental variables, showing the mean, interquartile range, tails of the distribution and outlying values for each variable using GGPlot2 in R (Wickham 2009). Wilcox ranked sum tests were used to compare the covariate values between BRUVs and RUVs to test whether or not environmental conditions were comparable between bait treatments (Hollander et al. 2013).

6.3.10.3 Multivariate assemblage structure

The multivariate structure of reef fish assemblages was compared between different benthic habitats within the same habitat scale to test the first hypothesis. Secondly, species turnover rates within the fish size-class categories was compared across habitat scales to test hypothesis 2.

6.3.10.4 Hypothesis 1: Differences in fish assemblage structure between benthic habitat

Prior to analysis, all data were pre-treated for analysis as described below.

6.3.10.4.1 Data standardisation and transformation

The environmental data were standardised to ensure that continuous covariates corresponded to a comparable range of values, as described in greater detail in Chapter 4. Covariates values were standardised using DECOSTAND in VEGAN (Oksanen et al. 2016).

Multivariate fish assemblages were represented by the capped abundances (MaxN) of multiple species. Abundances were capped at a maximum of 44 individuals per species, to mitigate the effects of large schools dominating the effects in statistical models (See Chapter 4 for details). Capped abundance data (MaxN) were $\log_{10}(x)+1$ transformed, to reduce the dominant effect of highly abundant schooling species on the assemblage structure (Anderson 2006). The dissimilarity between samples was calculated using modified Gower

distance. Note that were totals are presented outside of multivariate statistics, abundance values were not capped.

6.3.10.4.2 Transformation of dissimilarity distance

Lingoes transformation (addition) was applied to the dissimilarity distance matrix in all multivariate analysis to avoid negative eigenvalues incorrectly inflating the principal coordinate ordination axes contribution to the observed dissimilarity (Legendre and Anderson 1999; Legendre and Legendre 2012).

6.3.10.4.3 Multivariate precision and the removal of under-represented benthic habitats

Prior to the main analysis, the multivariate fish assemblage data were assessed for multivariate precision to test model assumptions and ensure accurate interpretation of the results. Under-represented habitats were defined as benthic habitats for which there were fewer samples than the number of benthic habitat categories (groups). Under-represented habitats were dropped from the multivariate analysis to satisfy the basic requirements of ANOVA (Zar 1999; Anderson et al. 2008). At the geomorphic zone level there was thus a requirement for a minimum four samples per geomorphic zone, at the broad benthic habitat scale six samples per habitat, and at the fine-scale, twelve samples per habitat. Where the assumption was violated, the under-represented habitat was removed from the data set. The number of samples required was then re-evaluated after an under-represented benthic habitat category was dropped from the analysis because once a category was removed, fewer benthic habitat categories required fewer samples to satisfy ANOVA assumptions. The change in precision of the results was compared between data sets using all samples to those where under-represented habitats were dropped from the analysis.

The effect of including and excluding under-represented habitats in the analysis on the multivariate precision was assessed using *pseudo* multivariate dissimilarity-based standard error (MultSE). The MultSE statistic is based on the residual mean square values from the PERMANOVA analysis of the data (Anderson and Santana-Garcon 2015). Calculations were carried out using the R script available from:

(<https://github.com/jslefche/multSE/blob/b60371cda6b381c888286666f9df780b3cbe44b9/R/multSE.R>).

The variability in the position of the centroid in the ordination space of the modified Gower dissimilarity measure was measured in MultSE using repeated sampling for a given sample size (see Anderson and Santana-Garcon 2015). The analysis was run using 10 000 bootstrapped iterations to determine the 95 % confidence intervals of precision with a decrease in the number of samples used in the analysis. An example of the results of the multSE analysis is provided for broad-scale benthic cover in Annex 6.1. Low levels of

precision were detected in the analysis where under-represented habitats were included, confirming the need to remove under-represented benthic habitats prior to the analysis.

6.3.10.4.4 *Multivariate analysis of differences in the fish assemblage structure within habitat scale*

The pre-treated fish assemblage and covariate data were then analysed using a two-way sequential permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001a, 2006; McArdle and Anderson 2001), implemented through the ADONIS2 function in VEGAN (Oksanen et al. 2016). PERMANOVA is based on permutations of the data, making an analysis of the data distribution free and allowing for any dissimilarity distance measure to be used (Anderson et al. 2008). Sequential PERMANOVA assesses the amount of variance explained by the covariates in the sequence that they were added to the model. In this study, PERMANOVA assesses the residual variance explained by benthic habitats after accounting for the effect of other covariates in the model. The distribution of samples was unbalanced, which could affect two-way PERMANOVA designs (Anderson et al. 2008). No interaction was specified in the PERMANOVA model between benthic habitat and rugosity, as there were insufficient samples within some of the benthic habitats to assess the effects of an interaction between all benthic habitat and rugosity levels. By not specifying an interaction the potential adverse effects of an unbalanced sample were dampened, but their interactive effect could not be assessed (Anderson et al. 2008).

The order in which variables were fitted to the models were carefully considered, as they have an effect on the results in two-way unbalanced designs (Anderson et al. 2008). Covariates were added sequentially to PERMANOVA models, based on the level of control that there was over the covariate value in the experimental design, as follows: percent water column, visible area, temperature, wave energy, fishing effort, rugosity, depth and benthic habitats. Depth was excluded from analysis at the geomorphic zone level, as they were highly correlated with each other.

Differences between pairs of benthic habitats were assessed using pairwise PERMANOVA tests as a *post-hoc* test following statistically significant differences between benthic habitats in the sequential PERMANOVA tests (Arbizu 2017).

6.3.10.4.5 *Dissimilarity between fish assemblages*

Principal Coordinates Ordination (PCO) was used to display the dissimilarity between samples in unconstrained ordination space using WCMDSALE (Oksanen et al., 2016). The standardised covariate values were fit to the PCO ordination plots using ENVFIT (Oksanen et al., 2016) to gain an understanding of the response of fish assemblages to a change in covariate values. Each fitted covariate was overlaid onto the ordination as a vector in the

direction of maximal change of that covariate. The averages of the eigenvalues were used to obtain centroids for benthic habitats (central point within a cloud of PCO points of the same benthic habitat category) (See Oksanen et al., 2016 for a detailed description). The distances to the centroid of PCO points from the same benthic habitat is indicative of the amount of species turnover between samples within the same benthic habitat. The amount of species turnover within a benthic habitat could therefore be compared between benthic habitats within a single scale, and across scales.

6.3.10.4.6 Species turnover between habitats

Species turnover within reef fish assemblages between habitats was measured using multivariate dispersion distance (Anderson 2006; Anderson et al. 2011), and repeated respectively for each of the habitat scales. Multivariate dispersion tests were carried out using the BETADISPER function in VEGAN (Oksanen et al. 2016) to determine the distance between samples and intergroup centroids. Samples were grouped according to benthic habitat categories, and the mean distance and standard error of samples to the centroid of the covariate-factor was determined at each habitat scale. Statistical significance of the differences in dispersion distance between benthic habitats categories was assessed using a permutational ANOVA, PERMUTEST (Oksanen et al. 2016) with 4 999 permutations of the data.

6.3.10.5 Hypothesis 2: Cross-scale species turnover

Cross-scale similarity of fish assemblages was calculated using the following steps. First, the dispersion distances of each sample to its benthic habitat (group) centroid was calculated for hypothesis 1. Secondly, the distances were then pooled into a single dataset across the respective scales. Thirdly, the pooled distance data was submitted to a one-way univariate permutational ANOVA (ADONIS2 in VEGAN using 4999 permutations), as recommended for a single covariate (Anderson and Millar 2004), to determine if species turnover was different across scale. The distances between samples and centroids were treated as Euclidean distances because that is the original distance represents once plotted in a PCO (Anderson et al. 2008). Scale, a three-level factor representing either geomorphic reef zone, broad-scale benthic habitat, or fine-scale benthic habitat was used as a single covariate to in the analysis to compare cross scale the distances. The first part of the method is the standard method for calculating dispersion distances in community ecology but comparing turnover across scales was novel. The novel cross-scale comparison was acceptable given that all PCO locations use the same methods to calculate distances. Despite sample sizes not being identical between the scales after removing under-represented habitats, multivariate analysis does not require an equal sample size, and therefore the method of analysis was acceptable (McArdle and Anderson 2001).

6.3.10.5.1 Cross-scale species turnover within size-class

The species turnover within size-classes of Elasmobranchii and Actinopterygii were compared across habitat scales, repeating the methods stated above to test the effect of fish size and habitat association.

6.4. RESULTS

6.4.1 Covariates summary

Overall 142 samples, 73 from Baited Remote Underwater Video systems (BRUVs) and 69 from unbaited Remote Underwater Video systems (RUVs) samples, were used in the analysis after covariate outliers were removed. The samples had a depth ranging between 3 and 58 m, with a mean $\pm$ standard error (SE) of 18.27 ± 1.6 and 18.31 ± 1.7 meters in RUVs and BRUVs, respectively (Figure 6.4). The overall mean temperature was 27.28 ± 0.14 °C with a minimum of 23.1 °C and a maximum of 30 °C (Figure 6.4). Depth and water temperature had a significant negative correlation ($\rho = -0.36$, $p < 0.01$) in BRUVs, but the relationship was not significant ($\rho = -0.11$, $p > 0.05$) in RUVs.

The mean wave energy was $7\,175 \pm 175.8$ J/m³ spanning a wide range of exposure conditions, ranging from 4 435 to 11 191 J/m³. The cumulative fishing effort from 2005 to 2015, yielded an average 392.6 ± 33.7 line-hours per site, and ranged between 65 and 1 692-line hours (L H) between sampling sites. The fishing pressure gradient was highest near to the Research Station on the northwest coast of Aldabra, and lowest along the east coast (Figure 6.5). Wave energy had a strong negative relationship with fishing effort in BRUVs ($\rho = -0.58$, $p < 0.001$) and in RUVs ($\rho = -0.53$, $p < 0.001$). The correlation was due to the fishing effort being greatest near the Research Station, which is in the wave-sheltered lee of the Atoll, while the fishing effort is lowest further away from the Research Station, where wave exposure is greatest. As multi-collinearity between covariates was below the threshold of r of 0.8 all variables were kept for analysis (Anderson et al. 2008).

The visible area (mean $\pm$ SE 87.7 ± 3.25 m²) varied widely between 6 and 166 m², likely as a consequence of variation in the Field Of View (FOV) caused by obstructions from benthic structures. The mean percentage water column in samples was 43.8 ± 1.12 % with low levels of variation, which were indicative that BRUVs and RUVs were consistently angled approximately horizontal in the water column, therefore recording both reef fish close to the substrate and above the reef. None of the covariates were significantly different between BRUVs and RUVs (Wilcox test, $p > 0.05$, for respective covariates) (Figure 6.4), therefore environmental conditions were comparable across the two sampling methods.

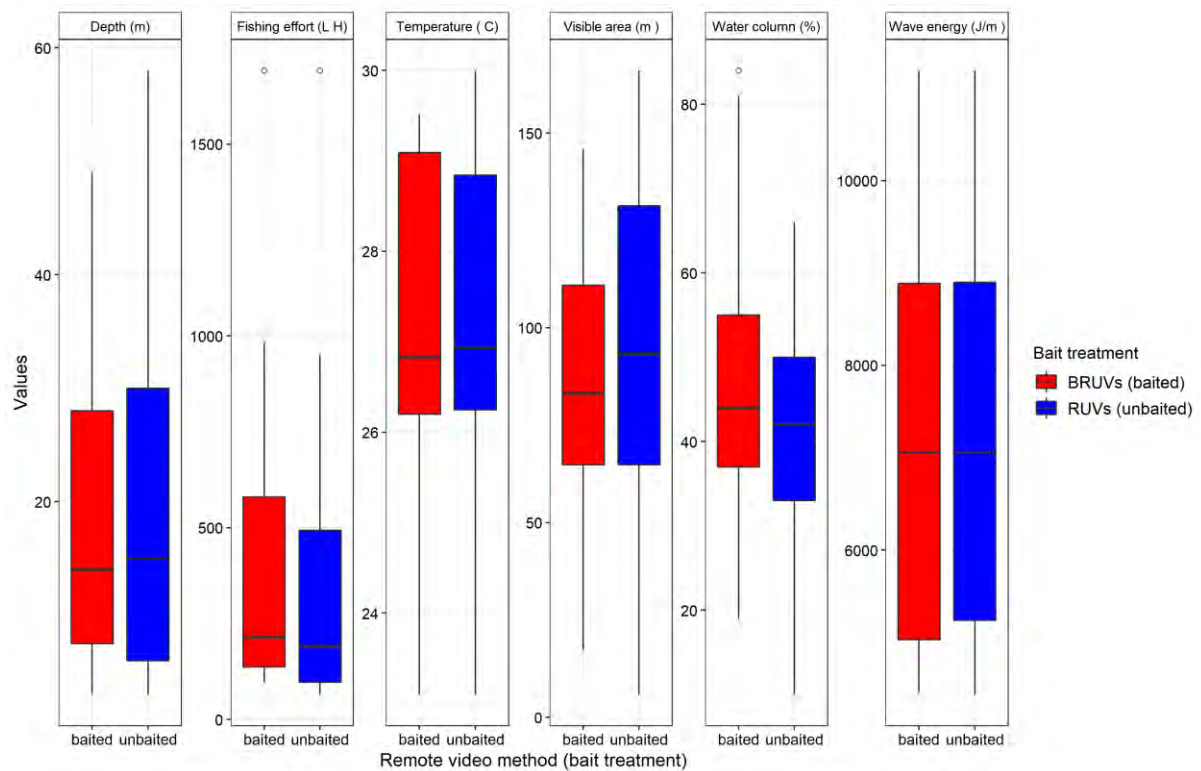


Figure 6.4. Boxplot showing the mean (thick black line inside the box), interquartile range (box), tails (thin black lines) and potential outlier values (circles), for the covariates from Baited Remote Underwater Video systems (BRUVs) and unbaited Remote Underwater Video systems (RUVs). (Fishing effort line hours abbreviated to L H).

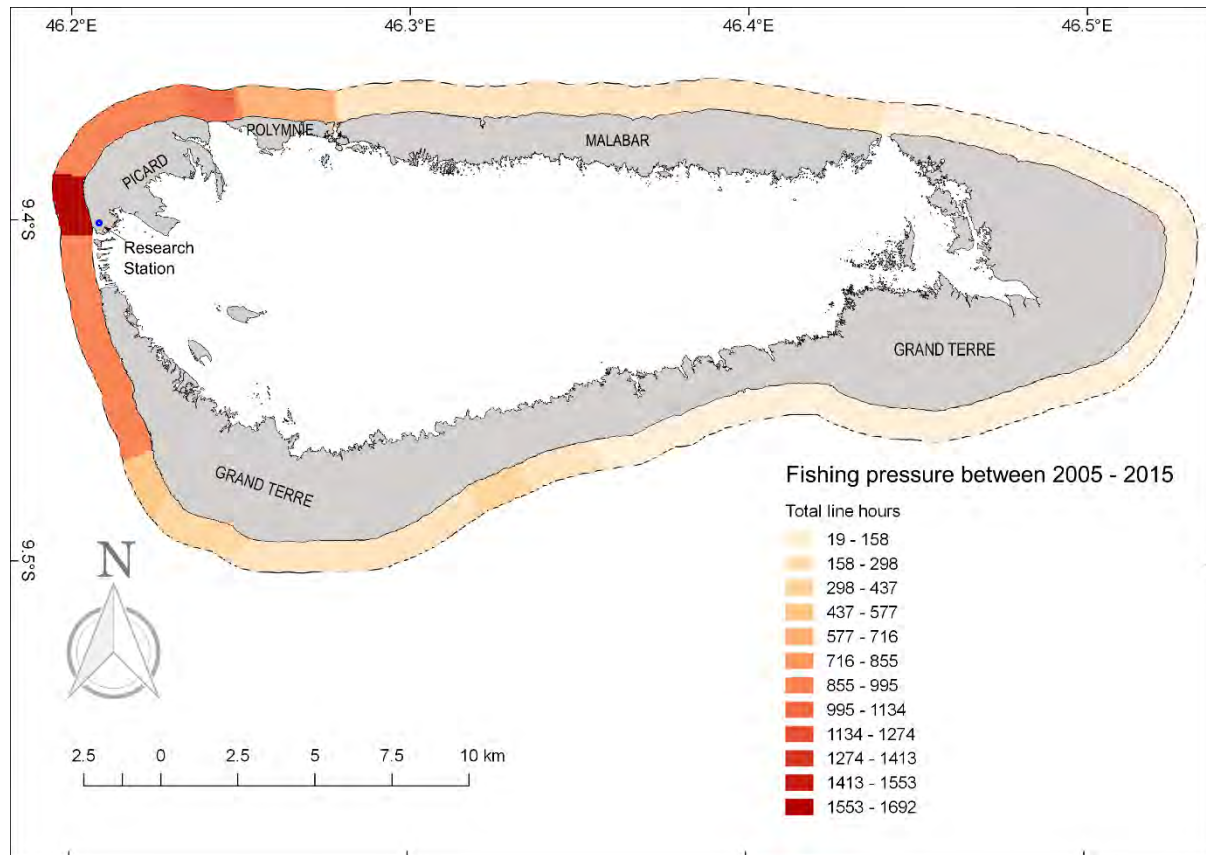


Figure 6.5. The total fishing effort within the Marine Protected Area (MPA) of Aldabra Atoll between 2005 and 2015, measured as the number of hours fished summed multiplied by the number of fishing lines used, giving line hours (L H).

6.4.2 Fish assemblage analysis

6.4.2.1 Multivariate fish assemblage structure in geomorphic reef zones observed in BRUVs

Species assemblage structure observed in BRUVs was significantly different between the geomorphic reef zones (PERMANOVA $F = 2.29$, $p < 0.001$), after accounting for the effect of the covariates (Table 6.6). The wave energy, temperature, rugosity and fishing effort were significant in explaining variation in the fish assemblage structure in BRUVs data (Table 6.6).

Table 6.6. Sequential PERMANOVA results for the species assemblage between geomorphic reef zones, observed using Baited Remote Underwater Video systems (BRUVs) with 4 999 permutations.

	Degrees freedom	Sum of squares	F	Pr(>F)	Significance
Percent water column	1	0.57	1.17	0.19	
Visible area	1	0.71	1.45	0.058	
Temperature	1	1.22	2.49	0.0004	***
Wave energy	1	1.49	3.06	0.0002	***
Fishing effort	1	0.79	1.61	0.028	*
Rugosity	4	5.18	2.65	0.0002	***

Geomorphic reef zone	3	3.35	2.29	0.0002	***
Residual	60	29.27			

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Pairwise PERMANOVA results indicated that the species assemblage structure observed in BRUVs was significantly different between each of the respective pairs of geomorphic reef zones (Table 6.7).

Table 6.7. Pairwise PERMANOVA indicating differences in reef fish species assemblages between pairs of geomorphic reef zones on the seaward reefs at Aldabra Atoll.

Habitat pairs	F.Model	R2	p	p.adjusted	Significance
Top of forereef slope vs Lagoon reef	2.276	0.090	0.001	0.006	**
Top of forereef slope vs Deep forereef slope	2.247	0.055	0.001	0.006	**
Top of forereef slope vs Platform	6.128	0.125	0.001	0.006	**
Lagoon reef vs Deep forereef slope	3.794	0.127	0.001	0.006	**
Lagoon reef vs Platform	3.978	0.117	0.001	0.006	**
Deep forereef slope vs Platform	6.234	0.119	0.001	0.006	**

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

The species turnover was significantly different between the four reef zones (PERMUTEST $F = 15.02$, $p < 0.001$), and there was a separation in the locality of samples in the PCO plot according to geomorphic reef zones (Figure 6.6). Differences in the locality of samples in the PCO plot indicate that assemblages within the same reef zone were more similar to each other than to assemblages in other reef zones. The samples from different geomorphic reef zones that overlapped in their location in the PCO plot, showed that fish observed on the lagoon reef and top of the forereef slope shared similarities in assemblage structure, while the top of the forereef slope and deep forereef slope shared similarities, and the deep forereef slope and reef apron shared similarities in assemblage structure (Figure 6.6). The results show that fish assemblages from adjacent geomorphic reef zones were more similar to each other than to more distant geomorphic reef zones.

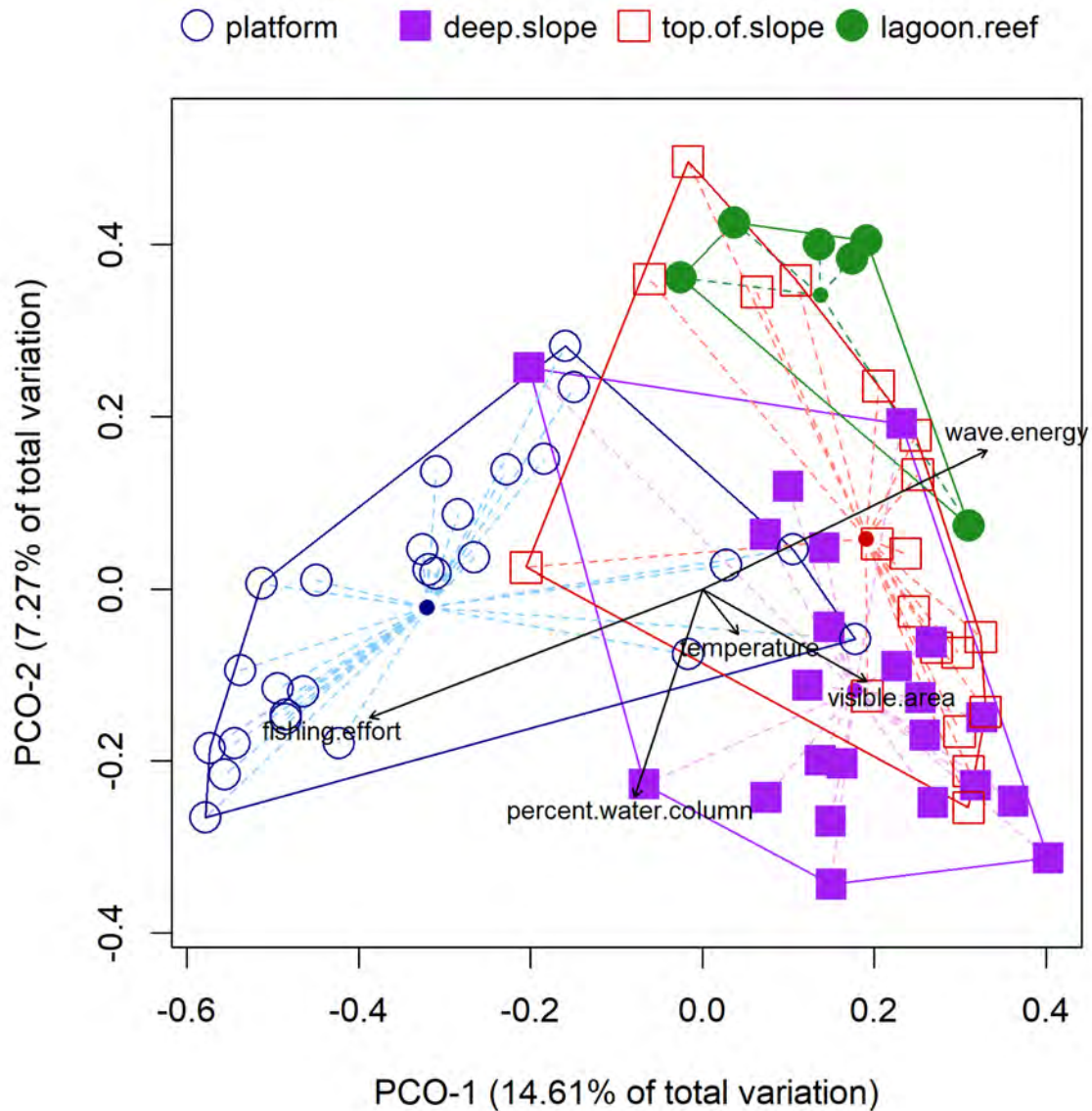


Figure 6.6. Principal Coordinate Ordination plot showing the dissimilarity between the fish species assemblages in the four geomorphic reef zones observed at Aldabra Atoll, using BRUVs. Symbol and colour reflect geomorphic zone category. The relative strength of the effect of covariates is indicated by the length and direction of arrows.

6.4.2.2 Multivariate fish assemblage structure in geomorphic reef zones observed in RUVs

Fish species assemblages observed using RUVs were also significantly different between geomorphic reef zones (PERMANOVA $F = 1.93$, $p < 0.001$). Wave energy, rugosity, fishing effort, temperature and visible area were significant in explaining variation in the fish assemblage structure (Table 6.8).

Table 6.8. Sequential PERMANOVA of fish species assemblage structure using Remote Underwater Video systems (RUVs) in four geomorphic reef zones at Aldabra Atoll in 3 to 58 m water depth between October 2012 and March 2015.

	Degrees freedom	Sum of squares	F	Pr(>F)	Significance
Percent water column	1	0.58	1.20	0.15	
Visible area	1	1.02	2.13	0.0032	**
Temperature	1	0.78	1.63	0.017	*
Wave energy	1	1.81	3.79	0.0002	***
Fishing effort	1	1.01	2.10	0.0038	**
Rugosity	1	2.51	5.23	0.0002	***
Geomorphic reef zone	3	2.77	1.93	0.0002	***
Residual	59	28.27			

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Fish species assemblage structure observed in RUVs was significantly different between all pairs of geomorphic reef zone, other than between the top of the slope and lagoon reef assemblages (Table 6.9).

Table 6.9. Results from pairwise PERMANOVA of fish species assemblage observed in Remote Underwater Video systems (RUVs) between pairs of geomorphic reef zones at Aldabra Atoll in 3 to 58 m water depth between October 2012 and March 2015.

Habitat pairs	F.Model	R2	p	p.adjusted	Significance
Deep forereef slope vs Top of forereef slope	1.936	0.045	0.001	0.006	**
Deep forereef slope vs Lagoon reef	2.742	0.095	0.001	0.006	**
Deep forereef slope vs Platform	5.947	0.129	0.001	0.006	**
Top of forereef slope vs Lagoon reef	1.724	0.065	0.015	0.09	
Top of forereef slope vs Platform	6.952	0.151	0.001	0.006	**
Lagoon reef vs Platform	2.735	0.102	0.001	0.006	**

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

Species turnover in the fish assemblage structure was significantly different between geomorphic reef zones (PERMUTEST F = 10.8, Pr(>F) < 0.001). Species assemblage structure observed in RUVs grouped together in their location in the PCO plot according to geomorphic reef zone, with separation between assemblages from the respective geomorphic reef zones (**Error! Reference source not found.**). A similar pattern of overlap between fish assemblages between adjacent geomorphic reef zones was observed in RUVs, as in BRUVs.

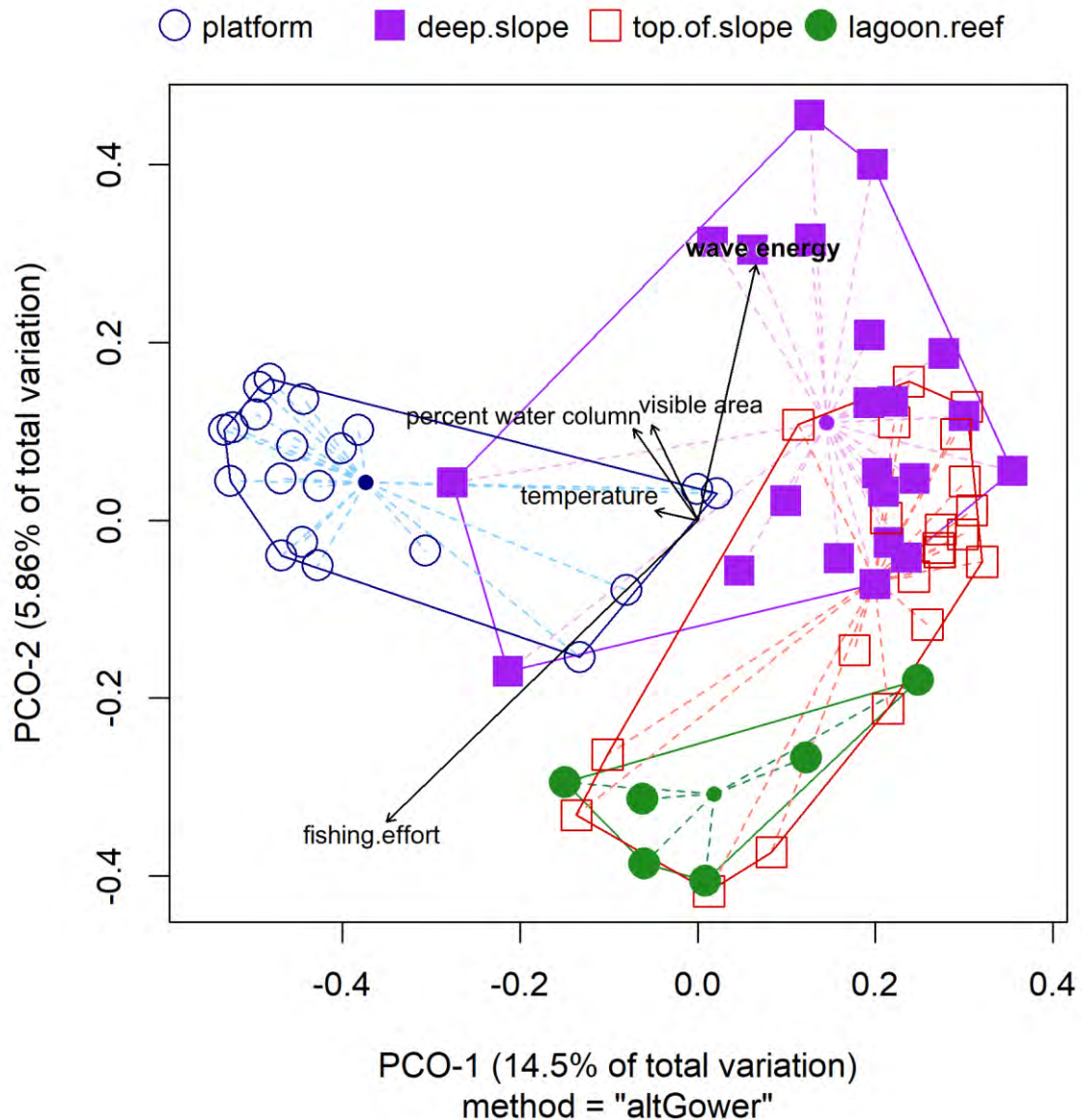


Figure 6.7. Principal Coordinate Ordination (PCO) plot showing dissimilarity between the fish assemblages recorded in the four geomorphic reef zones (coarse scale benthic habitat) as observed at Aldabra Atoll, using RUVs. Symbol and colour reflect geomorphic zone category. The direction and rate of increase of covariate values are indicated by the arrows in the plot.

6.4.2.3 Multivariate species assemblage structure in broad-scale benthic habitat from BRUVs

Sixty-eight samples from three broad-scale benthic habitats were included in the PERMANOVA analysis, after removing under-represented habitats. (Samples recorded in benthic habitat with fewer replicates than there were benthic habitat categories.) The Epilithic algal matrix and Seagrass benthic habitats were removed from the analysis as they

only two and three samples, respectively (Annex 6.1). There were no samples obtained from Macroalgal benthic habitat.

Species assemblage structure observed in BRUVs was significantly different among the three broad-scale benthic habitats categories (PERMANOVA $F = 1.4$, $Pr(>F) < 0.05$). Depth, temperature, rugosity and wave energy were significant in explaining variation in the assemblage structure observed in BRUVs (Table 6.10).

Table 6.10. PERMANOVA analysis of species assemblage observed using Baited Remote Underwater Video systems (BRUVs) in broad-scale benthic habitat at Aldabra Atoll in 3 to 58 m water depth between October 2012 and March 2015.

	Degrees freedom	Sum of squares	F	Pr(>F)	Significance
Percent water column	1	0.52	1.07	0.3	
Visible area	1	0.77	1.58	0.029	*
Temperature	1	1.16	2.39	0.0006	***
Wave energy	1	1.48	3.05	0.0002	***
Fishing effort	1	0.67	1.37	0.077	
Rugosity	4	5.26	2.70	0.0002	***
Depth	1	1.53	3.14	0.0002	***
Broad-scale benthic cover	2	1.36	1.40	0.026	*
Depth:Broad-scale benthic cover	2	1.11	1.14	0.18	
Residual	53	25.75			

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

Fish species assemblage structure observed using BRUVs was significantly different between each of the pairwise comparisons of assemblages in the broad-scale benthic habitat categories (Table 6.11).

Table 6.11. Pairwise PERMANOVA comparison of species assemblage across pairs of broad-scale benthic habitat categories observed in Baited Remote Underwater Video systems (BRUVs).

Habitat pairs	F.Model	R2	p	p.adjusted	Significance
Hard coral vs Rubble	4.144918	0.06461803	0.001	0.003	**
Hard coral vs Sand	5.213879	0.15239076	0.001	0.003	**
Rubble vs Sand	2.226728	0.05151276	0.001	0.003	**

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

Species turnover was significantly different among assemblages in broad-scale benthic habitat categories in BRUVs (PERMUTEST $F = 11.01$, $p < 0.001$), shown by the separation in location and variability in the spread of samples according to benthic habitat categories in the PCO plot (Figure 6.8). Species assemblages in hard-coral cover separated in their

location in the PCO plot from those in rubble or sand, supporting the findings of the PERMANOVA analysis.

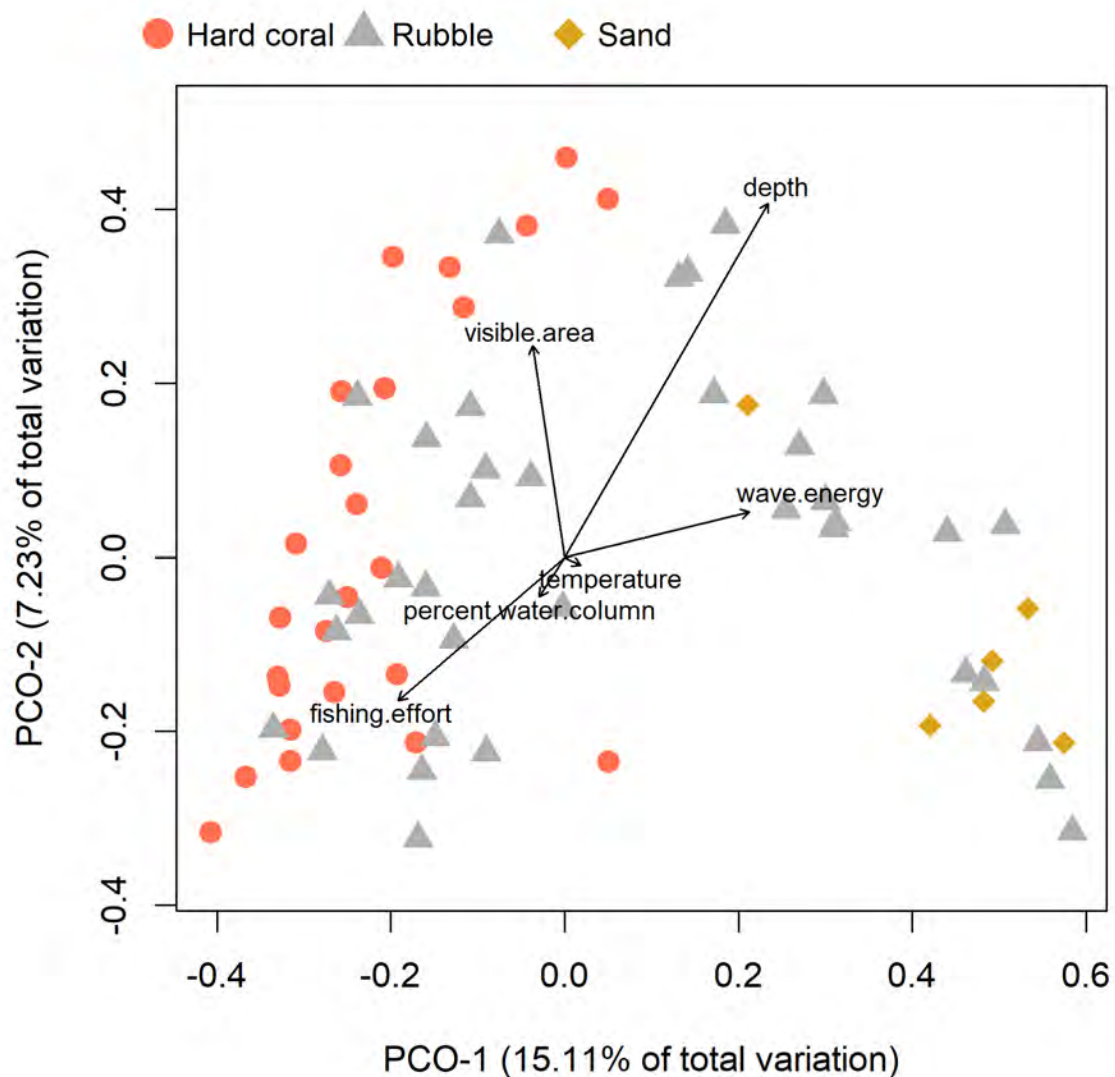


Figure 6.8. Principal Coordinate Ordination (PCO) showing dissimilarity of species assemblage structure at sampling sites in broad-scale benthic habitat at Aldabra Atoll, using BRUVs. Symbol and colour reflect broad-scale benthic habitat category. Length and direction of arrows indicate direction and rate of increase of covariate values.

6.4.2.4 Multivariate species assemblage structure in broad-scale benthic habitat from RUVs

Sixty-three samples of fish assemblages observed in RUVs from three broad-scale benthic habitats were included in the PERMANOVA after the removal of samples from the under-represented habitats. Underrepresented habitats included the two samples collected in Seagrass and four samples collected in Epilithic algal matrix which were removed, and there were no samples in Macroalgal benthic habitat (Annex 6.1). Macroalgal habitat was very rare

at Aldabra, and the sampling localities did not overlap with the few macroalgal habitats that were identified subsequent to sampling.

Fish species assemblage structure was not significantly different between the broad-scale benthic habitats (PERMANOVA $F = 1.27$, $\text{Pr}(> F) > 0.05$) in RUVs after the effects of the covariates were accounted for in the sequential PERMANOVA analysis (Table 6.12). The interactive effect of depth and broad benthic habitat category on the fish assemblage structure was also not significant (PERMANOVA $F = 1.24$, $\text{Pr}(> F) > 0.05$), suggesting that the effect of depth was consistent within the various broad-scale habitat categories. Depth, wave energy, fishing effort, temperature, rugosity and visible area were significant in explaining variation in the data (Table 6.12).

Table 6.12. Sequential PERMANOVA analysis of fish assemblages observed using RUVs in broad-scale benthic habitats at Aldabra Atoll in 3 to 58 m water depth between October 2012 and March 2015.

	Degrees freedom	Sum of squares	F	Pr(>F)	Significance
Percent water column	1	0.53	1.09	0.26	
Visible area	1	1.00	2.05	0.0036	**
Temperature	1	0.83	1.71	0.017	*
Wave energy	1	1.84	3.78	0.0002	***
Fishing effort	1	1.04	2.14	0.0026	**
Rugosity	1	2.06	4.25	0.0002	***
Depth	1	1.24	2.55	0.0006	***
Broad-scale benthic cover	2	1.23	1.27	0.074	
Depth:Broad-scale benthic cover	2	1.21	1.24	0.084	
Residual	51	24.78			

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

The locality of samples in the PCO plot indicated some grouping according to the benthic habitat category in which they were collected, indicating similarity of fish assemblage structure within the same broad-scale benthic habitat (Figure 6.9). The grouping of samples collected in Hard coral suggests that fish assemblage structure was more similar to samples within the same habitat than samples collected in Rubble or Sand.

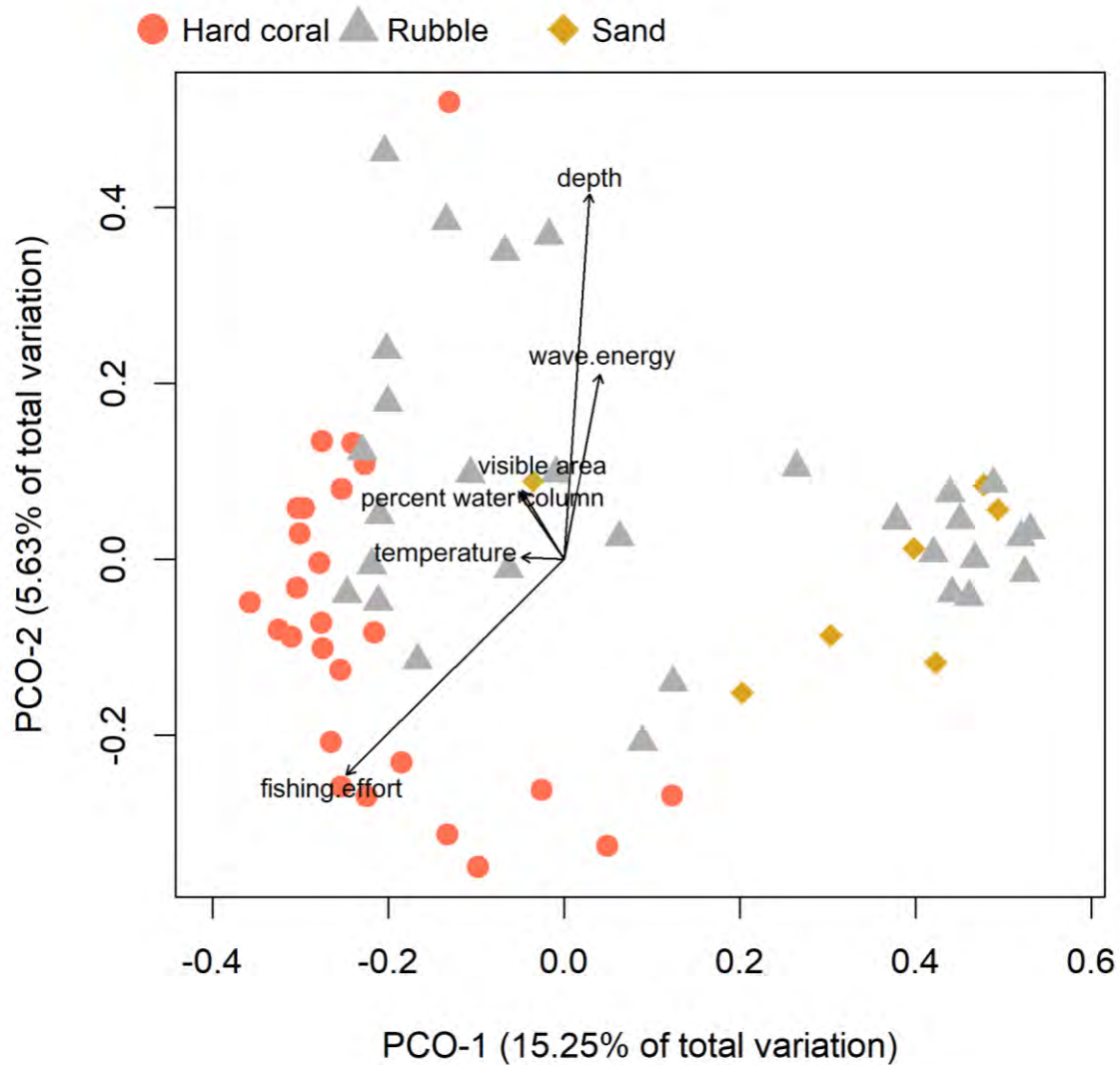


Figure 6.9. Principal Coordinate Ordination (PCO) showing the dissimilarity between fish assemblage structure in broad-scale benthic habitats at Aldabra Atoll in 3 to 58 m water depth between October 2012 and March 2015 using Remote Underwater Video systems (RUVs) samples. Symbols are coloured according to broad-scale benthic habitat category. The rate and direction of increase of covariates are indicated by the arrows.

The species turnover was significantly different among broad-scale benthic habitats (PERMUTEST $F = 12.1$, $\text{Pr}(> F) < 0.001$).

6.4.2.5 Multivariate species assemblages in fine-scale benthic habitats observed in BRUVs

Under-represented habitats that were removed prior to the analysis comprised "Fleshy macroalgae", "Heterogeneous sand macroalgae and EAM (Epilithic Algal Matrix)", "Heterogeneous seagrass macroalgae and EAM", "High density seagrass", and "Sand", leaving 65 samples in total for analysis distributed between six fine-scale habitat categories.

Fish assemblage structure observed in BRUVs was significantly different between the fine-scale benthic habitats (PERMANOVA $F = 3.38$, $p < 0.001$). Depth, wave energy, fishing effort, temperature, rugosity and the visible area were all significant in explaining variation in the fish assemblages observed in BRUVs (Table 6.13).

Table 6.13. Sequential PERMANOVA results for species assemblage structure observed in Baited Remote Underwater Video systems (BRUVs) at the fine-scale habitat at Aldabra Atoll in 3 to 58 m water depth between October 2012 and March 2015.

	Degrees freedom	Sum of squares	F	Pr(>F)	Significance
Percent water column	1	0.57	1.23	0.15	
Visible area	1	0.78	1.69	0.017	*
temperature	1	0.91	1.96	0.003	**
Wave energy	1	1.39	3.00	0.0002	***
Fishing effort	1	0.79	1.70	0.017	*
Rugosity	4	4.64	2.50	0.0002	***
Depth	1	1.80	3.90	0.0002	***
Fine benthic cover	5	3.38	1.46	0.0008	***
Depth:Fine benthic cover	5	2.48	1.07	0.26	
Residual	45	20.84			

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$

The species assemblage structure observed in BRUVs was significantly different from between nine of the pairwise comparisons out of 16 pairwise comparisons of assemblages in fine-scale benthic habitat (Table 6.13). Significant differences in fish assemblage structure were observed between coral dominated categories, including “Soft coral and *Physogyra* and *Isopora palifera*”, “Branching and corymbose and short staghorn coral” and “*Halimeda*” compared to “Epilithic algal matrix (EAM)”, “Sand and EAM and Gorgonian fans” and “Rubble and sand hard coral”.

1 **Table 6.14.** Pairwise PERMANOVA comparisons of fish species assemblage structure between six categories of fine-scale benthic habitats on
 2 seaward reefs in 0 – 55 m depth at Aldabra Atoll observed using Baited Remote underwater video systems (BRUVs).

Habitat pairs	F.Model	R ²	p.value	p.adjusted	Sign
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs Epilithic algal matrix (EAM)	2.52	0.16	0.002	0.030*	*
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs Branching and corymbose and short staghorn coral	1.26	0.04	0.106	1.000	
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs Halimeda	0.83	0.06	0.796	1.000	
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs Sand and EAM and Gorgonian fans	3.45	0.19	0.001	0.015	*
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs Rubble and sand hard coral	2.21	0.10	0.005	0.075	
Epilithic algal matrix (EAM) vs Branching and corymbose and short staghorn coral	3.22	0.11	0.001	0.015	*
Epilithic algal matrix (EAM) vs <i>Halimeda</i>	1.90	0.15	0.002	0.030	*
Epilithic algal matrix (EAM) vs Sand and EAM and Gorgonian fans	4.12	0.23	0.001	0.015	*
Epilithic algal matrix (EAM) vs Rubble and sand hard coral	3.50	0.16	0.001	0.015	*
Branching and corymbose and short staghorn coral vs <i>Halimeda</i>	1.41	0.05	0.027	0.405	
Branching and corymbose and short staghorn coral vs Sand and EAM and Gorgonian fans	5.80	0.17	0.001	0.015	*
Branching and corymbose and short staghorn coral vs Rubble and sand hard coral	4.58	0.12	0.001	0.015	*
<i>Halimeda</i> vs Sand and EAM and Gorgonian fans	2.47	0.16	0.002	0.030	*
<i>Halimeda</i> vs Rubble and sand hard coral	1.48	0.08	0.037	0.555	
Sand and EAM and Gorgonian fans vs Rubble and sand hard coral	1.84	0.08	0.010	0.150	

3 Significance levels: < 0.001 = ***, < 0.01 = **, < 0.05 = *

There was a significant turnover of species between fine-scale benthic habitats in BRUVs (PERMUTEST $F = 5.69$, $p < 0.001$). The PCO points, representing the dissimilarity between fish assemblage structures, grouped in their location in the PCO according to the fine-scale benthic habitat in which the samples were collected (Figure 6.10). The PCO suggested that fish assemblages sampled within “Soft coral and *Physogyra* and *Isopora palifera*” and “Branching and corymbose and short staghorn coral” shared similarities in their assemblage structure. Their assemblage structures were distinct from those sampled in “Rubble and sand hard coral” and “Sand and EAM and Gorgonian fans”.

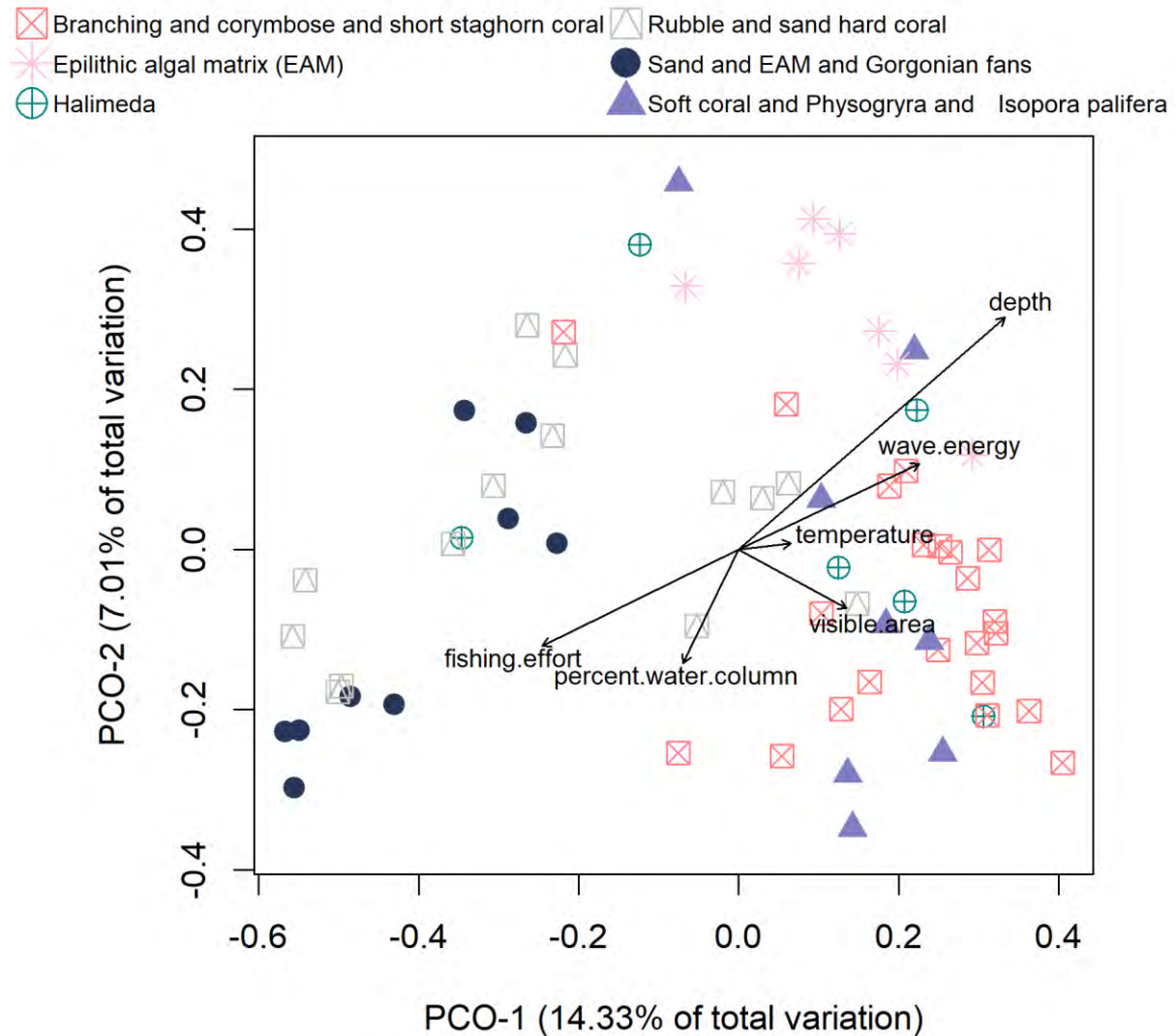


Figure 6.10. Principal Coordinate Ordination showing the dissimilarity between fish assemblages in various fine-scale benthic habitat categories at the seaward reefs at Aldabra Atoll in 3 to 58 m depth recorded using Baited Remote Underwater Video systems (BRUVs). Colours and symbols indicate the fine-scale benthic habitat category. Length and direction of arrows indicate direction and rate of increase of environmental covariates.

6.4.2.6 Multivariate analysis of fish assemblage structure in fine-scale benthic habitat from RUVs

Fifty-six samples from six fine-scale benthic habitat categories were analysed after removing under-represented benthic habitat categories. Fish species assemblage structure was significantly different between fine-scale habitats (PERMANOVA $F = 1.44$, $\text{Pr}(> F) < 0.001$) and the interaction of habitat and depth (PERMANOVA $F = 1.38$, $\text{Pr}(> F) < 0.01$) after taking the effects of covariates into account in sequential PERMANOVA (Table 6.15). Depth, wave energy, rugosity, fishing pressure and visible area were all significant in explaining variation in the fish assemblages observed in RUVs (Table 6.15).

Table 6.15. Sequential PERMANOVA results showing the effects of covariates on the fish species assemblage structure among fine-scale benthic habitat at Aldabra Atoll, observed in RUVs samples.

	Degrees freedom	Sum of squares	F	Pr(>F)	Significance
Percent water column	1	0.59	1.38	0.068	
Visible area	1	0.72	1.66	0.0152	*
Temperature	1	0.57	1.33	0.079	
Wave energy	1	1.56	3.62	0.0002	***
Fishing effort	1	0.98	2.27	0.0006	***
Rugosity	1	2.11	4.91	0.0002	***
Depth	1	1.03	2.40	0.001	**
Fine benthic cover	5	3.11	1.44	0.0006	***
Depth:Fine benthic cover	5	2.96	1.38	0.003	**
Residual	39	16.78			

Significance levels: < 0.001 = ***; < 0.01 = **; < 0.05 = *

The pairwise PERMANOVA confirmed that fish assemblages sampled in “Branching and corymbose and short staghorn coral” were significantly different from fish assemblages from all other benthic habitats, other than those sampled in “Soft coral and *Physogyra* and *Isopora palifera*”) (Table 6.16). Fish assemblages sampled in “Epilithic algal matrix” were also significantly different from assemblages from all other benthic habitats other than those in *Halimeda* (Table 6.16).

Table 6.16. Pairwise PERMANOVA of fish species assemblage structure in Remote underwater Video systems (RUVs) between pairs of six fine-scale benthic habitat categories at the seaward reefs of Aldabra Atoll in 3 to 58 m depth.

Pairs	F.Model	R ²	p.value	p.adjusted	Significance
Sand and EAM and Gorgonian fans vs Branching and corymbose and short staghorn coral	4.52	0.15	0.001	0.015	*
Sand and EAM and Gorgonian fans vs Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i>	1.60	0.10	0.037	0.555	
Sand and EAM and Gorgonian fans vs Epilithic algal matrix (EAM)	3.23	0.18	0.001	0.015	*
Sand and EAM and Gorgonian fans vs <i>Halimeda</i>	2.10	0.14	0.004	0.060	
Sand and EAM and Gorgonian fans vs Rubble and sand hard coral	0.83	0.06	0.813	1.000	
Branching and corymbose and short staghorn coral vs Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i>	1.83	0.07	0.006	0.090	
Branching and corymbose and short staghorn coral vs Epilithic algal matrix (EAM)	1.90	0.07	0.002	0.030	*
Branching and corymbose and short staghorn coral vs <i>Halimeda</i>	2.42	0.09	0.001	0.015	*
Branching and corymbose and short staghorn coral vs Rubble and sand hard coral	4.81	0.17	0.001	0.015	*
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs Epilithic algal matrix (EAM)	1.77	0.11	0.003	0.045	*
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs <i>Halimeda</i>	1.21	0.09	0.137	1.000	
Soft coral and <i>Physogyra</i> and <i>Isopora palifera</i> vs Rubble and sand hard coral	1.87	0.13	0.007	0.105	
Epilithic algal matrix (EAM) vs <i>Halimeda</i>	1.54	0.10	0.004	0.060	
Epilithic algal matrix (EAM) vs Rubble and sand hard coral	3.35	0.20	0.001	0.015	*
<i>Halimeda</i> vs Rubble and sand hard coral	2.09	0.16	0.014	0.210	

Significance levels: < 0.001 = ***, < 0.01 = **, < 0.05 = *

The species turnover in fish species assemblages observed in RUVs was significantly different between fine-scale benthic habitats (PERMUTEST $F = 3.69$, $\text{Pr}(> F) < 0.01$).

The fish assemblages grouped according to the benthic habitat category in which they were sampled, suggesting greater assemblage similarity within a habitat category than between different habitats (Figure 6.11). Fish assemblages sampled in “Soft coral and *Physogyra* and *Isopora palifera*” and “Branching and corymbose and short staghorn coral” grouped together, and close to those sampled in Epilithic algal matrix and *Halimeda*, suggesting a structural similarity between fish assemblages in these benthic habitats. Fish assemblages sampled in Sand with Gorgonian fans and Rubble grouped further away from the aforementioned assemblages, suggesting that these assemblages were more different from each other.

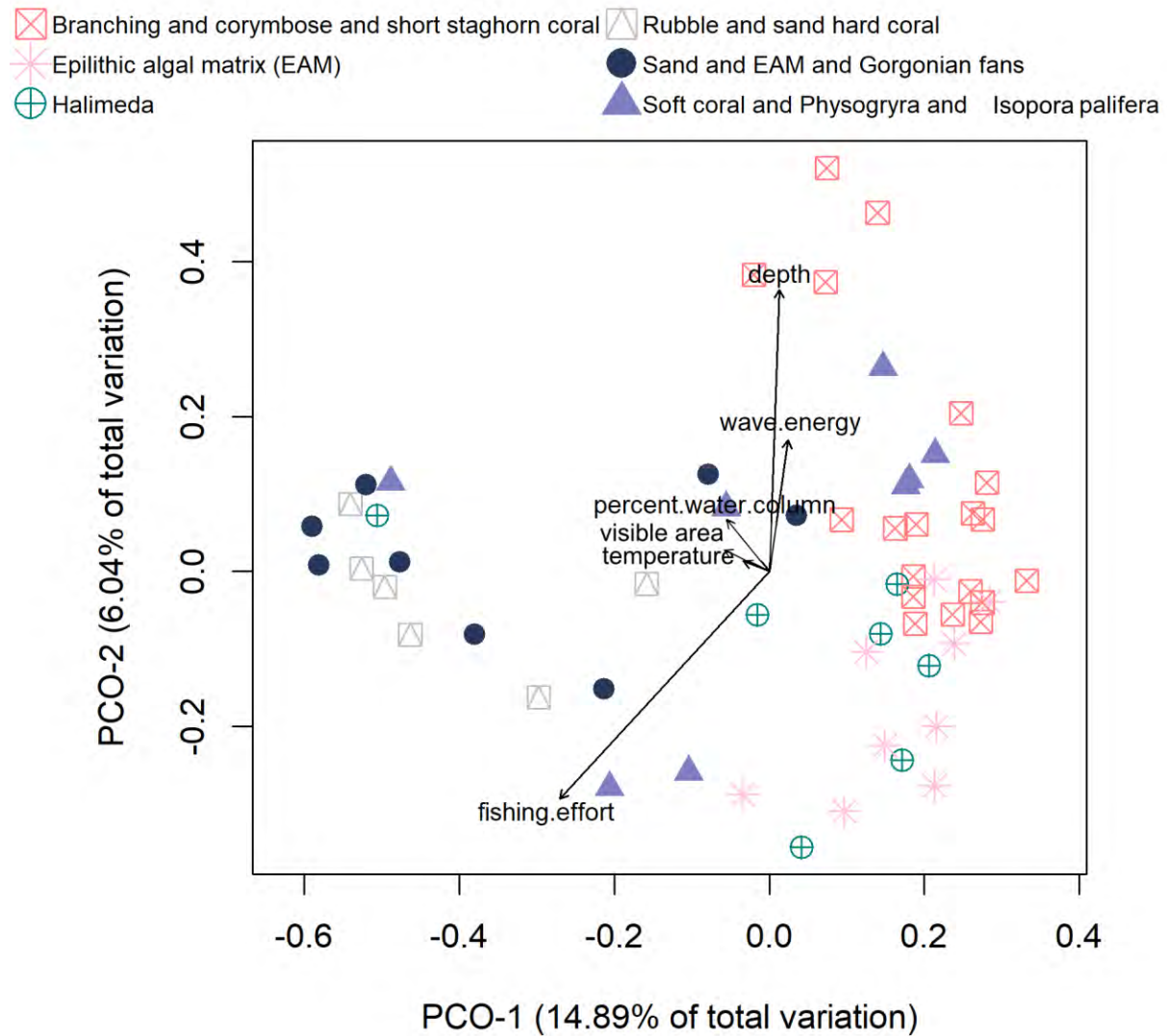


Figure 6.11. Principal Coordinate Ordination (PCO) showing the dissimilarity between fish assemblages among fine-scale benthic habitats in Remote Underwater Video systems (RUVs). Colour and symbol indicate the fine-scale benthic habitat category. The direction and rate of increase of covariates are indicated by the arrows.

6.4.2.7 Turnover in fish assemblage across habitat scale

The turnover of species from fish assemblages between benthic habitats was significantly different across habitat scales observed using BRUVs (univariate permutational ANOVA $F = 4.61$, $p < 0.01$) and RUVs (univariate permutational ANOVA $F = 6.55$, $p < 0.01$). Species turnover was the greatest between broad-scale benthic habitat categories and lowest between fine-scale benthic habitat categories in both BRUVs and RUVs (Table 6.17).

Table 6.17. Species turnover between the benthic habitats for each of the habitat scales (mean dispersion distance to centroids). The mean distance of samples to group centroids of the principal coordinates is the mean dispersion of samples within each habitat scale. Groups refers to the respective benthic habitat categories within a single habitat scale. Sample size (n).

Treatment	Scale	Mean dispersion distance	Standard error	n
Baited	Geomorphic zone	0.69	0.01	73
	Broad-scale benthic	0.72	0.01	68
	Fine-scale benthic	0.67	0.01	66
Unbaited	Geomorphic zone	0.68	0.011	69
	Broad-scale benthic	0.71	0.012	63
	Fine-scale benthic	0.65	0.011	57

6.4.2.8 Species variation within size-classes across habitat scales

The species turnover between benthic habitats in the BRUVs data was significantly different across the habitat scales within all size-classes of Actinopterygii fish, but not for any of the size-classes of Elasmobranchs (Table 6.18). Turnover of assemblage structure was greater between geomorphic reef zones and broad-scale benthic habitats than between fine-scale benthic habitats.

Table 6.18. Mean multivariate dispersion distance (mean distance) within fish size-classes from BRUVs for the three habitat scales, standard error (SE), number of samples (n), and univariate PERMANOVA results for each size-class (F, Pr(>F), and significance). “NA” was used to indicate that no comparison was possible for size-classes with too few samples.

Class	size	scale	mean distance	SE	n	F	Pr (>F)	Significance
<i>Actinopterygii</i>	very small	Geomorphic zone	1.065	0.01	67	3.42	0.0386	*
		Broad-scale	1.064	0.01	63			
		Fine-scale	1.026	0.01	64			
	small	Geomorphic zone	1.221 ^(2,3)	0.01	65	18.79	0.0002	***
		Broad-scale	1.140 ⁽¹⁾	0.01	60			
		Fine-scale	1.137 ⁽¹⁾	0.01	62			
	medium	Geomorphic zone	1.413 ^(2,3)	0.01	70	64.03	0.0002	***
		Broad-scale	1.255 ^(1,3)	0.01	65			
		Fine-scale	1.329 ^(1,2)	0.01	64			
	large	Geomorphic zone	0.869 ⁽³⁾	0.01	73	12.92	0.0002	***
		Broad-scale	0.872 ⁽³⁾	0.01	68			
		Fine-scale	0.800 ^(1,2)	0.01	66			
	very large	Geomorphic zone	1.168 ⁽²⁾	0.01	66	8.73	0.0008	***
		Broad-scale	1.173 ⁽³⁾	0.01	61			
		Fine-scale	1.100 ^(1,2)	0.01	60			
<i>Elasmobranchii</i>	small	Geomorphic zone	0.311	0.05	29	0.49	0.6188	
		Broad-scale	0.367	0.05	25			
		Fine-scale	0.307	0.04	25			
	medium	Geomorphic zone	0.165	0.01	59	0.12	0.8912	
		Broad-scale	0.159	0.01	56			
		Fine-scale	0.155	0.01	53			
	large	Geomorphic zone	0.665	0.03	40	1.06	0.3510	
		Broad-scale	0.677	0.03	38			
		Fine-scale	0.619	0.03	36			
	very large	Geomorphic zone	0.525	0.03	39	0.68	0.5166	
		Broad-scale	0.545	0.03	37			
		Fine-scale	0.495	0.03	33			
	very small	NA	NA	NA	10	NA	NA	

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$; Pairwise PERMANOVA post-hoc test, mean distance followed by superscript: ⁽¹⁾ significantly different to geomorphic reef zone, ⁽²⁾ significantly different to broad-scale benthic habitat, ⁽³⁾ to significantly different to fine-scale benthic habitat .

The species turnover across habitat scales was significantly different within very small, small, medium size-classes of Actinopterygii, and within large Elasmobranchs observed in RUVs (Table 6.19). There were no significant differences between the amount of species turnover across habitat scales within very large Actinopterygii and most size-classes of Elasmobranch (Table 6.19). Species variation was, again, greater between fish assemblages at the geomorphic zone and broad-scale benthic habitat level than between assemblages at the fine-scale. The greatest levels of species variation were observed in the medium size-class of Actinopterygii fish between benthic habitats at the geomorphic and broad-scale benthic.

Table 6.19. Mean multivariate dispersion distance (mean and standard error (SE) distance) within each size-class from RUVs for the three habitat scales. The number of samples (n), and significant differences between each size-class indicated by univariate PERMANOVA results (F, Pr (>F) and significance). "NA" was used to indicate that no comparison was possible for size-classes with too few samples.

Class	Size	Scale	Mean distance	SE	n	F	Pr (>F)	Significance
Actinopterygii	very small	Geomorphic zone	0.929 ⁽³⁾	0.01	67	27.403	0.0002	***
		Broad-scale	0.934 ⁽³⁾	0.01	61			
		Fine-scale	0.825 ^(1,2)	0.01	57			
	Small	Geomorphic zone	0.809 ⁽³⁾	0.01	65	31.464	0.0002	***
		Broad-scale	0.814 ⁽³⁾	0.01	59			
		Fine-scale	0.681 ^(1,2)	0.01	55			
	Medium	Geomorphic zone	1.111 ⁽³⁾	0.01	68	250.050	0.0002	***
		Broad-scale	1.103 ⁽³⁾	0.01	62			
		Fine-scale	0.794 ^(1,2)	0.01	56			
	Large	Geomorphic zone	0.864 ⁽³⁾	0.01	68	16.106	0.0002	***
		Broad-scale	0.869 ⁽³⁾	0.01	62			
		Fine-scale	0.768 ^(1,2)	0.01	56			
	very large	geomorphic zone	0.805	0.02	51	1.838	0.1596	
		Broad-scale	0.805	0.02	46			
		Fine-scale	0.761	0.02	42			
Elasmobranchii	Small	Geomorphic zone	0.229	0.04	14	1.655	0.1980	
		Broad-scale	0.285	0.09	10			
		Fine-scale	0.127	0.06	11			
	Medium	Geomorphic zone	0.074	0.02	22	2.612	0.8140	
		Broad-scale	0.089	0.02	21			
		Fine-scale	0.035	0.02	17			
	Large	Geomorphic zone	0.508 ⁽³⁾	0.06	16	5.226	0.0104	*
		Broad-scale	0.531	0.05	15			
		Fine-scale	0.255 ⁽¹⁾	0.08	11			
	very large	Geomorphic zone	0.365	0.12	6	3.0196	0.087	
		Broad-scale	0.222	0.11	6			
		Fine-scale	0	0	5			
	very small	NA	NA	NA	10	NA	NA	

Significance levels: $< 0.001 = ***$; $< 0.01 = **$; $< 0.05 = *$; Pairwise PERMANOVA post-hoc test, mean distance followed by superscript: (1) significantly different to geomorphic reef zone, (2) significantly different broad-scale benthic habitat, (3) to significantly different to fine-scale benthic habitat

6.5. DISCUSSION

This study compared the fish species assemblage structure within and across three scales of habitat, namely the geomorphic reef zones, broad-scale benthic habitats, and fine-scale benthic habitats of Aldabra Atoll. This study also compared the turnover (change in species diversity between samples relative to the overall diversity) of fish species within size-classes across these three scales of benthic habitat, to assess if there was a relationship between fish size and the scale of the habitat. The results of the study showed significant variation in fish assemblages between the different benthic habitats of the same scale, and significant species turnover within fish assemblages across benthic habitats of different scales. This study showed some size-classes of Actinopterygii had significant levels of species turnover across different scales of habitat but this was rarely the case with the elasmobranchs. The results from this chapter demonstrated that habitat was a significant driver of fish assemblage structure at all three of the hierarchical scales at which habitat was defined.

6.5.1 Fish assemblage structure and turnover between benthic habitats

In general, there were significant differences in the fish assemblage structure between the respective benthic habitat categories, at all three scales, after accounting for the effects of a range of other environmental variables. The significant difference in fish assemblages between the geomorphic reef zones was supported by previous studies (Parrish and Boland 2004; Fitzpatrick et al. 2012). The correlation among geomorphic reef zones and depth is likely to explain some of the variation observed between fish assemblages in different geomorphic reef zones. This was illustrated by the increasing dissimilarity of assemblage structure with depth in the PCO plots, and lower variance between fish assemblages from adjacent geomorphic reef zones than disjunct zones in pairwise comparisons. In fact, depth was a highly significant explanatory variable in all analyses, and its importance in structuring fish assemblages was consistent with previous studies (Brokovich et al. 2008; Heyns-Veale et al. 2016). In addition to a change in depth, geomorphic reef zones also represent a change in the gradient of the reef slope, temperature, and visibility, and typically contain a few broad- and fine-scale habitats. Geomorphic zones are therefore a useful high-level habitat grouping when multiple other environmental variables and finer scales of benthic habitat are unknown.

The differences in fish assemblages between broad-scale benthic habitats were only detected when using BRUVs, but not RUVs. The presence of bait in BRUVs was shown to alter the fish assemblage structure by attracting generalist carnivores in greater abundance

and making assemblages more distinctive than in RUVs (Chapter 4), a finding that is supported by previous studies (Harvey et al. 2007; Bernard and Götz 2012). The more distinctive fish assemblages observed using BRUVs may explain why differences in fish assemblages were detected between different broad-scale habitats for BRUVs but not RUVs. However, these conclusions would be strengthened by further sampling of the full complement of benthic habitat categories in future. The exclusion of under-sampled benthic habitats from the analysis is a shortcoming in this study which stresses the need for sampling designs to be based on habitat maps *a priori*, rather than assigning fish according to habitat after sampling, as has been suggested previously (Mellin et al. 2009).

The pairwise comparisons of fish assemblages between habitats (within the same scale) showed that fish assemblages were significantly different between all geomorphic zones and all broad-scale benthic habitats but not between all pairwise comparisons of fine-scale benthic habitat categories. There were no differences in the fish assemblages between the fine-scale benthic habitats that were of the same broader-scale benthic habitat category. For example, fish assemblages observed in hard coral dominated habitat, such as “Branching, corymbose and short staghorn coral” and “Soft coral, *Physogyra* and *Isopora palifera*” were not significantly different from each other, but both were significantly different from fish assemblages sampled in “Sand with Gorgonian fans”, and “Rubble, sand and hard coral”. These results suggest that variation in the reef fish assemblage caused by differences in benthic habitat, as observed using BRUVs or RUVs, may be adequately captured at the geomorphic or broad-scale benthic habitat level. Broad-scale habitat information may be suitable to represent the variation between reef fish assemblages observed using BRUVs or RUVs. However, broad-scale habitat may not adequately capture variation in different groups of fish, such as niche specialists with a strong association to particular micro-habitats (Ahmadia et al. 2012; Brandl et al. 2015), which BRUVs and RUVs record less effectively than SCUBA-based methods (Watson et al. 2005b; Colton and Swearer 2010).

Previous studies that have assessed fish assemblage associations with hierarchical scales of habitat, quantified habitat scales according to area-size class categories (Pittman et al. 2004; e.g. Friedlander et al. 2007; Wedding and Friedlander 2008; Sekund and Pittman 2017). The significant differences in the fish assemblage structure between habitats in this chapter was consistent with the aforementioned studies, finding significant differences in diversity and species richness among habitats occurring at spatial scales of 75 – 100 m, which roughly corresponds to the upper end of broad-scale and the lower end of geomorphic reef zone habitat as defined in my study (Pittman et al. 2004; Friedlander et al. 2007; Wedding and Friedlander 2008; Heyns-Veale et al. 2016; Sekund and Pittman 2017). Other

studies have shown that there are differences in the fish species diversity, species richness and biomass at the level of fine-scale benthic habitats, but not at broader benthic-habitat scales (Kuffner et al. 2007; MacNeil et al. 2009; Kendall and Miller 2010). The lack of consistency in support for the effects of broad-scale benthic habitats stems from inconsistencies in how the habitat assignment is applied and which parameters are used in the data analysis, making it difficult to compare findings among studies (Mellin et al. 2009). There is therefore still a need for a more standardised approach in defining or quantifying habitat to allow comparison of results among different studies. While not the objective of this study, the relationship between the patch size of benthic cover should be investigated in future studies, which may allow for better standardization of habitats, as used by Sekund and Pittman (2017).

6.5.2 Species variation across scale

There were significant differences in the turnover of fish species between benthic habitats across the habitat scales, with the highest turnover observed between broad-scale habitats, and the lowest turnover between fine-scale habitats in both the BRUVs and RUVs data. Fish assemblages associated with the broad-scale Rubble category had the greatest within-group turnover, sharing similarities in fish assemblage structure with those from the Sand category and with the Hard coral category. The higher levels of species turnover between broad-scale habitats than geomorphic reef zones may be explained by the very broad definitions used, such as Hard coral, which is a single category that in some instances exceeds the ecological niche space of geomorphic reef zones where the forereef is separated into the two distinct zones. A potential drawback of blindly using broad-scale benthic habitat maps to associate benthic data with fish assemblages is that it does not account for between-site heterogeneity from one sampling site to the next. This use of broad-scale benthic habitat from habitat maps may be ineffective to assess fish assemblages if it does not adequately represent differences in benthic composition at the scale at which fish assemblages change. Previous studies have used the percentage cover of the respective benthic types at each site to establish the correlative relationships between benthic species and fish assemblages, which avoids assigning uniform habitat categories that do not capture between-site heterogeneity (Mellin et al. 2007; e.g. Fitzpatrick et al. 2012).

6.5.3 Species variation within size-classes across scale

In general, there was a significant difference in the amount of species turnover between species size-class categories across the habitat scales in both the RUVs and BRUVs

datasets. The results of the study showed that turnover within fish assemblages in each size-class of Actinopterygii fish was greater between geomorphic reef zones, and between broad-scale benthic habitats than between finer benthic habitats. A higher level of species turnover was expected in habitats of larger scales, as the species turnover between fine-scale habitats within larger scale habitats acts cumulatively. However, I did not find evidence to support the hypothesis that the change in species composition of smaller fish size-classes would be more affected by a change in benthic habitat than in larger size-classes of fish, as shown for *Perca fluviatilis* of different size classes in a lake ecosystem (Byström et al. 2003). The difference between these findings could be explained by the relationship between species phylogeny and habitat association, which may be masked when assessing diverse reef fish assemblages, of which some species may be habitat generalists, with only a few niche specialists (Wilson et al. 2008). Species level assessments may uncover habitat associations which are not immediately obvious at the assemblage level.

The results of this study did however show that the structure of each Actinopterygii size-class assemblage was significantly different between the scales of benthic habitats. However, only the large elasmobranchs' size-class assemblage structures were altered by a change in the habitat scales, when observed using RUVs. A plausible explanation for this difference between elasmobranchs and Actinopterygii fish is that Actinopterygii fish have smaller home ranges (Green et al. 2015) and distinct assemblages associate with the benthic habitats included in this study. Furthermore, the consistent high turnover of species within elasmobranch size-class assemblages between different benthic habitats provides evidence that elasmobranchs of all size classes operate at scales that exceed the scales of habitats assessed at Aldabra Atoll. For example, reef sharks that were recorded in this study have high site fidelity and strong habitat associations, including species like *Carcharias melanopterus*, *Negaprion acutidens* and *Carcharias amblyrhynchos* among others (Stevens 1984; Gaspar et al. 2008; Bond et al. 2012, 2015; Filmalter et al. 2013; Vianna et al. 2013), and were observed in samples of each of the geomorphic reef zones. Even at the broadest scale assessed, the geomorphic reef zone, the transition between the lagoon reef, forereef slope and reef apron, typically occurs over less than 1 km in a direction perpendicular to the shoreline. Given that most species of shark assessed in this study regularly travel more than 1 km (Stevens 1984; Gaspar et al. 2008; Bond et al. 2012, 2015; Filmalter et al. 2013; Vianna et al. 2013), the lack of differences in turnover between scales used may not be that surprising. The variability in elasmobranch home-range size, between species, and even between individuals of the same species (Stevens 1984; Gaspar et al. 2008; Bond et al. 2012, 2015; Filmalter et al. 2013; Vianna et al. 2013) suggests species-based analysis may be more insightful to study habitat-use in elasmobranchs, rather than attempting assemblage

based analysis. Site management for elasmobranchs at Aldabra may be improved by establishing the home ranges of distinct populations of these species and ensuring the protection of core ranges (e.g. Bond et al. 2012). The indications of habitat use beyond the scale at which habitats occur at Aldabra, suggests further studies of inter atoll movement of reef sharks are necessary to inform species management practices, given that large-scale movement has been shown for reef sharks (Heupel et al. 2010).

The exception to the result was the large-elasmobranch group observed in RUVs which had significantly lower species turnover between fine-scale benthic habitats than at broad-scale benthic habitat and geomorphic reef zones. Low species turnover between benthic habitats in RUVs but not BRUVs, suggests that large-elasmobranch assemblages are distinctive under natural conditions, but readily move between habitats in the presence of bait. Further studying movement of large sharks in response to the presence of bait is required to test this hypothesis, as previous studies have suggested a change in search behaviour in the presence of bait (Strong et al. 1992; Vabø et al. 2004). While not explicitly tested in this study, the higher turnover in BRUVs than RUVs between habitats within the same size-classes suggests that the use of bait interfered with natural assemblage structure by exaggerating species habitat associations, which was consistent with the findings of Chapters 4 and 5.

The results presented here were limited to species-size-classes, based on the maximum attainable size of a given species, and did not include individual fish size. The correlations between individual fish sizes and habitat have been shown to be stronger than those between habitat and species-size (Nash et al. 2013). Furthermore, habitat association has been shown to change with ontogenetic development of fish (McCormick and Makey 1997; e.g. Mumby 2006; Wilson et al. 2008). The use of species-size instead of individual size may therefore miss patterns of size-related turnover of species between habitats. Future studies assessing the relationships between size-classes and the scale of benthic habitat should be based on individual size, which is more accurate than species size and provides more reliable correlations between fish and habitat association (Nash et al. 2013).

6.5.4 Effects of environmental parameters

The effects of depth and wave energy on the fish assemblage structure were significant at all habitat scales in both BRUVs and RUVs. The effect of depth and wave energy not only directly impacts on the structure of fish assemblages, but also indirectly through altering the benthic habitat and other environmental variables, such as light and sediment distribution (Bradbury and Young 1981; Dollar 1982; Penta et al. 2008; Warner et al. 2008; Chollett and

Mumby 2012). The significant role of depth and wave energy as environmental modifiers of the fish assemblage structure was consistent with previous studies (Clark 1997; Friedlander et al. 2003; Zintzen et al. 2012; Heyns-Veale et al. 2016), and shows the importance of stratifying ecological fish surveys over a range of depth and wave energy conditions to obtain a representative sample of the fish community, or standardising these conditions to ensure comparability across monitoring periods..

In this study, analysis controlled for the effects of habitat rugosity, a critical component of structural habitat complexity, which affects species richness, diversity and biomass (Gratwicke and Speight 2005; Graham and Nash 2013; Ferrari et al. 2017). Habitat complexity has been shown to operate at multiple spatial scales on fish assemblages, but typically requires detailed bathymetric data to derive landscape-scale metrics at broader scales (Wedding et al. 2008; Pittman et al. 2009; Nash et al. 2014; Sekund and Pittman 2017). When detailed bathymetric data become available for Aldabra, structural habitat complexity should be derived to further the understanding of its effects on the fish assemblage structure at multiple scales. Additional useful multiscale variables can be obtainable from habitat maps including measures of the shape of habitat patches, isolation, proximity and connectivity measures (Turner 2005; Mellin et al. 2009; Kupfer 2012). Including the distance from the lagoon may be an important additional variable to consider given that fish assemblage structures may change in response to habitat availability with a change in tide (Chapter 5).

6.5.5 Effects of fishing pressure

In general, the effects of fishing effort had a significant effect on the fish assemblage structure observed in both the RUVs and BRUVs. While the fishing effort was negatively correlated with wave energy, the effects of wave energy were accounted for prior to testing the effects of fishing effort on the residual turnover in the PERMANOVA analysis. The measure of fishing effort on the fish assemblage structure employed in this study may therefore be conservative, and the effects of fishing may be stronger in reality. These results provide evidence that the fishing effort is having an effect on the composition and structure of the fish community, which is in contrast to the conclusions of Pistorius and Taylor (2009) which were used to explain the recorded declines of fished species at Aldabra. The results of this study suggested that BRUVs and RUVs were 1) sensitive to the effects of fishing and therefore future sampling distribution for ecological studies at Aldabra require control or stratification of sampling designs to account for differences that fishing has on the fish assemblage, and 2) that BRUVs and RUVs are both appropriate methods to detect changes

in the fish assemblage resulting from fishing effort, which can inform management decisions at Aldabra. The use of individual fish size ought to provide an even more sensitive parameter to detect the effects of fishing, as a change in the size of fish usually precedes a change in composition or assemblage structure. The effects of subsistence fishing at Aldabra may therefore be having a bigger effect than previously thought (e.g. Pistorius and Taylor 2009). The results provide further evidence that even low levels of fishing pressure can have detrimental effects on the fish population structure (Dulvy et al. 2004b, 2004a; Goetze et al. 2011).

6.5.6 Conclusion

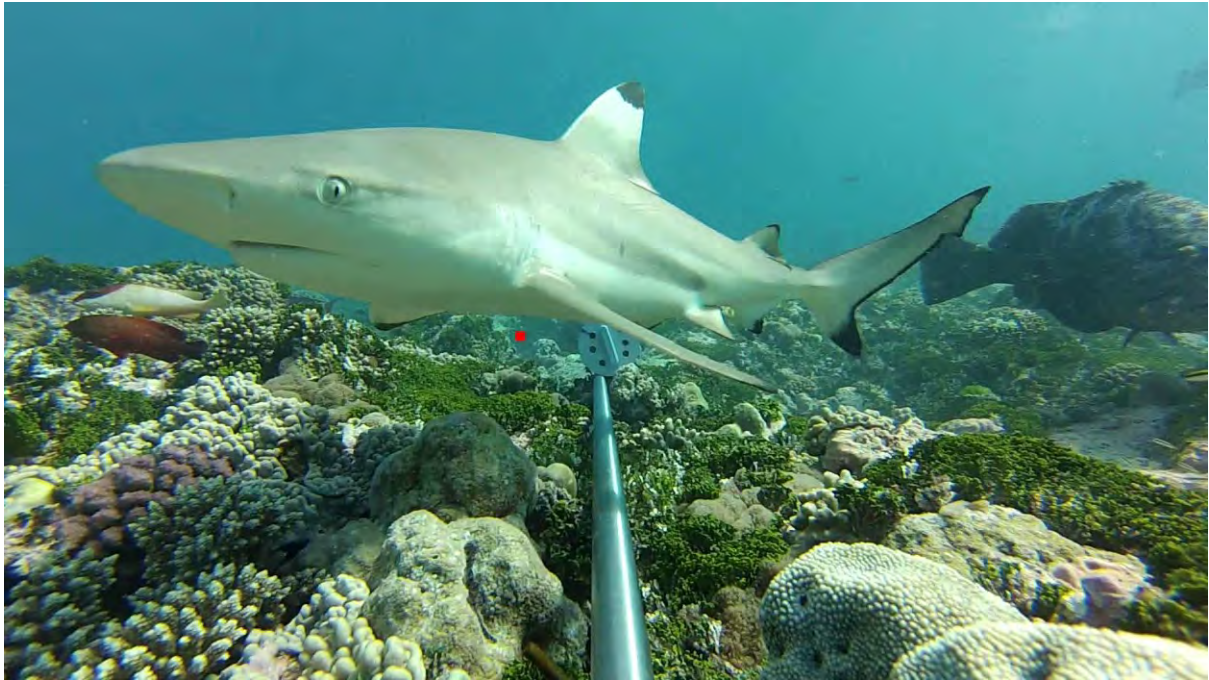
This study was the first to assess the effects of benthic habitats at multiple scales on the fish assemblage structure at Aldabra, and the first to compare fish assemblages observed in BRUVs and RUVs among multiple thematic benthic habitat scales. The significant differences between fish assemblages in different benthic habitats at all three scales have implications for site and resource management. For example, the findings highlight the importance of incorporating a representative set of benthic habitats, and the need for replication of these, to inform MPA designs to ensure protection to fish assemblages that differ between benthic habitats.

The pairwise comparisons of fish assemblages in fine-scale and broad-scale benthic habitats suggested that broad-scale benthic habitat was sufficient to capture significant levels of variation when using BRUVs or RUVs. The level of habitat information obtained from reef-mapping exercises may therefore be sufficient to account for the difference in habitat when assessing fish assemblages once off. However, when the objective is to detect a change in the fish assemblage, the lower levels of species turnover detected in all size-classes of Actinopterygii between fine-scale benthic habitats relative to between-broad-scale benthic habitats may be desirable. Data on fine-scale benthic habitats are better collected *in situ*, as habitat mapping studies at the fine-scale level are not often available, and have relatively low accuracy. The habitat association of Actinopterygii fish at all scales of habitat was contrasted by the lack of habitat association in elasmobranchs. The low levels of species turnover at all benthic habitat scales suggests that elasmobranchs operate on greater spatial scales than the scales at which habitat occurs within Aldabra Atoll. This highlights that conservation strategies should protect the entire Atoll and that protection of adjacent islands may be necessary to fully protect populations of elasmobranchs, which is consistent with previous recommendations for shark conservation (e.g. Heupel et al. 2010, 2015). The highly complex nature of fish assemblage structures in relation to benthic habitat

and the multitude of environmental variables that influence coral reef ecosystems means that continued research efforts are required to elucidate the patterns and processes that underpin fish assemblage structures (Bellwood and Hughes 2001).

While not the aim of this chapter, it was clearly shown that even light levels of fishing significantly altered the fish assemblage structure. It is recommended that fishing is better managed, limiting fishing to food security areas while closing most of the atoll's reefs to fishing. Less damaging fishing practices, such as pelagic fishing as opposed to bottom fishing should be promoted to reduce the impact on long-lived slow growing species. The comparatively light levels of fishing effort at Aldabra, relative to most other reefs in the Western Indian Ocean (WIO), strongly suggests that fishing in the WIO is having a significant impact on the structure and therefore the functioning of reef fish assemblages throughout the region and warrants further investigation.

Chapter 7. General discussion



Black tip reef shark over a shallow reef on the west coast of Aldabra observed using a Baited Remote Underwater Video system (BRUVs)

Tropical reef ecosystems are some of the most diverse ecosystems in the world, and nearly a quarter of all marine fish are associated with their habitats (Spalding 2001). Tropical reef ecosystems provide productive shallow habitats such as coral reefs, seagrass beds and mangroves in which fish find food or shelter from predation (Beets and Friedlander 1999; Nagelkerken et al. 2002). The connectivity between these habitats mediates the completion of reef fish life cycle phases and enhances biomass on coral reefs (Nagelkerken et al. 2002; Gillanders et al. 2003; Mumby et al. 2004a, 2006; Dorenbosch et al. 2005; Adams et al. 2006). The profuse diversity harboured by coral reefs, and its significant value to millions of people who rely on reef fisheries are under constant threat from multiple stressors such as global climate change, alien species, pollution and overfishing (Bellwood et al. 2004; Veron et al. 2009; Cinner et al. 2012). The rapid degradation of tropical reef ecosystems requires urgent action to understand these systems to inform appropriate management action before they are irreversibly changed (Pauly 1995; Graham and McClanahan 2013).

The impacts of environmental and anthropogenic disturbances on tropical reef ecosystems have been the subject of detailed studies, but the associations between reef fish assemblages and benthic habitats, and how environmental drivers change this relationship is highly variable and remains a key challenge to studies of reef ecology (Friedlander and Parrish 1997; Friedlander et al. 2003, 2010; Graham and McClanahan 2013; Robinson et al. 2018; Samoilys et al. 2018).

The relationship between reef fish and benthic habitat, and the relative influence of environmental variability on coral reef ecosystems has been impacted on by multiple pervasive anthropogenic and environmental stressors, making it difficult to understand the true nature and complexities of these associations (Baum and Myers 2004; Knowlton and Jackson 2008). The urgent need for baseline ecological data on benthic communities and reef fish has been met by international efforts to study remote sites least affected by anthropogenic impacts (e.g. National Geographic's Pristine Seas expeditions, NOAA's monitoring of remote reefs in the Pacific, Catlin seaview survey). These remote sites represent the remaining areas where ecosystem processes are thought to be intact, referred to as pristine or wilderness sites (Graham and McClanahan 2013).

Most coral reefs in the Western Indian Ocean (WIO) have been heavily modified by direct anthropogenic impacts, in particular overfishing, against a backdrop of rapid degradation of coral reefs as a result of climate change (McClanahan et al. 2007b; Graham et al. 2017). This thesis presented results from Aldabra Atoll, a remote, isolated, near-pristine coral atoll with a history of minimal and well-recorded local human disturbances. The results from this thesis therefore provide a valuable ecological reference point of near-natural benthic habitat

and fish assemblages and their relationship for the Western Indian Ocean (WIO) region (Stoddart 1968a, 1971; Downing et al. 2005a; Stobart et al. 2005). Ecological reference points from an isolated oceanic atoll may not fully capture all the ecological nuances of mainland reefs in the WIO, which may be influenced by greater connectivity between habitats along the length of coastline. There are however very few intact reefs remaining at mainland coastlines in WIO (Francis et al. 2002; McClanahan et al. 2007b; Graham and McClanahan 2013). Given the lack of intact reefs remaining along the mainland coast of the WIO, reference points from remote and intact reefs like Aldabra may represent the best comparable baseline conditions for WIO reefs. Obtaining ecological reference points from oceanic atolls has become common practice elsewhere such as the Pacific (Sandin et al. 2008; Friedlander et al. 2010) and central Indian Ocean (Graham and McClanahan 2013).

7.1.1 Benthic habitat at coral reefs

Knowledge of the types of benthic habitat and their spatial distribution underpins the relationship between habitat and fish, and it is a fundamental starting point for inquiries into the resilience of reefs, and connectivity among tropical reef habitats (Mumby et al. 2004a; Bellwood et al. 2006; Mumby 2006; Almany et al. 2007). Habitat mapping from remotely sensed imagery is a popular method that provides a snapshot of the spatial distribution of benthic habitat over large areas. Habitat maps provide the basis for measuring large-scale change in response to environmental or anthropogenic disturbances (e.g. Palandro et al. 2003; Iovan et al. 2015). The recent developments in satellite imagery, computational processing capabilities and software make remote sensing a particularly powerful tool to assess changes in habitat at various scales (Blaschke 2010; Butler 2014; Beijbom et al. 2015; Gorelick et al. 2017).

This thesis created habitat maps at three scales, namely geomorphic reef zones, broad-scale habitat, and fine-scale habitat for Aldabra Atoll in November 2011. The habitat maps were therefore the starting point to investigate atoll-wide relationships between habitats and reef fish assemblages. Furthermore, the habitat map provided the data to understand the role of environmental drivers in determining these spatial distributions of the benthic habitats around Aldabra. The habitat map also provided a reference point of the state of benthic habitats after nearly 14 years following the 1998 bleaching event, in which up to 41 % of the coral bleached or suffered mortality at Aldabra's seaward reefs (Spencer et al. 2000; Stobart et al. 2005).

Repeated and intense mass-bleaching events, arising from global climate change, are one of the most significant threats to coral reefs today, causing benthic habitat change in all

tropical oceans and significantly degrading the reefs in the WIO (Turner et al. 2000a; Turner and Klaus 2005; Graham et al. 2006; Sheppard et al. 2008; Hoegh-Guldberg et al. 2017; Hughes et al. 2018). Aldabra's reefs appear to have been less affected by the 1998 mass-bleaching event compared to a number of other reefs in the WIO (Spencer et al. 2000; Graham et al. 2006). Aldabra's more southerly geographical position may have been a factor that meant it was less exposed to bleaching conditions than the rest of the Seychelles (Spencer et al. 2000; Sheppard and Obura 2005; Stobart et al. 2005). Worldwide, many reefs, such as the granitic islands in the Seychelles and Caribbean, have undergone phase shifts from productive coral reefs to macroalgal-dominated habitats characterised by low productivity (Hughes 1994; Graham et al. 2006). The pervasive effects of climate change are therefore causing extreme changes to the benthic habitats at some locations, with limited recovery of coral, and some irreversible changes to benthic cover type (Graham et al. 2013; Chong-Seng et al. 2014).

Various outcomes of this study, including the habitat maps and the reef fish assemblage, indicate that Aldabra's reefs have made some recovery from the 1998 bleaching event, consistent with a previous study that tracked the initial recovery process (Stobart et al. 2005). Furthermore, the thesis provides evidence of habitat recovery, such as a three fine-scale habitat categories characterised by high coral, covering a total area of 8.8 km², the absence of substantial areas of dead coral (0 km²), and a scarcity of macroalgal cover (0.9 km²). The diverse fish assemblage observed at Aldabra included abundant herbivores and a continuous presence of large predators that are associated with ecosystem processes such as herbivory and predation that promote reef recovery (Hughes et al. 2010; McClanahan et al. 2011). The habitat maps also provide multiple scales of information on the current distribution of habitat at Aldabra upon which to assess future bleaching events, such as those that occurred during the summers of 2015/2016 and 2016/2017, subsequently damaging coral reefs in the Indian Ocean (Cerutti et al. Submitted; Sheppard et al. 2017).

The habitat maps developed in this study provided evidence that there has been no detectable permanent phase shift to widespread and persistent macroalgal-dominated communities following the 1998 bleaching event. By November 2011 a relatively large area of reef was characterised by high levels of Hard and soft coral, and there was only a very small area that was dominated by macroalgae on Aldabra's forereef slope. Furthermore, this study characterised the deep forereef slopes as having relatively high levels of *Physogyra lichtensteini*, which is susceptible to bleaching. The recovery of this vulnerable scleractinian coral is indicative that the reef has some degree of resilience to mass bleaching (McClanahan et al. 2007a; Obura et al. 2010). The resilience and recovery of Aldabra's reefs

may be a consequence of intact ecosystem processes, for example predation and herbivory, which regulate reef dynamics such as controlling macroalgal growth and encouraging calcifying processes (Hughes et al. 2007; Ledlie et al. 2007; Stevenson et al. 2007; McClanahan et al. 2011). This has also been the case in the Chagos archipelago, where high recovery was correlated with high fish biomass and intact ecosystem processes that various trophic groups of fish deliver (Sheppard et al. 2008). In contrast, at the inner islands of the Seychelles, phase shifts to macroalgal communities correlate with high fishing pressure and low abundance of herbivores (Graham et al. 2006). The apparent resilience of Aldabra's coral reef ecosystem elevates the significance for continued conservation of this reef ecosystem to maintain it as a reference point of benthic habitat. Furthermore, it highlights the importance to assess other island systems in the region and compare the results to my study to understand how intact or impacted different sites are.

This study (Chapter 2) showed that there were only limited reefs that extended beyond 30 m depth at Aldabra, and Hard coral habitats dominated the reefs between 5 and 20 m depth. Previous studies at Aldabra have shown that there was up to 20 % mortality of hard coral at depths exceeding 20 m (Stobart et al. 2005). The lack of coral reefs beyond 30 – 35 m at Aldabra suggests that there may not be a depth refugium at the atoll. The lack of a depth refuge suggests that the corals at Aldabra may be vulnerable to shallow-water impacts such as elevated sea surface water temperatures and storm wave energy. The intact fish community (see Downing et al. 2005a for post-1998 bleaching assessment) at Aldabra may therefore be playing a very important role in maintaining this apparent resilience at Aldabra (Stobart et al. 2005). Anthropogenic pressures such as fishing that degrade key ecosystem processes and regulate reef dynamics could compromise otherwise resilient sites, like Aldabra, and these activities should therefore be at the forefront of site management priorities.

7.1.2 Effect of environmental drivers on benthic habitat

It is essential to understand how environmental drivers affect the benthic community as it provides information about the natural constraints that determine habitat distribution on coral reefs (Robinson et al. 2018). Depth, which regulates light, wave intensity and pressure, and exposure to wave energy which is strongly related to the abrasion on the reef, collectively determine the biological zones on the coral reef (Barnes et al. 1971; Aronson and Precht 2016). Studying the effects of depth and wave energy on the benthic habitat at Aldabra provided the opportunity to understand how these processes determine the benthic habitat communities at an ecological reference site without the confounding effects of anthropogenic

impacts. Depth and wave exposure were able to predict the probability of occurrence of broad-scale benthic habitats at Aldabra and thereby provided insight into the typical broad-scale habitats likely to characterise reefs at oceanic islands in the WIO. Shallow Seagrass and the Epilithic algal community had the greatest probability of occurring in shallow water (0 – 2m), while the probability of occurrence was greatest for Hard-coral reefs between 10 and 18 m. Increased wave energy caused the maximum probability of occurrence of respective benthic habitats to shift to a greater depth.

The understanding gained of the relationship between depth and wave energy and the benthos allows predictions of the distribution of habitats at data-poor sites (e.g. Kelly et al. 2001; Chollett and Mumby 2012) such as Aldabra's neighbouring atolls, Cosmoledo, Astove and Assumption which are characterised by similar environmental conditions. Moreover, it allows prediction of the response of benthic habitat to a change in these key environmental variables.

Environmental drivers such as temperature, depth and wave energy are changing with global climate change (Hearn 1999; Petit et al. 1999; Fitt et al. 2001; Hemer et al. 2013). In addition to elevated water temperatures, rising sea level and an increased frequency of extreme weather conditions pose a significant threat to coral reefs and seagrass beds (Fourqurean and Rutten 2004; Fabricius et al. 2008; Beeden et al. 2015; Perry et al. 2015). The ability of corals to keep up with rising sea levels has been deemed to be unlikely, especially in the light of reduced reef accretion rates as a result of ocean acidification (Hoegh-Guldberg et al. 2007; Perry et al. 2015). Chapter 3 in this thesis showed that benthic habitat, and hence the benthic communities that comprise these, occurred in deeper water with increasing exposure to wave energy. However, light-dependency restricts the depth to which habitats and benthic communities are able to occur, and therefore it is unlikely that all habitats will simply be able to shift to greater depths in response to increased wave energy (Duarte 1991; Hoegh-Guldberg 1999). Shallow benthic habitats such as seagrass may therefore ultimately become pinched off between depth limits and the destructive effects of high wave energy, especially in areas that are expected to be exposed to increased wave energy.

In turn, the loss of habitats such as coral, seagrass and mangroves removes the protection that these habitats provide against wave energy, and thereby exacerbates the impact that wave energy has on people (Sheppard et al. 2005). Sea level rise and increased storm wave energy as a consequence of climate change are significant threats to the infrastructure and livelihoods of 600 million people living near to the coast and have already affected small island states (Lewis 1990; Farbotko 2010). While storm damage is a natural disturbance on

coral reef ecosystems, the long-term recovery of habitats, the biological community response and the effects on coastal erosion in the aftermath of more frequent and more intense storms is not fully understood and requires further investigation.

7.1.3 Reef fish assemblage structure and diversity

High levels of herbivory and predation are two essential processes that sustain coral reef ecosystems and thereby play an integral role maintaining the benthic habitat (Graham et al. 2006; Ledlie et al. 2007; MacNeil et al. 2015). Overfishing is the most significant anthropogenic driver of changes to the reef fish assemblage structure (Friedlander and DeMartini 2002; Knowlton and Jackson 2008). Fishing pressure tends to selectively remove fish from the top levels of the food chain first. The loss of top predators has been shown to cause a meso-predator release, which affects lower trophic levels, and can influence herbivore communities (Mumby et al. 2006, 2012; Ferretti et al. 2013). Some fisheries target herbivorous fish, and together with a meso-predator release multiple impacts can reduce the number of herbivores on the coral reef (Bellwood et al. 2012; Heithaus et al. 2008). Overfishing of top predators and reductions of herbivores thereby compromise predation and herbivory which maintain coral reef dynamics (MacNeil et al. 2015; Graham et al. 2017).

Aldabra's isolation, long history of protection, and near absence of any direct anthropogenic impacts means that the reef fish assemblage was ideal to study an almost intact fish community (Stoddart 1968a; Seaton 1991). Furthermore, Aldabra's reef fish population has been protected for over 30 years since the MPA was officially proclaimed in 1981, which ought to have provided sufficient time for the reef fish populations to make a full biomass recovery (MacNeil et al. 2015) from the mild levels of historical exploitation (Stoddart 1971). Despite there being measurable effects caused by the existing subsistence fishery, the biomass (4880 kg/ha) of Aldabra's reef fish assemblage is still well above (Friedlander et al. 2015a) what is considered a fully recovered fish biomass (ca 1000 kg/ha) (MacNeil et al. 2015) and more than double what is typical fish biomass at other remote tropical reefs (McClanahan et al. 2019). The reef fish diversity and assemblage structure of Aldabra may therefore be regarded as near, or relatively pristine. Data on the relatively pristine reef fish assemblage from Aldabra provide useful metrics to inform the management objectives of more degraded reefs in the WIO (McClanahan et al. 2015). It was therefore important to understand 1) the biases of the methods used to quantify the fish assemblage, to ensure accurate interpretation of the data, in order to provide 2) the reef fish diversity and abundance as ecological reference points for a near pristine site.

7.1.3.1 Accuracy in reef fish assemblage observations

The first challenge to observing the reef fish assemblage was to understand the biases of the survey methods used to record the reef fish assemblage, to ensure accurate interpretation of diversity and abundance estimates. The implications of inaccurate observations of the perceived natural fish assemblage could lead to an inaccurate understanding of the trophic structure of marine food webs, which in turn could mislead site management decisions (Bijoux et al. 2013; McClanahan et al. 2015).

In this thesis, two methods of observation were compared to distinguish between reef fish assemblage structure under baited and natural conditions, namely, Baited Remote Underwater Video systems (BRUVs) and Remote Underwater Video systems (RUVs). Few studies have previously compared the effectiveness of using BRUVs and RUVs to survey tropical reef fish (e.g. Watson 2005; Harvey et al. 2007), but none of these have taken place in an environment that could be considered essentially unimpacted by anthropogenic activities. Aldabra provided the opportunity to test this in an environment where fish assemblages are intact, and relatively high levels of abundance for predators were expected (Potts 1983; Stevens 1984; Friedlander et al. 2015a).

In contrast to some previous studies (e.g. Harvey et al. 2007), this thesis showed that the presence of bait increased the number of generalist carnivores and piscivores but significantly reduced the diversity and abundance of herbivores and corallivores on the seaward reefs at Aldabra. The results suggest that the presence of bait, which increased the predator densities, may have caused an avoidance effect, which reduced the number of herbivores and corallivores observed in BRUVs. Avoidance behaviour in response to the presence of predators is consistent with previous research that has shown that predators exert an important role in structuring fish assemblages (Heithaus et al. 2008; Roff et al. 2016). A possible explanation for the difference in the findings of this thesis and the study by Harvey et al (2007), may be that there is a threshold in the minimum density of predators that deters prey species from the vicinity. Sites like Aldabra with relatively high levels of predators may breach this predator density threshold around BRUVs, which may have led to the altered fish assemblage in which there were fewer herbivores and corallivores than observed in RUVs.

The results of the BRUVs and RUVs data sets are complementary because RUVs provide data on the unaltered fish assemblage which may be a more accurate representation of herbivore and corallivores, while BRUVs provided an effective means to observe large mobile predators. Together they provide a holistic view of the structure of the reef fish assemblage structure at a pristine tropical atoll. The non-extractive and effective means by

which BRUVs and RUVs collect data, along with the advantages in observing mobile predators over traditional SCUBA survey methods (Watson et al. 2005b; Colton and Swearer 2010), makes RUVs and BRUVs highly appropriate methods by which to observe the reef fish assemblage at pristine, protected areas like Aldabra Atoll. Further to impacting the fish assemblage structure, it appeared that BRUVs were unable to detect natural variation in the assemblage structure with a change in tide and time of day. This has important implications which should be taken into account in future studies. For example, BRUVs surveys might be more robust to effects of cyclical environmental drivers of fish assemblage, but if the effects of these parameters on the fish assemblage are of interest RUVs is a more appropriate method.

7.1.3.2 Ecological reference points of reef fish diversity and abundance

Both BRUVs and RUVs data sets showed high levels of herbivores, piscivores and generalist carnivores, which are key elements in determining the ecological process that influence the reef dynamics. The mean and standard deviation of herbivore abundance per RUVs sample was 18.3 ± 31.6 individuals which was dominated by the acanthurids (10.2 ± 10.5), with the scarid, *Chlorurus sordidus* (2.16 ± 3.65) and the large herbivore *Naso brevirostris* (1.93 ± 9.3) being the most abundant herbivorous species on the reef. Herbivores play an important role in maintaining reef resilience by promoting coral recovery and suppressing macroalgal growth (Hughes et al. 2007; Ledlie et al. 2007).

The relatively high abundance of top predators suggests that predation processes were fully functional. Intact predation processes have been shown to maintain high levels of herbivorous fish through control of meso-predator abundance. Their presence also induces behavioural changes in reef fish, marine mammals and sea turtles (Dulvy et al. 2004a; Mumby et al. 2006, 2012; Heithaus et al. 2008). Changes in behaviour such as time spent grazing in different habitats has important ecological implications for algal growth and therefore indirectly affects the benthos (Mumby et al. 2006; Heithaus et al. 2008; Graham et al. 2010; Roff et al. 2016).

In this study, seventeen species and 207 individuals of elasmobranch were recorded from 61 BRUVs samples at the seaward reefs of Aldabra between 0.1 and 53 m depth. Nine species of shark (excluding rays) were recorded using BRUVs at a rate of 3 hr^{-1} ($N = 61$) at Aldabra, exceeding rates reported for the eight species of shark recorded at the Chagos (1.95 hr^{-1} , $N = 138$), which have declined by 90 % between 1970 and 2006 due to poaching (Graham et al. 2010; Tickler et al. 2017). The vulnerability of sharks, even at relatively pristine marine protected areas, due to the effects of distant fishing fleets, highlights the need for large MPAs and protective measures, such as banning fishing for sharks, which better protect

these species throughout their large home-ranges. Despite high vulnerability, given the opportunity to recover through effective protection measures, reef shark populations have been shown to increase significantly faster than would be predicted from their life cycle characteristics (Speed et al. 2018). The very high levels of shark abundance at Aldabra elevates its conservation importance as a refuge for reef-associated sharks in a time of the ongoing worldwide collapse of shark populations and loss of apex predatory function (Baum and Myers 2004; Heithaus et al. 2008; Ward-Paige et al. 2010).

The rich reef fish assemblage of Aldabra has been estimated to be an order of magnitude greater than what has been reported from small MPAs in the populated granitic Seychelles islands (Graham and McClanahan 2013; Friedlander et al. 2015a). However, the far-reaching effects of global climate change and international fishing pressure on highly mobile species like sharks, are likely to affect every reef on the planet to some degree. The effects of mass coral bleaching have been previously shown not to alter reef fish assemblages at Aldabra, but changes can easily go undetected owing to lag effects in the community response (Downing et al. 2005a; Graham et al. 2007). Even if Aldabra's reef fish assemblage appears to have remained stable through mass-bleaching events, it is likely to have been affected by historic shark fishing, recent incidents of poaching, an exploitative research survey and continued light levels of subsistence fishing (Stevens 1984; Travis 1990; Grandcourt 2005; Neville et al. 2007; Pistorius and Taylor 2009; Fardial 2015). These direct effects are taking place against the backdrop of significant repeated stressors to the benthic environment at Aldabra following the 1998 and then recent 2015 – 2017 bleaching events (Cerutti et al. Submitted; Stobart et al. 2005; Cerutti 2017).

Despite this continued backdrop of global environmental pressures, mild historical exploitation and very light levels of present day subsistence fishing, Aldabra's reef fish have very high biomass levels comparable to those recorded in the remote Northern Hawaii line Islands, Palmyra in the Pacific and the Chagos in the central Indian Ocean (Friedlander and DeMartini 2002; Stevenson et al. 2007; Sandin et al. 2008). While there are differences between the reef fish assemblage structure between the Aldabra and the Northern Hawaii Islands, Palmyra, Chagos, these sites have a common characteristic of high abundances of herbivores and predators (Sandin et al. 2008; Graham and McClanahan 2013; McClanahan et al. 2015). Aldabra's reef fish assemblage is therefore an important modern-day baseline and reference point to inform management objectives for the WIO's more degraded reefs systems (Friedlander and DeMartini 2002; Sandin et al. 2008; Friedlander et al. 2015a; McClanahan et al. 2015).

7.1.4 Cyclical environmental drivers of assemblage structure

The cyclical change of tide and time of day were shown to alter the reef fish assemblage during spring tides on the forereef slopes of Aldabra's west coast between 1 and 53 m depth. The greater species richness and overall higher relative abundances of reef fish observed during spring midday low tide compared to the morning or evening high tides suggests that fish move between different habitats with change in the tide and time of day which was a finding consistent with previous studies (Unsworth et al. 2007; Krumme et al. 2008; Félix-Hackradt et al. 2010; Birt et al. 2012; Kruse et al. 2016). The difference between reef fish assemblages recorded during different tide and time of day combinations at Aldabra were possibly as a result of the flooding of the lagoon during high tide which allows fish access to the shallow ($\pm 2\text{m}$ during high tide) lagoon. It follows that when fish then leave the seaward reefs during the high tide to access potential feeding opportunities in the lagoon during high tide, the counts on the seaward reefs drop. However, further studies of lagoon fish assemblage at Aldabra are required to support this. Fish have been shown to undertake migrations between reefs, mangroves and seagrass beds with a change in tide, and change their behaviour from resting to feeding with a change in the tide and time of day (Mumby 2006; Unsworth et al. 2007; Krumme et al. 2008). Understanding fish movement with tide and time of day and connectivity between different marine habitats is therefore important to inform conservation strategies and research programmes.

The differences in fish diversity, abundance and assemblage structure between tide and time of day were better detected using RUVs than BRUVs, supporting the conclusion of the fourth chapter which indicated RUVs better represented fish assemblages under natural conditions. Given the increase in the popularity of BRUVs and RUVs as monitoring tools used to assess the status of reef fish assemblages, this study has shown the necessity to account for the effects of tide and time of day within the design of sampling programmes to ensure that an accurate interpretation of data is used to inform management decisions (Malcolm et al. 2007; Birt et al. 2012; Bijoux et al. 2013; Whitmarsh et al. 2017).

7.1.5 Reef fish associations with habitat and environmental gradients

Reef fish differ in their habitat requirements and the range over which they operate, yet most studies of reef fish assemblages use a single scale of habitat when assessing reef fish relationships with habitat. A mismatch between the scale of the habitat defined by a study and actual scale of the habitat with which fish associate may lead to inaccurate estimations of the effects of habitat degradation on fish assemblages. It is therefore important that the habitat used when studying reef fish matches the scale of the habitat to which fish associate.

In my study, phylogenetic and size-class functional groupings of the fish assemblage were used to assess habitat associations as there is limited redundancy in high diversity communities and the community level response to disturbance has been shown to be detectable at the functional level (Bellwood et al. 2003; Nyström 2006; Meyer et al. 2007a; McCauley et al. 2012; Mouillot et al. 2013; Green et al. 2015). In future, assessments of habitat associations should be examined for individual species to allow for the high degree of niche specialisation of reef fish (McCormick and Makey 1997, Spalding 2001, Wilson et al. 2008, Slatyer et al. 2013) to be incorporated in our understanding of habitat association and improve predictive models that stem from this.

In this thesis, it was shown that habitat significantly contributed to the variability between fish assemblages after accounting for other environmental drivers including depth, structural complexity (rugosity) of habitat, wave energy and temperature. In general, the association between fish and habitat was significant at all scales of the habitat, showing that patterns in reef fish assemblage structure occur at multiple scales. The significant effect of habitat was consistent with previous studies in lagoon habitat (Nagelkerken et al. 2000; Friedlander et al. 2003; Chittaro 2004; Wilson et al. 2008). The effect of habitat rugosity was found to be significant in all analyses, and consistent with previous research showing that the three-dimensional structure of habitat is as important as the type of benthic cover itself (Graham and Nash 2013; Ferrari et al. 2017; Richardson et al. 2017). The strong effect of depth and wave energy in structuring the fish community was consistent with previous studies (Clark 1997; Friedlander and Parrish 1998; Friedlander et al. 2003). Accounting for the effects of environmental variables was therefore important to ensure an accurate understanding of the relative importance of the habitat in structuring reef fish assemblages.

The close association between benthic habitat and reef fish means that degradation of habitat quality will impact reef fish assemblages. Degradation of habitat may impact on reef fish assemblage through the removal of feeding areas and loss of structural complexity which reduces sheltering opportunities from predation (Syms and Jones 2000; Jones et al. 2004; Munday 2004; Graham et al. 2007; Halpern and Floeter 2008; Wilson et al. 2008; Paddack et al. 2009; Richardson et al. 2017). A change to the reef fish assemblage structure is likely to change dynamics that regulate key ecosystem processes like predation and herbivory on the reef (Bellwood et al. 2003; Graham et al. 2006). Herbivory and predation play vital roles maintaining the resilience of coral reefs and can prevent phase shifts to low productivity macroalgal-dominated systems after disturbance events (Hughes et al. 2007; Ledlie et al. 2007; Mumby et al. 2012; Ferretti et al. 2013; Heupel et al. 2014). The loss of these ecosystem processes and shifts to macroalgal-dominated benthic communities have

the potential to lead to declines in fish resources, which will impact the livelihoods of coastal communities (Cinner et al. 2012).

The associations between reef fish and habitat were evident in all size-classes of fish that were evident from the large amount of species turnover of bony fish (Actinopterygii) between habitats, at all three scales of habitat that were investigated. This suggests that the habitat scale at which species composition changes was not dependent on the attainable size of the species observed. Habitat association of reef fish is known to change with ontogeny (Mumby 2006). However, habitat associations of fish during the different stages of its life cycle was not be taken into account in this study because the methods of data capture did not allow size estimation of individual fish. The use of individual size measurements has been shown to provide more accurate estimations of the effects of different scales of habitat rugosity on fish body-depth abundance distributions than the maximum attainable size of a species (Nash et al. 2013, 2014). In this study, elasmobranchs were not associated with any habitat, irrespective of the elasmobranch size or the scale that was used to define the habitat. This suggests that while elasmobranchs may have preferred habitats within the coral reef, they move between the variety of habitats at all three scales. This was consistent with previous studies, which have concluded that effective conservation of sharks will require ecosystem-level protection of habitats throughout their range (Chapman et al. 2005; Speed et al. 2010; Knip et al. 2012).

7.1.6 Fishing disrupts trophic structure

Globally, fishing has the greatest impact on fish assemblages (Graham et al. 2005; Brander 2007), even depleting fish under minimal pressure (Goetze et al. 2011). While not a focus of the thesis, the effects of the limited and localised subsistence fishing pressure at Aldabra were shown to alter reef fish assemblage structure, highlighting the need for careful management of any fishery at baseline reference sites. A secondary outcome of assessing the effects of fishing on the assemblage structure using BRUVs at Aldabra was demonstrating the method's value as a monitoring tool to study the impacts of light levels of fishing.

The combination of very light levels of fishing by SIF, incidental poaching events and past extractive research methods in addition to distant offshore fishing by tuna fleets remove large long lived species, such as potato grouper, and highly mobile apex predators such as tunas, bull sharks, tiger sharks and silky sharks from the fish assemblage (Romanov 2002; Grandcourt 2005; Pistorius and Taylor 2009; Huang and Liu 2010; Poisson et al. 2014). The specific impacts of the subsistence fishing at Aldabra is not well understood and require

separation from the effects of other forms of fishing impacts. The SIF has implemented several policies to minimise the impacts of its fishery. For example, the subsistence fishery deliberately avoids catching, and indeed has very low incidents of catching sharks. The subsistence fishery targets meso-predators, such as *Lethrinus nebulosus*, *Lutjanus bohar* and *Variola louti*, but it also removes long-lived, slow growing species like *Epinephelus tukula*, *E. polyphekadion* and *E. lanceolatus* from the reefs every year (Pistorius and Taylor 2009). The subsistence fishery has become spatially restricted by introducing closed areas within the MPA in 2015 (Aldabra Management Plan 2016) and efforts to return such species to sea when feasible have been trialled with assistance from Seychelles Fishing Authority. Future research will investigate the effects of closed areas to provide more concrete evidence of the effects of the that subsistence fishing has on the reef fish assemblage structure at Aldabra (Aldabra Management Plan 2016). Many of these species undertake long-distance migrations (e.g. Speed et al. 2010; Daly et al. 2014; Poisson et al. 2014) exposing them to both coastal and oceanic fishing fleets in the Indian Ocean. The lack of regular observations of very large apex predators may be caused by declines in their populations arising from bycatch in commercial tuna fishing in the Indian Ocean (e.g. Romanov 2002; Huang and Liu 2010) but also from fishing near coastal states (Robinson and Sauer 2013). The removal of commercial fishing effort in Southern Seychelles during the next phase of MPA expansion in Seychelles may prove critical for protecting highly mobile species at Aldabra. The damaging effects of fishing on the fish assemblage structure, such as many of the more degraded reefs in Seychelles and along the East African Coastline, is highlighted by the fact that even very light levels of fishing can have measurable effects on the assemblage.

7.1.7 Application of the results to inform management of degraded reefs

Aldabra's subsistence fishing is a prime example of the tough decisions that managers face in weighing up conservation ideals against human needs and societal well-being. Light (and managed) levels of fishing have been allowed to continue within Aldabra's MPA to provide a reliable source of protein to its small society. Fishing within the MPA at Aldabra is controversial because the site is an ecological baseline of global importance. Furthermore, all people on the island are staff employed by the management authority, SIF, to protect, monitor and manage the site. This study disproved the notion that the light and managed levels of subsistence fishing has a negligible effect on the fish assemblage at Aldabra. The evidence of fishing impacts at Aldabra presented here calls for a change in the management of the fishery. Recently SIF developed a zoning plan (Aldabra Management Plan 2016) and a fisheries monitoring programme in an effort to improve the management of the subsistence

fishery. The implementation of fishing and no-take zones along with self-enforcement by collecting GPS and landings data on board during fishing trips may alleviate the local pressures on vulnerable and highly resident species of grouper.

Further management considerations should consider further options to restrict the damaging effects of fishing, such a switch to only pelagic fish with high turnover rates, or a complete ban of fishing. While supplying protein to staff is essential for health and well-being, fishing within the MPA of a key ecological reference site seems contrived if other means to obtain protein are available. The solution to supplying staff with protein without fishing at Aldabra may require investing in additional shipping of protein and storage facilities at Aldabra to meet the staff demands. The removal of all fishing effort from Aldabra would be of global significance, as this promotes full recovery of top predators and the important process that they regulate within the coral reef ecosystem. Furthermore, it would represent a commitment to the conservation of one of the last remaining pristine sites in the WIO. Improving this aspect of Aldabra's MPA management is an opportunity to set management authority apart from so many others that have failed.

Throughout much of the world's reefs, the immediate societal needs, such as food and money, and a lack of regulation overshadows conservation efforts. The degraded reefs of East Africa and much of the inner islands of Seychelles are a testament to the effects of continued over-exploitation of the reef fish, which have systematically eroded key ecosystem functions such as herbivory and predation (Ledlie et al. 2007; McClanahan et al. 2007b; McCauley et al. 2012). The lack of these key ecosystem processes has led to phase shifts to macroalgal dominated habitat. A significant result from the series of studies which established critical thresholds for a number of metrics have defined the critical points where ecosystem functions break down, was that key ecosystem processes like predation and herbivory recover at a total fish biomass of approximately 1200 kg/ha (Graham et al. 2005; MacNeil et al. 2015; McClanahan et al. 2015). These studies have provided quantitative targets which provide clear objectives for coral reef management in the WIO. This estimate of biomass levels (1200 kg/ha) where key ecosystem process return to the reef is a minimum value which is well below the top end of 7000 kg/ha recorded at the Chagos¹ (McClanahan et al. 2011, 2015), or Aldabra (4900 kg/ha) (Friedlander et al. 2015a). The difference between the 1200 kg/ha and 7000 kg/ha biomass metrics do not yet quantify how well the ecosystem processes like herbivory and predation are functioning and this relationship between biomass and ecosystem function may be a fruitful avenue to explore in

¹ Note that sampling in the Chagos covered a very limited depth range which may have inflated biomass estimations relative to the study at Aldabra which covered a wider depth range.

future research. Benthic and reef fish communities in small MPAs near high population centres may make recoveries that will progressively return key ecosystem functions with increasing fish biomass (McClanahan et al. 2011). The recovery period of these key ecosystem functions present at 1200 kg/ha and has been estimated to take 35 – 60 years (McClanahan et al. 2011, 2015). The time that it will take for reefs to make a full recovery to pristine biomass levels and associated ecosystem processes such as those recorded at the Chagos is not yet known but is likely to take a significant amount of time (Graham and McClanahan 2013). The long time to recovery where unique features, an abundance of large predatory fish, and high levels of reef resilience are present, serves as a reminder that once these features are lost, it is very difficult to return to baseline levels (McClanahan et al. 2007b; Graham and McClanahan 2013; Graham et al. 2017). The unique benthic and reef fish communities and the high abundance of herbivores and large carnivores recorded at Aldabra in this study are consistent with features of intact ecosystems. The long-term persistence of Aldabra's intact benthic and reef fish community requires continued protection, more effective fishing regulations and an expansion of its MPA boundaries, to ensure the full protection of this valuable baseline site in the WIO.

Obtaining abundance and size class data across a gradient of fishing pressure in WIO will improve our understanding of the effects of fishing on the fish assemblage structure. Carrying out BRUVs surveys in other parts of the WIO, is therefore an important consideration for future work to test the generality of the findings from this thesis. It is recommended that stereo-BRUVs, which are well suited to measure fish size (Langlois et al. 2012), used carry out an assessment of the abundance of size classes in locations with differing levels of fishing pressure.

7.1.8 Outcomes

Identification and implementation of management actions that allow coral reefs to rebuild the components and processes that enhance resilience, promotes diversity and increases productivity remains the core challenge to coral reef management (Graham et al. 2013; MacNeil et al. 2015; McClanahan et al. 2015). While several regulatory mechanisms have been shown to be effective to conserve fish stocks, marine protected areas (MPAs) are recognised as a key management tool to restore fish biomass (Roberts et al. 2001a, 2005; Côté et al. 2005; Edgar et al. 2014).

This thesis provided critical evidence that indicates the need to expand the MPA around Aldabra to protect 3.5 km² of forereef which fell outside of the 1 km boundary MPA. After initial immediate protection of this 3.5 km² of reef, the Government of Seychelles signed the

proclamation order (15 October 2018 – 7.2 Annex.) to expand the MPA to a rectangular area within which the seamount on which Aldabra rests to a depth of approximately 3 km (Figure 7.1). The inclusion of the seamount was recommended to Seychelles' Blue Economy programme by SIF in order to provide a buffer zone around Aldabra. The buffer zone not only places a greater distance between fishing activities and the vulnerable reef fish communities on the forereef slope, but it affords more protection to wide-ranging vagile species like sharks, dolphins and trevally, and highly migratory species like humpback whales, dugong and green turtles (Potts 1983; Stevens 1984; Hermans and Pistorius 2008b; Mortimer et al. 2011; Hamylton et al. 2012a). The larger Aldabra MPA also protects the deep-water habitats and species that are known to occur within the waters over the Aldabra seamount (Forster 1984; Mortimer et al. 2011; Friedlander et al. 2015a). The area's designation as a Seychelles Special Reserve is the highest national designation which matches the IUCN category 1a and is consistent with Aldabra's existing MPA status (Stoddart 1968a; Seaton 1991; Jennings et al. 1996). The new Aldabra MPA covers a total area of 2615.52 km² and extends up to the deepest point between Aldabra and its nearest neighbouring island, Assumption island (Figure 7.1).

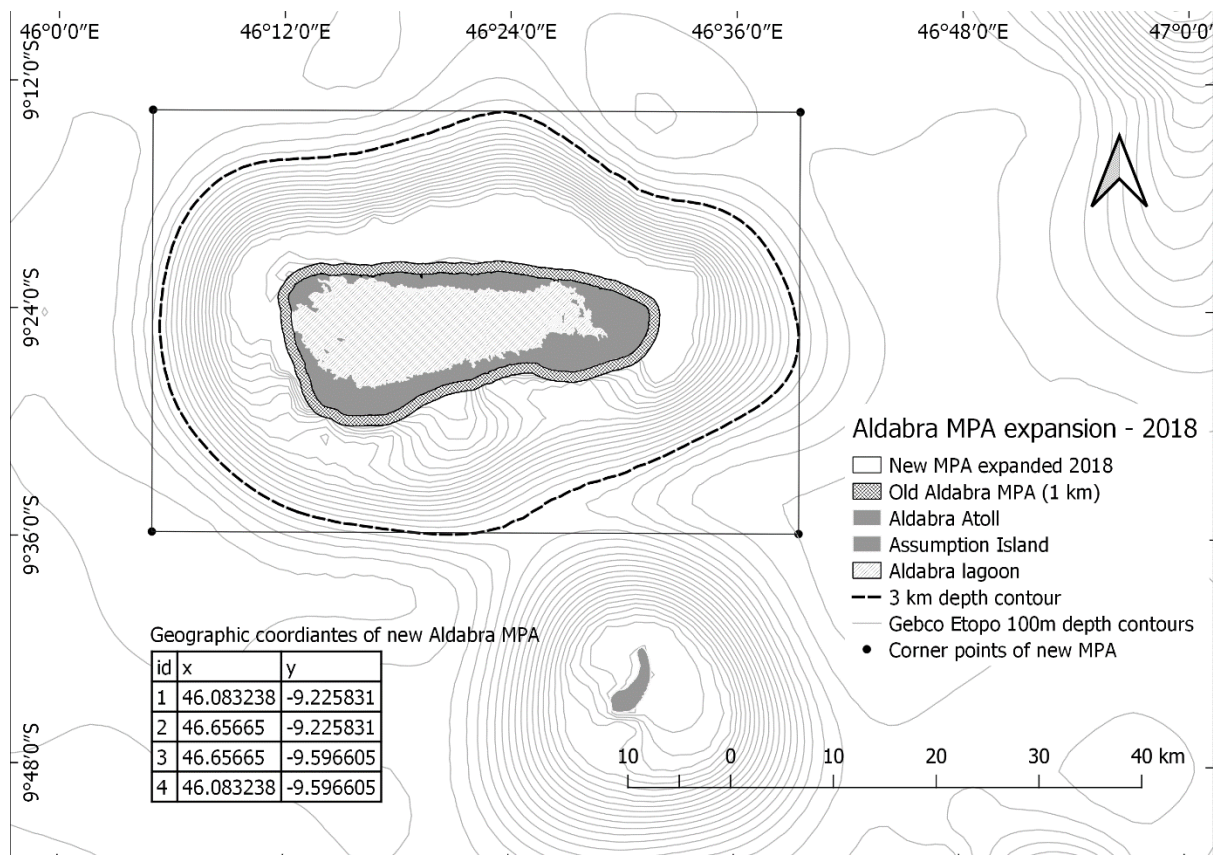


Figure 7.1. The newly expanded Aldabra Marine Protected Area (MPA) adds 2176.32 km² to the existing MPA (89.75 km²) and the lagoon MPA (155 km²) covers an area of 2421.1 km². The expanded area includes the Aldabra seamount to a depth of 3 km as indicated by the contour lines.

This expansion of the Aldabra MPA was the first phase of a planned series of an MPA expansion programme as part of Seychelles' Blue Economy programme. The Nature Conservancy and Government of Seychelles' plan to include a greater area around the Aldabra group of islands with a total area of 210,000 km² planned by 2020. The ambitious MPA expansion plans may provide a further buffer zone around the recently expanded MPA boundary and will contribute 30 % of the Seychelles overall goal for MPAs of 1.37 million km². Furthermore, the benthic habitat map was reflected in the site management plan and used to inform the zoning of the MPA (Aldabra Management Plan, 2016).

The case for the preservation of Aldabra, once threatened by the development of a BBC radio station and US military base, has long been fought by scientists and naturalists from around the world (Stoddart 1968b). This MPA expansion is a significant achievement which provides debt alleviation and contributes towards the national goals to achieve CBD targets. Moreover, the expansion of the Aldabra MPA represents a victory for the preservation of the marine diversity and the safeguarding of intact ecosystem processes which have been irreversibly lost from so many reefs around the world. Aldabra remains one of the most remarkable tropical reef ecosystems in the Indian Ocean and the world, and long may it remain so.

7.2. ANNEX: MPA EXPANSION PROCLAMATION ORDER

S.I OF 2018

NATIONAL PARKS AND NATURE CONSERVANCY ACT

(Cap 141)

National Parks and Nature Conservancy (Aldabra) Special Reserve (Designation) Order, 2018

In exercise of the powers conferred by section 5 of the National Parks and Nature Conservancy Act read with the Transfer of Statutory Functions (Seychelles National Environment Commission) Order, 1998, the Minister of Environment, Energy and Climate Change hereby makes the following Order—

1.	This Order may be cited as the National Parks and Nature Conservancy (Aldabra) Special Reserve (Designation) Order, 2018.	Citation
2.	The area described in the Schedule is hereby designated as the Aldabra Special Reserve.	Designation of Special Reserve
3.	A copy of the map describing the area in the Schedule has been filed in the Office of the Director of Surveys under reference number ML-ADN-171.	Copy of the Map
4.	The National Parks (Special Reserve Aldabra) (Designation) Order, 1981 is hereby repealed.	Repeal of S.I 86 of 1981

SCHEDULE

CORDINATES

Coordinates for Aldabra Special Reserve

ID	X coordinates	Y coordinates
1	46.083283	-9.225831
2	46.65665	-9.225831
3	46.65665	-9.596605
4	46.083283	-9.596605

MADE this 15th..... day of October....., 2018.

A handwritten signature in blue ink, consisting of a large, stylized 'C' followed by a small flourish.

**WALLACE COSGROW
MINISTER FOR ENVIRONMENT,
ENERGY AND CLIMATE CHANGE**

7.3. ANNEX: RECOMMENDATIONS TO THE MANAGEMENT OF ALDABRA

Coral reefs all over the world are undergoing rapid significant changes at unprecedented rates since 1980 as a consequence of an increased frequency of coral bleaching events. While it is difficult to make changes to management that can address global pressures such as climate change, it is essential to promote reef resilience through minimising local anthropogenic impacts that break down the ability of the reef to cope with bleaching events. Furthermore, it is essential that changes to coral reef ecosystems at pristine sites like Aldabra are monitored to provide evidence of the larger environmental processes that drive change. This evidence is the basis to inform national, regional and international policies at a time when coral reefs, and indeed other ecosystems, are facing an anthropogenically induced climate crisis. The Seychelles Islands Foundation (SIF), which manages two UNESCO World Heritage Sites, Aldabra Atoll and Vallée De Mai, have an important role to play in informing the development of the environment and sustainable development policies in the Seychelles. In addition to the extraordinary ecological value of Aldabra, it is revered by the Seychellois and plays an important role in the political mindset of conservation in the Seychelles. The Seychelles Islands Foundation therefore has an important role to set a compass for best practice in research and management in the Seychelles.

With the expected increase in thermal stress at Aldabra's coral reefs within this decade, it is becoming (and will become) ever more important that the SIF have and maintain a marine monitoring programme that allows the detection of changes to the coral reef ecosystem at Aldabra Atoll. This thesis established baseline conditions for the benthic habitats and reef fish communities prior to the 2015-2017 global coral bleaching event. Based on the results of this thesis the following recommendations are made to SIF with respect to its marine monitoring programme and management practices, which will decrease local impacts on the reefs of Aldabra:

1.) The reef fish community

Healthy reef fish populations with an abundance of large predators and herbivores have been shown to be essential for maintaining a resilient coral reef ecosystem (Friedlander and De Martini 2002; Hughes et al. 2007). Baited Remote Underwater Video systems (BRUVs) and Remote Underwater Video systems (RUVs) are already used at Aldabra to monitor the reef fish assemblage in a monitoring programme that followed the data used in this thesis (Haupt and Bernard 2015). This thesis showed that BRUVs were better suited for monitoring predatory fish, while RUVs were more appropriate for monitoring herbivores and corallivores

(Chapter 4). It was also shown that changes in reef fish assemblages associated with the time-of-day and tide were detected by RUVs but not BRUVs. (Chapter 5). This suggests that SIF could use BRUVs under a variety of tides and times and expect to obtain comparable data, while RUVs should be standardised according to these parameters.

1.1) It is therefore recommended that SIF continue to use BRUVs for its annual monitoring programme to monitor reef fish assemblages because they will be less sensitive to environmental patterns than RUVs.

1.2) RUVs should be used for fine-scale ecological studies.

1.3) It is important that BRUVs and RUVs surveys span a wide depth range from habitats over the shallow lagoon reef, the fore reef slope to the reef apron at (50m), as depth and geomorphologic zone were shown to be two of the most significant environmental predictors of reef fish assemblage structure throughout this study.

1.4) The significant differences in the reef fish assemblages between different habitats (Chapter 6) suggests that it is important to monitor the reef fish in a variety of benthic habitats, especially at the broad scale, as defined and mapped in this study. These habitats included: Hard-coral-dominated reef, seagrass beds, sandy terraces, rubble-dominated reef, and epilithic algal-matrix-dominated reefs.

The habitat map showed that there were substantial differences in the differences in the distribution of different benthic habitats around the atoll, as a factor of depth and exposure to wave energy. The spatial distributions of wave energy and recent fishing pressure were correlated and had significant effects on the reef fish assemblage structure, and the following strategy should improve our understanding of their respective influences:

1.5) The sampling strategy for BRUVs and RUVs should include sites that are open to fishing and sites that are not fished, to build on the understanding of the effects of fishing on the reef-fish assemblage structure detected in this study. It is important that ,as far as possible, the sites that represent non-fished areas are large enough to avoid the effects of nearby fishing pressure on the larger more mobile species.

1.6) Wave energy

In order to incorporate the effects of wave energy on the fish assemblage, sampling should be undertaken around the atoll to obtain a wide variety of exposure gradients. The effects of wave exposure gradient may be slower to change and therefore it may only require an atoll-wide survey every five years to ensure that representative data of the fish community are available for analysis. Including data from fished and non-fished sites will help discern the effects of wave exposure and fishing with more certainty than has been shown in this thesis. Furthermore, *in situ* measurements of wave energy would provide greater certainty about the exposure levels at Aldabra and the effects of wave energy on the benthic and fish assemblages.

1.7) The size of predatory fish is a critical component to the fish community dynamics. The different roles played by different sizes of predatory fish (with different diets) is an important predictor of their trophic positions and roles in the ecosystem. It will therefore be essential to monitor the size of reef fish, especially large predatory sharks and fish. In this study, BRUVs and RUVs were used, and species sizes were based on the maximum attainable sizes of different species. This method therefore assumed that all individuals of a species were the same (maximum-species) size. Detecting a change in size is an early indicator of change to the assemblage structure and therefore important to monitor. Stereo-BRUVs are well suited to obtain the size of the fish assemblage and should be carried out as soon possible and repeated every three to five years. This should replace the annual (mono) BRUVs programme, or be done in conjunction with it to document the effect that a) local fishing pressure has on the species composition, relative abundance and size-class distributions of reef fish, b) understand the effects of environmental change on the trophic structuring of reef fish.

1.8). Cease fishing at Aldabra Atoll, or restrict catches to pelagic mesopredators.

In this thesis, it was shown that fishing influences the reef fish assemblage structure. While it was not the main purpose of the study, it showed that the reef fish assemblage was significantly altered by the fishing effort gradient at Aldabra, even after accounting for a range of environmental variables. Fishing at Aldabra targets medium to large generalist carnivores and piscivores, unintentionally landing large groupers, such as potato grouper and giant grouper, and very large giant trevally, and even sailfish (Pistorius and Taylor 2009). Large predators play an important role in maintaining the balance in the assemblage structure, in particular on herbivores, which have direct and indirect effects on the benthic community. It is therefore essential that the removal of these large predators be limited or

ceased as soon as possible, especially given the slow recovery of their populations. If subsistence fishing is continued, it is recommended that only pelagic species are targeted. Pelagic species have faster turnover rates, range more widely, and are more likely to be sustainably fished. For example, bluefin trevally becomes sexually mature at about 35 cm after 2 years (Williams 1965), while first maturity in goliath grouper (which is similar to giant grouper) is estimated at 129 cm after 6 years and have a life span of approximately 37 years (Artrero et al. 2015).

The results from Chapter 6 strongly suggest that intensive fishing or fishing by destructive means would affect the fish assemblage structure dramatically, and should therefore be prohibited. The magnitude of the impact of a previous research fishing venture (Grandcourt 2005) at Aldabra removed a similar amount of fish from the reef, predominantly large grouper, to that associated with a recent poaching incident in 2016. The impacts from these events are likely to still be evident in the reef fish community today, given that some species of species of grouper live longer than 30 years (Grandcourt 2005). Careful assessments of research proposals that use fishing methods are required to ensure that impacts are managed and minimised or prohibited if damaging.

1.9.) Expansion of the protected area estate around Aldabra

This thesis showed that elasmobranchs had weak associations with the habitats that occur within Aldabra seaward reef than finfish, and that elasmobranchs moved and appeared to utilise all habitats, at least in the presence of bait. Many of the species of shark recorded in this study are known to undertake migrations among islands. The recent efforts from the Government of Seychelles to expand Aldabra's Marine Protected Area (MPA) should seek the cooperation of the Island Development Company (IDC), responsible for the management of nearby Astove, Assumption and Cosmoledo, to protect species that move between these islands.

2.) Benthic habitat

2.1) Remote sensing of monitoring of the distribution of benthic habitats

At the broad-scale, habitats such as coral reefs, seagrass beds, remotely sensed habitat mapping should be repeated every five to ten years to detect large-scale changes in the distribution of these broad-scale habitats. While these changes are likely to take a longer time to occur, remote sensing provides complete spatial coverage of the atoll, while SCUBA methods are restricted to small portions of the reef and are often restricted to coral-dominated forereef slopes. Understanding how the distribution of broad-scale habitats

changes in response to environmental drivers will provide essential information on a variety of benthic habitats, such as seagrass communities and coral communities.

2.2.) Monitoring of benthic cover, coral reef diversity and recruitment

While this study used remotely sensed imagery to establish a baseline on the character of the reef habitats and their spatial distribution, there is a need to understand the changes at a finer scale. This includes changes in diversity, proportional hard-coral cover within benthic community, and the overall benthic community composition at a finer scale where the effects of climate change act before large-scale changes in habitat are detected. A decrease in hard-coral cover and an increase in rubble or macroalgae will be essential indicators to monitor alongside the fish community composition to understand the critical point at which the ecosystem undergoes a phase shift, and what the role of a healthy fish community is in preventing this. Some of these aspects are currently addressed by SIF's Aldabra Reef Monitoring programme and should be continued to ensure detection of coral bleaching events are recorded.

3.) Environmental conditions

3.1) Bathymetric data

Obtaining more accurate bathymetric information for Aldabra will allow a significant improvement in our understanding of the drivers of biotic communities over the scale of the atoll. Bathymetric information will also allow the development of improved wave-energy models and should be a priority in light of understanding the new habitats included within the expanded MPA of Aldabra.

3.1.) Storm wave energy

This thesis showed the importance of prevailing wave energy in determining the type of reef habitats but was limited by the short time-frame that the data spanned to develop storm wave energy models. The disruptive forces of wave energy from storms on coral reefs play an important role in shaping the reefscape. Understanding how storm wave energy will change with a changing climate will therefore be essential to predict the future of coral reefs at Aldabra. Further investigation of the impacts from predicted increases in storm wave energy with the concomitant sea level rise at Aldabra should be pursued to develop a more complete understanding of likely outlook for the reefs of Aldabra.

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