Unveiling the depths of the Motiti archipelago: Biodiversity and stressors of mesophotic sponge reefs

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Abstract

Compounding environmental stressors exacerbated by global warming are threatening marine ecosystems worldwide. In New Zealand, recent events such as Cyclone Gabrielle and unprecedented marine heatwaves have brought these concerns to light. Sponge communities dominate the mesophotic reefs of the Motiti archipelago in the Bay of Plenty, which are under ‘no-take’ protection and yet were largely unexplored prior to this research. This study utilised remotely operated vehicle footage and taxonomic identification to establish a baseline of the diversity and current state of Motiti’s mesophotic sponge communities, which are sentinels of the health of their environment. Comprehensive analysis revealed a rapid shift in assemblage composition taking place at the time of surveying, potentially towards species more resilient to sedimentation and elevated temperatures. Additionally, this study reports the discovery of new sponge species, extends geographical occurrence records, identifies large-scale necrosis in line with the 2022 Bay of Plenty marine heatwave, and presents the ‘rapid sponge death’ hypothesis. Conservative findings support previous studies that point towards temperate mesophotic sponges being climate change ‘losers’, highlighting the urgent requirement for regular, long-term monitoring of this sponge diversity hotspot to inform management plans. This study also provides a basis for future research endeavours which are now paramount to understand the complex interactions and the extent of change occurring in this functionally important ecosystem.

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Preface

Emma Donald on a diving trip to collect and photograph sponges at Karewa Reef, August 2023.

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Chapter 1

General Introduction

1.1 Overarching context

The stakes have never been higher for marine conservation. The most recent 2023 Intergovernmental Panel on Climate Change (IPCC) report unequivocally showed that human-caused global warming has already inflicted substantial damage and increasingly irreversible loss in coastal and open ocean ecosystems (IPCC, 2023). In New Zealand, we are seeing more frequent and severe marine heatwaves in addition to increasingly warmer summers, with average sea-surface temperature increasing by 0.2ºC per decade in coastal waters between 1981 and 2018 (Pinkerton et al., 2019; Thomsen et al., 2019; Chiswell & Sutton, 2020; Ministry for the Environment & Stats NZ, 2022). Compounding this are increasing levels of other critical stressors, such as ocean acidification (Keegan et al., 2022), shifting oceanic currents (Boyd & Law, 2011; van Gennip et al., 2017) and especially coastal sedimentation, which is naturally high in New Zealand due to steep topography, exacerbated by the increasing frequency and extremity of weather events (Basher, 2013; Cummings et al., 2020; Crawshaw, 2022; Keegan et al., 2022). In recent times, storms such as Cyclone Gabrielle have brought to light the catastrophic impacts of extreme weather events (Noll & Andrews, 2023). The aftermath of the historically significant flooding around New Zealand from Cyclone Gabrielle was evident in the large sediment plumes, which smothered coastal marine environments (e.g., Figure 1) (Harrington et al., 2023). This study therefore comes at a critical time when understanding of our marine ecosystems, and the multiple stressors they are facing, is paramount to informing management plans.

Figure 1. Photos taken in March 2023, just after Cyclone Gabrielle, show fine sediment smothering shallow reefs (<25 m deep) around Motiti Island, Bay of Plenty, NZ. Top left: Smothered benthos; Top right: Sediment smothered kelp fronds; Bottom left: Rotting kelp canopy; Bottom right: Sediment smothered kelp fronds.

1.2 Mesophotic reefs

Mesophotic ecosystems are those situated between approximately 30 – 150 m depth and are largely understudied worldwide, including in New Zealand (Baker et al., 2016; Turner et al., 2017; Harris et al., 2021; Harris, 2022). The lack of attention they receive in comparison to shallow reefs is primarily due to their location beyond the occupational scientific diving depth limit of 30 m (Boffa Miskell Limited, 2020). Technological advances in surveying and photography equipment such as drop cameras, remotely operated vehicles (ROVs), and autonomous underwater vehicles (AUVs), have allowed scientists to bypass the depth and time limitations of SCUBA diving surveys. In the past, deep water research equipment was out of reach for most scientists due to its high costs (Boavida et al., 2016; Buscher et al., 2020). However, the recent development of smaller, cheaper ROVs is now allowing the deeper ocean to become much more accessible while still being capable of collecting high-quality data (Boavida et al., 2016). Consequently, there is now considerable international effort to gather information on these ecosystems (Slattery & Lesser, 2012; Kahng et al., 2014; Kane et al., 2014; Andradi-Brown et al., 2017; Turner et al., 2019). The only limitation however, in using smaller, cheaper ROVs is the difficulty in grabbing samples of the species being filmed, necessitating the use of diving or alternative sample collection methods alongside remote surveying.

Mesophotic ecosystems are known to host unique biodiversity and rich assemblages of endemic and rare species yet are suggested to be among the least protected marine ecosystems in the world (Soares et al., 2018, 2020; Donald, 2021). They contribute large amounts of complex 3-dimensional benthic habitat to coastal areas which provide critical ecosystem functions such as potential refuge from local and global anthropogenic stressors for some species, habitat for the survival and recovery of some endangered, threatened and declining species including fishery resources, biological connectivity between regions and depths, and nursery habitat for fish, coral, sponges and algae (Kahng et al., 2014; Lesser et al., 2018; Soares et al., 2018; Turner et al., 2019; Soares et al., 2020; Harris, 2022).

Declining light availability is the primary driver of the ecology of mesophotic ecosystems. As light declines with depth, photosynthetic organisms are gradually excluded, and the ecosystem shifts from being algae-dominated to invertebrate-dominated (Lesser & Slattery, 2021). It is the community composition, relative abundance and functional role of the invertebrate benthic fauna that controls the ecological dynamics of mesophotic ecosystems (Harris et al., 2021). Although kelp forests are largely excluded from mesophotic reefs by declining light, they are linked to the benthic community living below them by the carbon they sequester and subsequently introduce into the marine system, which forms an important part of the sponge food web (Filbee-Dexter & Wernberg, 2020; Mc Cormack, 2021). It is important to note that in recent times, the reasons for declining light at depth are related to increasingly turbid waters, termed ‘coastal darkening’, caused by increased sedimentary contribution from terrigenous sources (i.e., sediment run-off from land and freshwater catchments) (Mustaffa et al., 2020). The implications of coastal darkening on invertebrate communities inhabiting mesophotic reefs are unknown. However, previous research has indicated that coastal darkening could have negative implications for coastal carbon cycles, limiting the contribution of primary producers (e.g., kelp and phytoplankton) to carbon sequestration, and therefore weakening their interactions with the food web (Mustaffa et al., 2020; Blaine et al., 2021).

1.3 Previous research on Temperate Mesophotic Ecosystems

Two categories of mesophotic ecosystems can be found in the literature: mesophotic coral ecosystems (MCEs) and temperate mesophotic ecosystems (TMEs). This is due to the pioneer studies on this depth range starting on tropical coral reefs in the 1970s (e.g., Lang, 1974), while TMEs began to be explored a few decades later (as cited in Cerrano et al., 2019). Although TMEs remain largely unexplored in comparison to MCEs, interest in these so called ‘twilight zones’ has grown over the past decade (Cerrano et al., 2019). As a result, much of our understanding of TMEs draws on the knowledge already available from research on MCEs.

A variety of benthic communities inhabit TMEs around the world such as coralligenous reefs, formed by the accumulation of calcareous encrusting coralline algae (Ballesteros, 2006); cold-water reef building corals (Costantini & Abbiati, 2016); sponge grounds (Idan et al., 2018); turf invertebrate matrices (<50 m depth); and bryozoans (Bell et al., 2022). However, regional and global knowledge of mesophotic ecosystem spatial distribution is patchy. Studies increasingly reveal high rates of species discovery and geographic endemism (Kosaki et al., 2017; Pomponi et al., 2019; Pyle et al., 2019; Spalding et al., 2019; Donald, 2021), pointing towards the high proportion of biodiversity likely still to be found and highlighting the need for further research into these precious communities (Maldonado et al., 2017; (Turner et al., 2019).

1.4 Importance of sponges in benthic TME communities

To be able to address the pressing issues associated with global warming (IPCC, 2023), an understanding of how ecosystems function and the roles that species play within them is required to inform management plans (de la Mare, 2005; Bell et al., 2022). Benthic TME communities are indicators of reef health, as they accurately reflect prevailing sedimentation regimes (Battershill & Bergquist, 1990; Bell et al., 2015). They are sentinel communities that could be monitored to track the shifts in marine environments expected in the near future, as the climate rapidly changes across the globe (IPCC, 2023). In New Zealand, colourful and curious arrays of marine sponges (phylum Porifera) typically characterise the macrofaunal communities found on mesophotic rocky reefs (Harris et al., 2021). Sponges are ancient, multicellular animals that have a unique internal network of progressively optimized filter-feeding cavities, chambers, and canals (Battershill et al., 2010; Godefroy et al., 2019). Their main functional roles within TMEs are increasing habitat complexity, biodiversity enhancement, and benthic-pelagic coupling. Because of the substantial influence of these functional roles within benthic TMEs, sponges are known as environmental engineers (Cerrano et al., 2019).

Sponges grow in a plethora of complex morphologies and act as habitat formers on the reefs that they dominate, such as the mesophotic rocky reefs of New Zealand. Their variety of 3D structures combined with their high abundance makes an important contribution to habitat complexity (Maldonado et al., 2012; Harris et al., 2021). This increase in habitat complexity creates niches in the reef for shelter and refuge of other organisms (Kenchington et al., 2013; Gerovasileiou et al., 2016; Idan et al., 2018; Harris et al., 2021), in turn enhancing local biodiversity and richness (Dayton et al., 1974; McClintock et al., 2005; Wulff, 2008; Bo et al., 2012). Sponge reefs also have ecologically important functionality as spawning and nursery grounds for commercially important species such as fish, crustaceans and cephalopods (Battershill & Bergquist, 1990; Marliave et al., 2009; Orejas et al., 2009; Battershill et al., 2010; Baillon et al., 2012; Rossi, 2013; Paoli et al., 2017). By providing these ecosystem services, sponge communities lay the foundation of a healthy and biodiverse ecosystem, supporting its resilience against environmental and anthropological pressures (Thrush et al., 2011).

Marine sponges play a key role in benthic-pelagic coupling as they provide a trophic link between the water column and the benthos (Coppari et al., 2016; Maldonado et al., 2017). They are able to take up dissolved organic matter (DOM) and make it available to higher trophic levels as particulate organic matter (POM) either through producing detritus or being predated upon (Maldonado et al., 2012; Bart et al., 2021). Sponges also take up POM through suspension feeding on particulate carbon, nitrogen and phosphorous compounds (Folkers & Rombouts, 2020). Their ability to cycle essential nutrients *en masse*, recognised in recent literature as the ‘sponge loop’, supports biodiversity and productivity and likely makes sponges one of the most important functional components of TMEs (Achlatis et al., 2019; Bart et al., 2021; Harris, 2022).

Another way that marine sponges contribute to benthic-pelagic coupling is through the retention and filtration of organic carbon. Coastal marine-derived carbon makes up 60-73% of the sponge diet (Mc Cormack, 2021), such as from that sequestered by kelp forests, which are a major blue carbon sink (Filbee-Dexter & Wernberg, 2020). Terrestrial-derived carbon contributes up to 40% of the sponge diet at approximately 2181-3231 kg of carbon km^{-2} day^{-1} processed by the average sponge meadow, which makes sponges a key link between terrestrial and marine food webs (Mc Cormack, 2021).

1.5 New Zealand sponge research

Although there has been a rich history of sponge research in New Zealand, much of the earlier work focused on taxonomy (e.g., Bergquist, 1961a, 1961b, 1968, 1970; Bergquist & Warne, 1980; Pritchard et al., 1984; Bergquist & Fromont, 1988; Kelly-Borges & Bergquist, 1994; Bergquist, 1996; Kelly-Borges & Bergquist, 1997; Kelly, 2007; Battershill et al., 2010; Sim-Smith et al., 2022). Only a handful of research projects addressed the ecology of sponge communities, in particular studies on the drivers of biodiversity patterns and effects of environmental stressors. Even fewer were those focused within the mesophotic zone. Currently a significant gap exists in the research of sponge community ecology on mesophotic reefs around New Zealand, and as a corollary of this, relatively little is known about sponge taxonomic assemblages in this habitat (Table 1). This is especially the case in the Bay of Plenty (BoP), the focal region for this study and an important region for New Zealand in providing a sentinel community likely to evidence shifts in marine biogeography in a changing climate.

Table 1. Summary of the most relevant research on marine sponges in New Zealand in order of newest to oldest.

Author & year	**Study focus**	**Key findings**	**Knowledge gaps identified**
Bell et al., 2023	Documented the distribution of bleached and necrotic sponges of three common New Zealand sponge species and examined how it related to regional variation in the duration and intensity of recent marine heat waves.	Sponge bleaching and necrosis reported from 5 – 60 m depth from Northeastern New Zealand (Auckland/Coromandel up to the Poor Knights Islands), Cook Strait and Fiordland. Up to 45% of sponges observed in the Northeastern region showed signs of necrosis. The greatest impacts appeared to occur on *Ecionemia alata* and *Stelletta conulosa*, which are two of the most common and important habitat-forming species in New Zealand's subtidal rocky ecosystems. Of the nearly 800 sponge species reported from New Zealand, only a small number of species appear to have shown tissue	Although New Zealand has experienced several MHWs over the recent decades, this study has been the only one to document biological impacts on sponges in coastal ecosystems. There is a lack of knowledge on temperature impacts on temperate sponges, and this study suggests that temperate sponges may be more susceptible to the impacts of marine heat waves and climate change in comparison to tropical sponges.

		necrosis in response to the marine heat waves.	
Harris, 2022	Described how sponges are distributed through the infralittoral and mesophotic zones of rocky reefs in New Zealand and assessed the role of trophic relationships between sponges and microbial food sources in determining sponge distribution, population dynamics, and carbon retention in these habitats.	Significant variation in sponge abundance and presence of substrate-free space (from Chapter 2 – Harris et al., 2021) was not explained as no correlations could be found. Suggested that food availability is the most likely driver of these patterns and therefore the distribution of temperate sponges may be determined by bottom-up effects. Suggested the high abundance of sponges relative to other benthic invertebrate groups in resource-poor environments is due to their trophic plasticity, generalist feeding strategies, and dissolved organic carbon consumption. Sponges make a significant contribution to the transfer of carbon (>100% of available	Significant knowledge gap in how sponges are distributed and function in TMEs outside of the Mediterranean. This thesis addressed said gap but realistically it only skimmed the surface. Historic limitations of TME research due to access and technological constraints has led to studies having to infer knowledge from shallow water sponge communities. This has left a gap for *in situ* research of TME sponge communities.

		carbon in the benthic boundary layer per hour) to the benthos through the infralittoral and mesophotic zone of New Zealand reefs.	
Harris et al., 2021	Measured changes in the benthic community composition of rocky reefs from 5 to 120 m at the Poor Knights Islands, Fiordland Marine Area, and the Taranaki Bights.	Abundance varied significantly with depth at 75% of sites while morphological composition changed with depth at all sites. Sponges can cover more than 70% of the available space in the deeper areas of rocky TMEs. Sponge assemblages make an important contribution to habitat complexity in benthic TME communities. Depth related patterns in the benthic community were location specific.	Species-level studies of benthic TME communities will help to elucidate any common patterns. Suggested that TME research should prioritise multivariate analysis of ecological drivers of benthic community distributions, including abiotic drivers.
Donald, 2021	Preliminary research discovering the presence of vibrant sponge reefs on the	Created a record of species observed and found a high level of biodiversity on Nukutai Reef.	Only surveyed a small area of Nukutai Reef and only one out of four transect was analysed for this study. A large knowledge

	mesophotic reefs of the Motiti Island archipelago.	The mixed fish and sponge assemblages both suggest that warm tropical and cold temperate waters have an influence the Bay of Plenty.	gap still exists regarding all other mesophotic reefs around Motiti Island. Explorative and qualitative only. Suggested that there is much more to be discovered on the mesophotic reefs of the Motiti archipelago.
Mc Cormack et al., 2020 Mc Cormack, 2015	First sponge diversity study in BoP.	High level of Porifera biodiversity in BoP is due to the variety of habitats sampled combined with the complex oceanography (northern subtropical and southern temperate waters both influence). 34 (or 18 if being conservative) undescribed species identified.	Bay of Plenty sponge grounds are largely unexplored, this study was limited to shallow reefs by SCUBA diving maximum depths. Classical taxonomy in New Zealand can be complemented by mtDNA barcoding.
Berman & Bell, 2011	Provide a baseline for sponge species diversity of Wellington south coast.	Diverse sponge assemblage present, unusually dominated by calcareous species of the genus *Clathrina*. Possibly explained by low nutrient levels.	Sponges (shallow subtidal) well researched north of Auckland, but there are large areas around the rest of NZ that have not been fully surveyed for sponges.

			Possible seasonal changes in abundance in study area.
Battershill & Bergquist, 1990	Described dynamics of stability and instability of sponge characterised habitats in NZ.	Sponge assemblages acutely correlated to physical benthic regimes, especially sedimentary dynamics.	Limited knowledge of how physical factors and sponge reproductive strategies influence variation in sponge recruitment in their natural habitat.
Ayling, 1983	Described the growth cycles of 11 NZ subtidal thinly encrusting sponge species.	Temperate thinly encrusting sponge growth is very slow, but rapid growth (up to 30 times greater than undisturbed growth rate) can occur in some species as a mechanism to regain lost substrate space after disturbance.	Investigated disturbance and recovery from scraping (imitating predation) but a gap still exists in understanding the recovery dynamics of sponges from other disturbance and stress types, such as disease.
Ayling, 1980	Long-term investigation of the reproductive biology of NZ sponges in association with disturbance and substrate type.	Seasonal cycles of sexual reproduction.	Northern NZ coastal sponge reef settlement dynamics need more detailed research to understand their aggregated dispersion patterns.

1.6 The Bay of Plenty and Motiti Archipelago reefs

The research reported here is situated within the Motiti archipelago, made up of numerous reefs scattered around Motiti Island, which is situated approximately in the middle (Figure 2). These reefs are all highly heterogeneous pinnacles of rock rising from depths of around 80 m and support an abundance of marine life (for detailed descriptions and summarised current knowledge of these reefs, refer to Donald (2021)). Three no-take Motiti Protection Areas (MPAs) have been in place since August 2021, while the wider Motiti Natural Environment Management Area (MNEMA) is still open for recreational fishing (Figure 2). The shallow areas of these reefs have been well explored as they are a popular spot for recreational diving and fishing, as well constituting an important cultural kai moana (seafood) area. The Rena shipwreck in 2011, which ran aground on Ōtāiti (Astrolabe Reef), led to a boom in environmentally related research in the region, contributing to the current knowledge of this reef system (Battershill et al., 2016; Schiel et al., 2016).

Although much of the Motiti archipelago is now safeguarded from extractive activities by the MPAs, our understanding of the spatial distribution and variability of species assemblages supported by the mesophotic reefs, extending from the various islands and subtidal reef systems there, remains limited. Even less is known about the ecology of these deeper reefs. The sole source of knowledge regarding Motiti's mesophotic reefs stems from the exploratory survey carried out by Donald (2021). In this initial (drop camera) survey, the discoveries of two probably new and ten possibly new species were made, pending retrieval of samples to confirm taxonomy. Among the readily identified sponges (due to their distinct morphology), some were characterised as naturally rare or uncommon (Donald, 2021), being known previously from the Far North (Poor Knights Islands). The fish and sponge species recorded represented a diverse assemblage with a mix of northern and southern affinities, signifying the influence of both the warm-water EAUC and cold-water Wairarapa Eddy (WE) in the BoP. This preliminary exploration provided but a first glimpse into the mesophotic zone of the Motiti archipelago, unveiling the wealth of knowledge yet to be uncovered in this reef system.

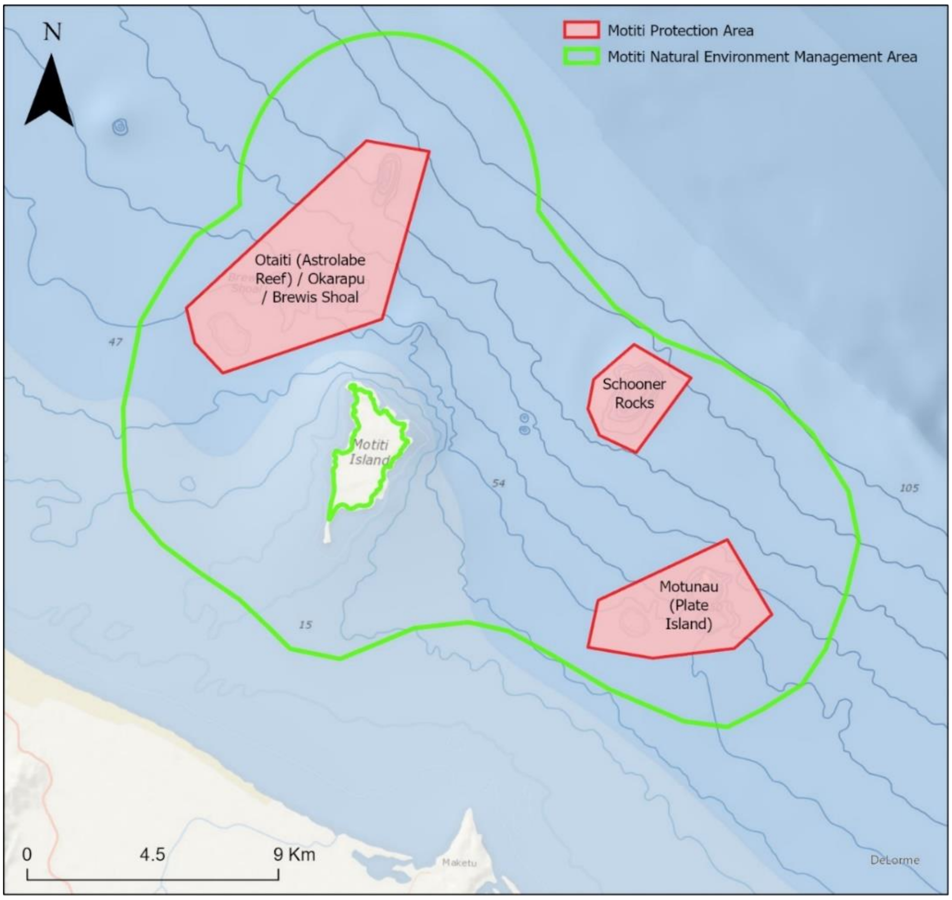


Figure 2. Map of the reefs surrounding Motiti Island, overlaid with the three no-take MPAs.

1.7 Thesis preface

1.7.1 Aims & objectives

The primary objective of the thesis is to establish a baseline of the diversity and current state of the benthic communities, characterised by sponges, inhabiting Motiti's mesophotic reefs. Furthermore, the aim is to enhance our understanding of the role of biophysical processes and environmental stressors influencing this ecosystem, to inform future management of the MNEMA and TMEs worldwide.

1.7.2 Thesis format

This thesis has been designed in publishable components, but with modifications in the interests of reducing repetition. Chapter One serves as a general introduction, providing the context for this research and discussing the key themes of mesophotic reefs, TMEs, the importance of sponges in benthic TME communities, previous relevant research in New

Zealand and background information on the Motiti reefs. Chapters Two and Three are research chapters. Chapter Two focuses on the biodiversity of Motiti’s mesophotic sponge communities, investigating local variability in diversity and biogeographic affinities. Chapter Three focuses on key environmental stressors and their potential impacts on Motiti’s mesophotic sponge communities, namely heat and sedimentation stress. Chapter Four serves as a general discussion, linking the two research chapters and exploring the broader implications of this research in the context of current literature and the current climate.

Chapter 2

Biodiversity & Biogeographic Distributions

2.1 Introduction

The shifting dynamics of marine environments in response to global warming have spurred a re-evaluation of the biogeography and diversity of sponge assemblages in deeper waters (IPCC, 2023). Sponge communities are excellent indicators of long-term environmental conditions due to their sentinel nature in reflecting the prevailing conditions of their habitat (Battershill & Bergquist, 1990; Bell et al., 2015). By tracking any changes in the biogeographic distributions of sponge species, shifts in oceanic currents can be detected based on known sponge distributions and thus affinities to warm or cold water (Maldonado & Uriz, 1995; Mc Cormack, 2021). It is important to understand the geographic population connectivity (i.e., how oceanic currents may connect spatially separated populations) between marine communities when considering the resilience of mesophotic ecosystems (Turner et al., 2019). Isolated populations can face issues with recruitment limitation of new individuals and thus become more susceptible to degradation than those able to be replenished with larvae or other propagules (fragments and buds in the case of sponges), transported by oceanic currents from surrounding areas (Kenchington et al., 2019; Guy & Metaxas, 2022). The diversity of sponge assemblages is inherently woven into this, as both are based on the make-up of species within a community. Alterations in species diversity or composition within a sponge community serve as an indicator of changing environmental conditions, as these communities reflect their surrounding environment (Battershill & Bergquist, 1990; Bell et al., 2015). It should be noted that it is crucial to conduct reliable taxonomic identification to underpin any study of this nature (Mc Cormack, 2021). Investigating both facets—sponge species distribution and community diversity—can yield a deeper understanding of the ecological dynamics at play, facilitating more comprehensive and effective management strategies to mitigate the anticipated impacts of a range of stressors likely to accompany global warming (van Gennip et al., 2017; Bell et al., 2023; IPCC, 2023).

2.1.1 New Zealand Biogeography

The biogeography of New Zealand’s marine system is influenced by the mixing of major oceanic currents. Warm subtropical currents flow down from the north on the East Auckland Current (EAUC) while cold subantarctic currents flow up from the south, splitting and forming eddies around the irregular coastline (Figure 3). In the Bay of Plenty (study area of this thesis), Mc Cormack (2015) suggested that the mixing of warm northern and cold southern oceanic currents contributes to the high level of biodiversity found on the reefs here. A recent preliminary survey by Donald (2021) provided additional evidence to support this, showcasing the resulting unique assemblage with both subtropical and subantarctic affinities. If the EAUC shifts spatially or in magnitude (van Gennip et al., 2017), the impacts of this will likely be able to be seen by monitoring the sponge reefs in this region.

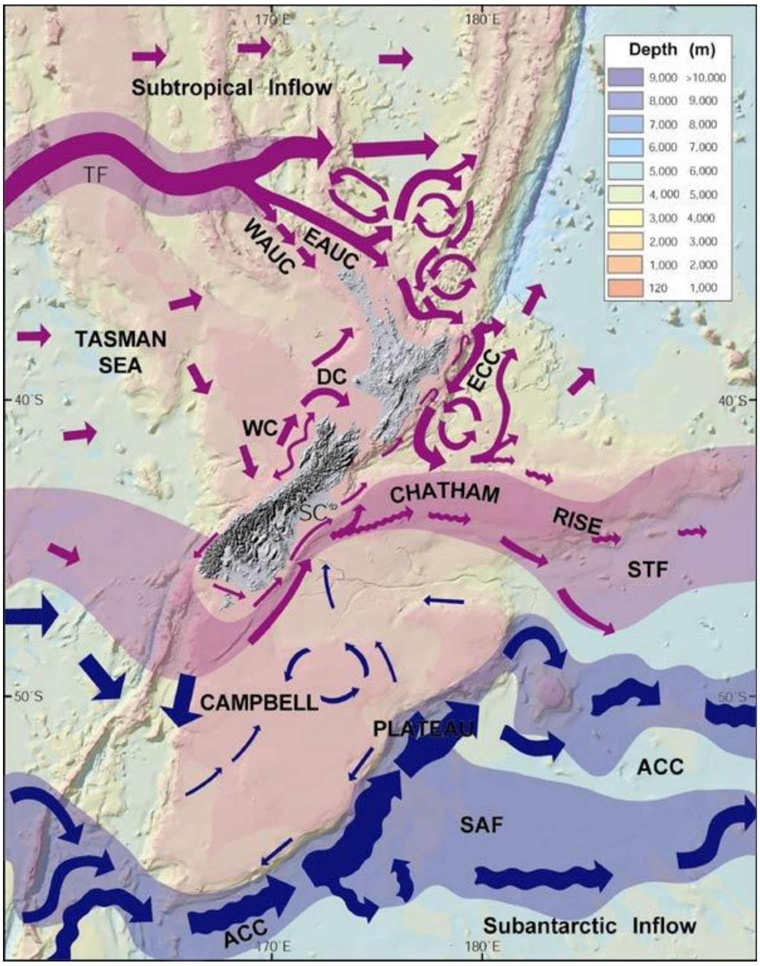


Figure 3. Major ocean currents and water masses around New Zealand, directions are illustrated by labelled arrows (from Stevens & Chiswell, 2006). Abbreviations stand for the following: ACC – Antarctic Circumpolar Current; DC – D’Urville Current; EAUC and

WAUC – East and West Auckland Currents; ECC – East Cape Current; SAF – Subantarctic Front; STF – Subtropical Front; TF – Tropical Front; WC – Westland Current.

2.1.2 Motiti biodiversity

Preliminary research suggests that there is exceptional benthic diversity unique to the Motiti archipelago (Donald, 2021). Much like other sponge gardens around the world (Bart et al., 2021), the Motiti mesophotic reefs are a biodiversity hotspot. The diversity of benthic assemblages here appears highly patchy at local (<10 km) scales, reflecting varied biophysical environments (Donald, 2021). It is clear that this is a vibrantly biodiverse reef system that has ecologically important functionality as nursery grounds for commercial fish species (Battershill & Bergquist, 1990; Battershill et al., 2010; Hill, 2017), as well as playing a crucial role in benthic-pelagic coupling and carbon flux (Maldonado et al., 2012; Bell et al., 2015), although the full extent specific to this region has yet to be examined (Tau Ki Ākau, 2023). They also have significant cultural importance as the reefs and the species they host are taonga for Motiti mana whenua, Ngāti Whakahemo and Te Patuwai. Motiti Island and the surrounding reefs have a rich Māori cultural history (Bay of Plenty Regional Council, 2019). The recent establishment of three no-take Motiti Protection Areas (MPAs), all of which contain mesophotic reefs, has provided a unique opportunity to safeguard and monitor a complex deep reef ecosystem that is relatively easy to reach and likely to be influenced over time by shifting environmental conditions (Bell et al., 2022).

2.1.3 Aims

This chapter addresses the biodiversity of the benthic mesophotic communities in the Motiti archipelago, focusing on sponges. The aims of this chapter are to:

(1) Investigate the diversity and geographic distribution of Motiti's mesophotic sponge communities.

(2) Assess any local variability in sponge diversity.

2.2 Methods

2.2.1 Survey sites

Multibeam Echosounder (MBES) depth data from the 2012/2013 LINZ HS39 Bay of Plenty Hydrographic Survey were used to select ROV survey sites and plan transect locations, as it was the highest quality hydrographic information available for the study region. Deep reef sites (>30 m) were identified based on steep topography changes and rocky reef structures confirmed using rugosity datasets. Te Poroiti Reef, Nukutai Reef and Motuhaku Reef were chosen as survey sites based on the criteria that they must be within the MNEMA, deeper than the 30 m scientific diving limit and over biogenic habitat (i.e., rocky reef) (Figure 4). These three reefs, along with all other outer reefs in the Motiti archipelago, constitute highly complex rocky habitats ranging from bedrock platforms to steep cliffs, from cobble and boulder fields to caves and overhangs (Donald, 2021; Ross et al., 2018). All are rocky pinnacles rising steeply from depths of approximately 42 – 80 m (Boffa Miskell Limited, 2020). The nearshore reefs around Motiti Island itself are more prone to sediment inputs (higher average concentration of total suspended solids) compared to the offshore reefs, Te Poroiti and Motuhaku (Crawshaw, 2022). Preliminary research by Donald (2021) used a drop camera to explore a small area of Nukutai Reef but no research has been published on the mesophotic zones of Te Poroiti Reef or Motuhaku Reef.

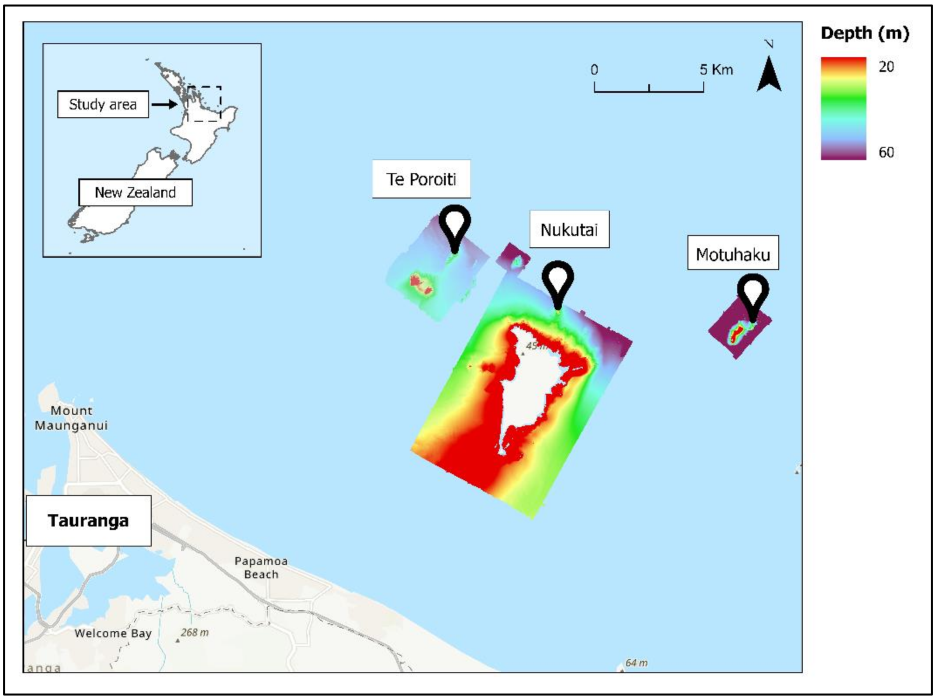


Figure 4. The three ROV survey sites are marked by red triangles at Te Poroiti Reef, Nukutai Reef and the northern end of Motuhaku Reef.

2.2.2 Remotely Operated Vehicle (ROV)

Image collection was carried out from 4th – 6th August 2022. Discovery Marine Limited (DML) (a partner with the University of Waikato for benthic marine mapping), was contracted to access the chosen locations and carried out the ROV fieldwork along with the author, using their survey vessel TUPAIA. Weather conditions were primarily fine, varying between 5-12 knot southerly winds, 0.5-1.2 metre swell and 0.2-0.5 metre chop.

Transect locations were pre-determined and were selected to provide coverage on all sides (i.e., compass faces) of each reef location, starting at the sandy seabed and travelling up to a shallow point on the reef. The purpose of placing transects on all sides was to take into account any effect of predominant ocean currents on sponge assemblage characteristics, as they may be influenced by reef topography, reef position, or reef aspect. Five video transects were carried out at Te Poroiti Reef and Motuhaku Reef, while four were completed at Nukutai Reef (Figure 5). The underwater position of the ROV was estimated with 2-5 m accuracy using a combination of the vessel's onboard GNSS positioning system and underwater features that were identified in the MBES data, such as prominent rocks, crevices and the known depth.

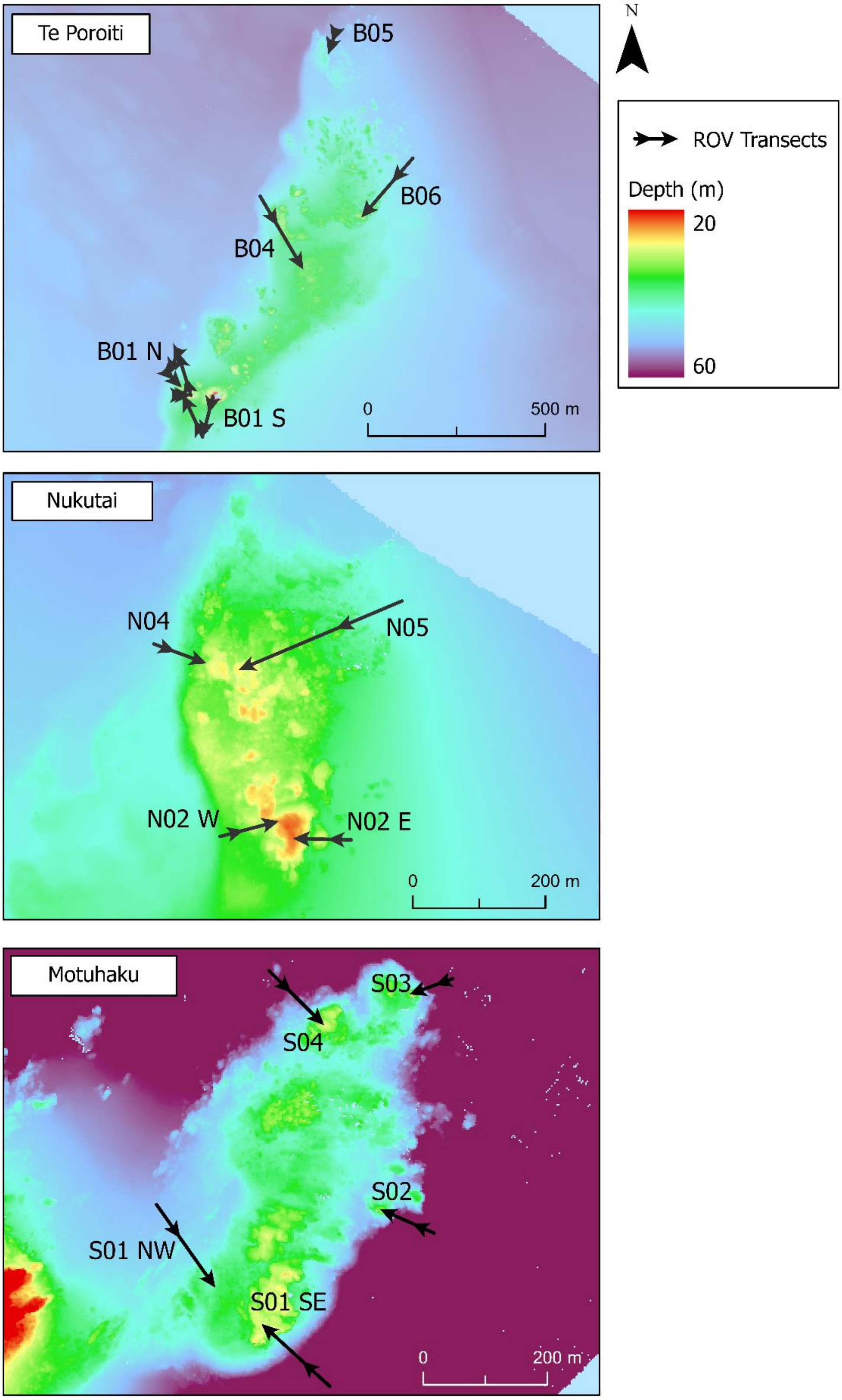


Figure 5. Labelled ROV transect locations at Te Poroiti Reef, Nukutai Reef and Motuhaku Reef are shown by the black lines, with arrows indicating the direction of ROV travel.

An observation class Chasing M2 Pro ROV was used to collect all footage (Figure 6), with a 200 m tether cable connecting the ROV to the topside control equipment on the vessel. Two visual data collection methods were utilised in this survey. Firstly, the inbuilt ROV camera (4K/12M pixel camera, 1/2.3 SONY CMOS, EIS stabilization feature) to collect a live video feed and, secondly, a GoPro Hero 9 Black was mounted atop the ROV facing 15° down from the horizontal line of the ROV, to take benthic photographs every 2 seconds along each transect. The addition of the GoPro as an auxiliary camera provided a more perpendicular angle than the ROV inbuilt camera could, which ensured parallax error was minimised as much as possible (Harris et al., 2021; Lesser & Slattery, 2021). The addition of a second camera also allowed the analyst to combine vertical images with oblique video footage to make identification easier in the resulting footage. A two-point laser scale spaced 10 cm apart provided a scale of reference. The date, time, depth and heading metadata from the ROV camera was used throughout analysis rather than the GoPro image metadata because there is a slight time offset between the two in each transect. Digital settings used for both cameras during surveying as well as the time offsets can be seen in Appendix A: Table 1. There is one exception in transect S04 metadata, where the depth data was estimated due to failure of the ROV camera to record the whole transect. Although the GoPro camera still captured images for analysis, it was not able to record depth. The depth was estimated using the below calculation:

Transect length = 124 m

Transect time = 41 mins

Average speed = 3.024 m/min

$$s = u * t$$

Where s = distance

u = speed

t = time

The distance along the transect for each image was calculated and matched up against 0.5 m interval point extracts of depth along the transect line, based on transect start and finish co-ordinates and using ArcGIS Pro. It is important to note that these calculations assume speed is constant throughout the transect, which it is not and therefore the depths for transect S04 are estimates based on average speed.

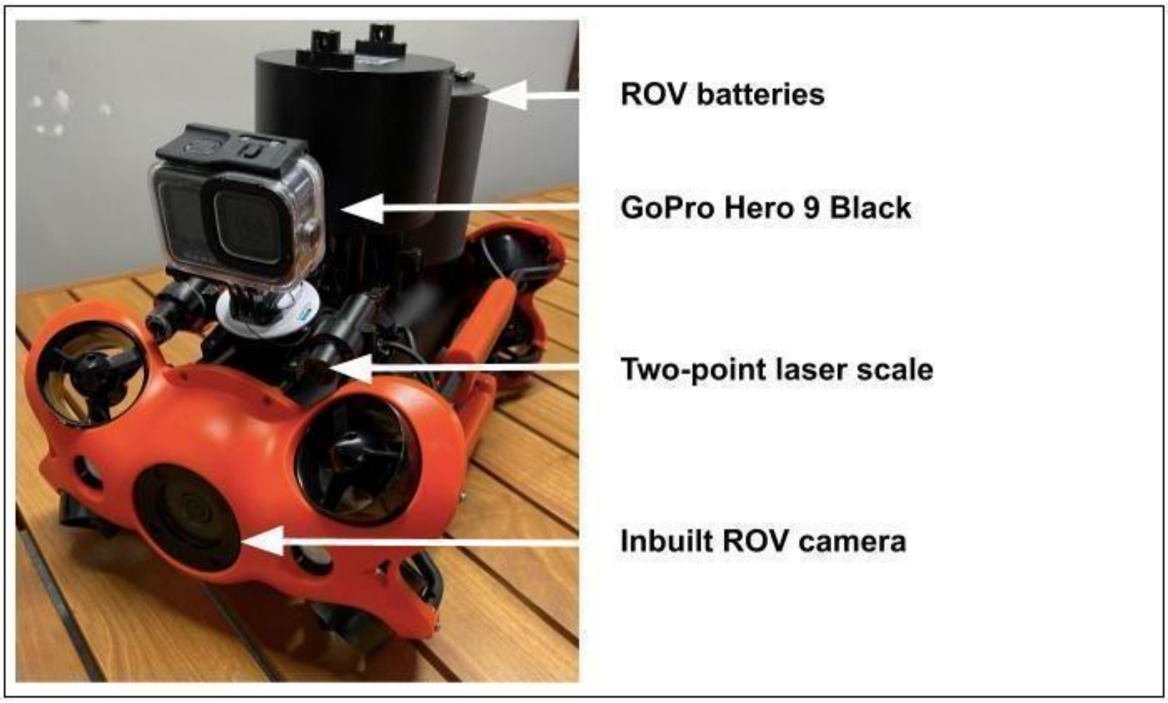


Figure 6. Chasing M2 Pro ROV used by DML to collect footage of Motiti Island's outer reefs, with GoPro and two-point laser scale added on.

2.2.3 Transect methodology

The survey vessel was positioned at the start of each transect using the GNSS positioning system combined with the onboard navigation software (QINSy) and an overlaid map of the historical MBES depth data. The ROV was deployed and first dove to the seabed then navigated on a fixed heading along the transect. Vessel position coordinates were logged as it followed above the ROV with a person on deck managing the length and direction of the tether. The ROV was flown approximately 1 m above the sea floor, facing (pitching) down by approximately 20^{o} to be as perpendicular to the benthos as possible. With the addition of the GoPro, the camera to substrate angle was approximately 55^{o} (oblique) throughout each transect (perpendicular being 0^{o}). This angle fluctuated due to the nature of navigating over highly complex reef structure, so images had varying fields of view.

ROV transect methods vary amongst the literature in regard to flying vertically up the reef and horizontally across the reef following depth contours (McIntyre et al., 2016; Harris et al., 2021). However, flying vertically up the reef was the only feasible option for these surveys due to the highly complex nature of the reef, known from bathymetry data. Flying horizontally would have restricted the view of where the ROV was going due to the inbuilt live feed camera facing forwards, which may have led to damage of the reef biota and ROV or entanglement.

2.2.4 Image post-processing

A total of 6,320 images were captured across all transects. Image post-processing began with removing unnecessary footage from the beginning and end of each transect. Next, the original folders for each transect were copied to create separate folders in which all near-duplicate (same field of view) and low-quality images (blurry, over-exposed, under-exposed, mid-water column, or <30 m deep) were deleted. The images were then narrowed down further by creating another folder for each transect containing only the high-quality images appropriate for carrying out taxonomic identification of sponges. A maximum of 30 images were analysed per transect, selected using a random number generator when more than 30 high quality images were available. The number of images analysed from each transect can be seen in Appendix A: Table 2.

2.2.5 Web-based annotation platform

Web-based annotation platforms offer a range of advantages over traditional image or video annotation software installed on individual computers. They enable remote collaboration and supervision by experts involved in a project, facilitate online storage of data for easy access from any computer, provide a contemporary and user-friendly interface equipped with helpful tools, and often incorporate AI capabilities to assist in annotation and analysis.

Three platforms were trialled to determine the one best suited for analysing the image sets in this study: BIIGLE; ReefCloud; and SQUIDLE+ (Table 2). These three platforms were compared based on functionality for labelling all identifiable sponges in an image and applicability to New Zealand reef systems. BIIGLE was chosen primarily because it has a free-form annotation method. Free-form annotation allows users to identify and annotate any objects of interest (OOI) in an image and not be limited to fixed- or random-point intercept methods, which often miss rare or small sponges in small sets of images. Other key features of note in BIIGLE include the ability to store images and footage online, the option to collaborate with experts or guests on your project and have their labels attach additionally to your OOI rather than replace your label, the Largo tool (Label Review Grid Overview) which allows you to review all OOI with the same label and quickly change, attach new labels or delete them, and the user-friendly, easy to navigate layout of the platform (Zurowietz & Nattkemper, 2021). BIIGLE is also constantly being updated with new features at the request of users.

Table 2. Comparison of the three web-based annotation platforms considered for use in this study.

	Pros	Cons
BIIGLE	User-friendly interface that accommodates temperate ecosystems. Allows free-form annotation in addition to fixed- and random-point intercept annotation methods. Used by the NZ National Institute of Water and Atmospheric Research (NIWA) so can easily collaborate in the future. Constantly updated, many new features based on requests from users.	Artificial intelligence (called 'MAIA') only identifies objects of interest and does not assign labels automatically, so annotation is limited to manual only.
SQUIDLE+	User-friendly interface that accommodates temperate ecosystems. AI automatically assigns labels.	Incomplete and does not currently support users.

Reef Cloud	User-friendly interface. AI assigns labels automatically based on training data. Is being improved constantly and AIMS staff provide support for users.	The user interface is geared toward coral reef ecosystems only. Restricted to random- or fixed-point intercept annotation methods.

2.2.6 Image analysis

The freeform annotation method available in BIIGLE was used to outline and label each individual sponge to the highest taxonomic level possible, generating count abundance data. Sponges that looked like they were joined together were counted as one. Where signs of tissue necrosis, bleaching or general stress were evident, that individual was given a second label to record the proportion of sponges in poor condition. Due to the difficulties with camera angle discussed in Chapter 1, analysis was restricted to only the immediate field of view where sponges were considered discernible in high enough detail for taxonomic identification.

After the author completed the whole image set, they were reviewed for a second time again by the same author in the interests of quality assurance and consistency. Expert sponge taxonomist Prof. Christopher Battershill (University of Waikato) supervised the identifications by collaborating online via BIIGLE, with the video footage playing alongside on a separate screen to give an additional 3D view for better perspective of each image. Identifications were discussed amongst experienced sponge and marine invertebrate taxonomists and ecologists who have dived throughout Aotearoa over many decades.

Although all identifications were made to the highest taxonomic level possible, there was invariably some level of uncertainty in identifying sponges through images without analysing a sample and examining spicules to confirm. To account for this, many species and morphotypes were grouped to a higher level, usually genus, to ensure that each identification category certainly represents at least one species that is different, which is what is important for diversity measures. Consequently, this allowed measurements of diversity at the species level, where some species were represented by ‘sp.’, some similar looking groups of species within the same genus represented by ‘spp.’, and some distinctive morphotypes represented by Operational Taxonomic Units (OTUs) – for example, the commonly seen ‘thin encrusting red Poecilosclerid’ and ‘fluffy cluster sponge’. Although this limited the scope of analysis somewhat, it was the most thorough analysis we could do with the resources available at the time, where limitations included restrictions on diving (due to weather and Covid), gear, funding and time. It was important that this analysis was done to the best of our ability now because of possible threats to this ecosystem, such as unprecedented sediment plumes from Cyclone Gabrielle (Harrington et al., 2023; Noll & Andrews, 2023) and the ever-pressing climate change (IPCC, 2023). Evidence for such occurrences and the likelihood that these reef systems are already being impacted is provided below in the discussion.

2.2.7 Sponge sample collection

The ROV image identifications were backed up by sample collections in comparable reef systems at depth (20+ m at Karewa Island, Motiti Island, and Ōtāiti and Okarapu reefs) and in areas heavily shaded (rocky canyons, overhangs and fissures) that would constitute similar habitat to those deeper (darker) reefs systems out of normal SCUBA diver reach. These specimens were processed taxonomically and assigned to genus and species where possible. *In situ* and deck/laboratory photographs were also taken for cross reference. After collection, sponge samples were immediately stored in 70% isopropanol once on board the boat. After one month they were transferred to 100% ethanol.

As samples could not be collected of every species seen in the images, key species were targeted for sample collection. The key species targeted were those that could not clearly be identified in the images and those which seemed to be new, or at least new to the area. A pilot study was conducted on the rocky reefs near Rabbit Island on March 14th, 2023, to trial using a Chasing M2 Pro ROV with a manipulator arm to collect sponge samples. Rabbit Island was the chosen location because it is the nearest similar rocky reef to Tauranga harbour, sitting about 500 m offshore from Mount Maunganui beach and about 20.2 km closer than the study sites. However, it was determined that this ROV was not fit for collecting samples because the manipulator arm was not strong enough to cut/grab some sponge tissue. A larger ROV would be sufficient for this task, such as a Boxfish, but due to the short time frame of this project and logistical limitations, samples were instead collected by SCUBA diving in March

2023 (see Appendix B for dive collection details, notes, and images). Furthermore, it was beyond the scope of this thesis to carry out further deep dive collections using technical divers as time and abnormally severe weather conditions limited this option (Cyclone Gabrielle and ensuing bad weather patterns).

2.2.8 Sponge sample preparation

To identify the sponges collected, a spicule mount and a thick section were prepared for each sample. Before beginning preparation, all 25 mL Pyrex test tubes were rinsed with distilled water, dried and numbered. A table was made on paper to keep track of which number test tube each sample was in. The following steps were then followed for the preparation of each sample. Between handling each sample, tools were washed with distilled water.

Spicule mount preparation:

Nitric acid was used to digest organic matter, leaving behind the glass spicules for analysis (for species other than the Calcarea, none of which were collected in this study). First, a cross-section was cut to include the pinacoderm, matrix and base. This was cut into small fragments (2 – 5 mm in diameter) to maximise surface area:volume ratio and added to the relevant test tube for spicule preparation. Inside the fume hood, a few drops of distilled water were added to each test tube using a squeeze bottle, followed by just enough nitric acid (65% concentration) to cover the fragments. Monitoring was required for 10 minutes after the addition of nitric acid as some samples reacted more strongly than others. In the case of a strong reaction, a few drops of distilled water at a time were added to the test tube to dilute and prevent bubbles overflowing. Once the fragments had been left to digest for at least 6 hours, with the addition of a few extra drops of nitric acid if needed to ensure all organic matter was dissolved, ~15 mL of distilled water was added to reduce viscosity and thus allow spicules to settle. After 1 hour of settling to avoid loss of microscleres, excess solution was decanted, and spicules were cleaned by stirring and adding another ~15 mL of distilled water. This was repeated once more, and then repeated but using ethanol instead of distilled water to give the spicules a final thorough rinse. Excess ethanol was then decanted, and the left-over solution swirled to get the spicules in suspension so they could be poured into 15 mL labelled clear vials with screw-top lids. Spicules were left to settle for 2 minutes, then transferred to their relevant labelled slide using a 1 mL plastic pipette with the end cut off so that it had a large enough opening pick up megascleres. Once the ethanol had evaporated from the slide, Canada balsam was used to mount a cover slip on top.

Thick section preparation:
At least two perpendicular thick sections of 1.0 – 1.5 mm thickness were hand-cut in wedge shapes using a clean scalpel, where the thickest end was at the pinacoderm and the thinnest in the matrix. The thick sections were placed onto a labelled slide and left until the isopropanol air dried. Canada balsam was then used to mount the cover slides on top of the thick sections.

2.2.9 Sponge sample analysis

Both thick sections and spicule mounts were analysed under a high-powered compound microscope. Identifications were made using the traditional alpha-taxonomy approach (for a full explanation, see Mc Cormack (2015)) with reference to the primary literature, along with some newer monographs (Bergquist, 1961a, 1961b, 1968, 1970; Bergquist & Warne, 1980; Pritchard et al., 1984; Bergquist & Fromont, 1988; Dawson, 1993; Bergquist, 1996; Kelly, 2007; Battershill et al., 2010; Kelly, 2022; Sim-Smith et al., 2022). These identifications were verified by Prof. Christopher Battershill (University of Waikato) and Prof. Michelle Kelly (NIWA). Final identifications followed the most up to date taxonomic classifications as recognised by the World Register of Marine Species (WoRMS) – at time of submission.

Spicule and thick section photos were taken with the microscope camera. Spicule measurements were taken using the digital scale available on Olympus cellSens, a computer program connected to the high-powered compound microscope. A desktop photo was taken of each sample using an Olympus Tough TG-6 4K camera and tripod at a set height. Each sample was briefly removed from storage in isopropanol and dabbed with a paper-towel to minimise glare from the light.

2.2.10 Statistical analysis

Statistical analyses only included results from ROV footage, as samples were not taken at the same survey sites due to their purpose being only for back up of visual identifications. All statistical analyses for this chapter were carried out using PRIMER v7 (Clarke & Gorley, 2015). Species richness counts from images were pooled and analysed at transect level, number of transects being replicates for each site (i.e., reef). The species accumulation curves were calculated using permuted sample order (9999 permutations). The two most common and proven measures of taxonomic distinctness (TD) in marine ecology (as cited in Jiang et al., 2020) were used in this study; average TD (Δ+) and variation in TD (Λ+) (for in-depth explanation refer to Clarke & Warwick, 1998). Because average TD is based on presence/absence data, results are comparable across varying sampling efforts, biogeographic and time scales, which ensure the results of this study are comparable to future studies in the interests of informing long-term MPA management (Clarke & Warwick, 1999). Moreover, the issue of abundance counts being likely underestimated and skewed toward larger macrofauna, due to the image quality and camera distance to the benthos, is ameliorated by the robust properties of Δ+ and Λ+ (Clarke & Warwick, 1998; Clarke & Gorley, 2015; Jiang et al., 2020).

Many studies have discussed the caveats of relying on TD indices to assess environmental disturbance caused by anthropogenic activities (e.g., Clarke & Warwick, 1999; Hu & Zhang, 2016). But in this case, they provide robust assessment due to the use of TD indices within only one Phyla (Porifera), as well as data being checked to ensure no indication that careful application was needed (e.g., if any sites with 'lower than expected' Δ+ values had low species numbers but a high Λ+ value) (Clarke & Warwick, 2001). TD indices have proven good measures of species diversity in marine ecosystems for over two decades now (as cited in Jiang et al., 2020) and using both complements analysis, as they shed light on different aspects of the taxonomic structure of the communities in question (Clarke & Warwick, 2001).

To calculate TD indices, step lengths were given constant increments ($\nu = 1$) and final path-length weights were standardised by default to set the maximum path length (ω) to 100 (Table 3). A randomisation test was run in PRIMER to produce a 95% ‘confidence funnel’, which determines whether any reefs had a ‘lower than expected’ average taxonomic spread while maintaining comparability between semi-uncontrolled habitat types (i.e., controlled by only observing rocky reef, but uncontrolled slope, rugosity, aspect, etc.) (Clarke & Warwick, 1998, 1999).

Table 3. Step lengths (ν) and final path-length weights (ω) for each taxonomic level.

Taxon	Branch (ν)	Weight (ω)
Species	1	20
Genus	1	40
Family	1	60
Order	1	80
Class	1	100

OTUs were not able to be included in analysis of TD due to the lowest taxonomic level of identification being order and, in some cases, only phylum. Those identified to genus level were counted as one species, since even those marked as 'spp.' represent at least one different species within the community. All OTUs and sponges identified to genus or family level that are in included in the total species richness can confidently be treated as different species. They have been grouped appropriately to ensure this, as previously discussed.

To test for variation between means of Δ+ and Λ+ amongst reefs, permutational multivariate ANOVAs (PERMANOVAs) were undertaken with PRIMER v7 (Clarke & Gorley, 2015) and with the PERMANOVA+ add-on (Anderson et al., 2008). Resemblance matrices for the values of Δ+ and Λ+ across transects were based on Euclidian distances, 9999 permutations were run, and F values were tested by permutation (Clarke & Gorley, 2015).

2.2.11 Limitations in data collection

The Chasing M2 Pro ROV did succeed in collecting sufficient footage for an extensive analysis of the targeted reefs, but it seemed that the vehicle was at the limit of its suitability for this type of project. The power supply and internal sensors failed while it was underwater, which led to repeat visits to the reefs and wear and tear on the vehicle. Another difficulty was encountered with the recording of positioning data. A small ultra-short baseline (USBL) acoustic positioning system was investigated to enable more accurate positioning of the ROV underwater but unfortunately, this equipment did not cooperate well with DML's other hardware and was not deemed suitable for the project. Despite these difficulties, the Chasing M2 Pro ROV was a cost-effective alternative to the larger, more robust commercial ROVs available which increase substantially in cost and complexity.

Varying camera to substrate angles resulted in most images being at oblique angles. The issue this raises is that oblique angle images introduce parallax error, geometric distortion and scaling error, making any measurement taken from a laser scale inaccurate whether that be measurement of sponges or quadrat area (Lesser & Slattery, 2021). Therefore, no measurements could be made using the laser scale which ruled out the use of some common measurements for abundance and species density data, such as biomass.

2.3 Results

The results presented in this section address the diversity and geographic connectivity of Motiti’s mesophotic sponge communities by assessing ROV footage and specimen samples at the lowest taxonomic level possible. Species richness was relatively similar amongst the three surveyed reefs, at an average of 15 species per transect at Te Poroiti and Nukutai, while Motuhaku had an average of 21 species per transect (Figure 7). Keep in mind that while these numbers provide context, they are not comparable to other studies due to the dependency of species richness values on sampling design and effort (Clarke & Warwick, 1999).

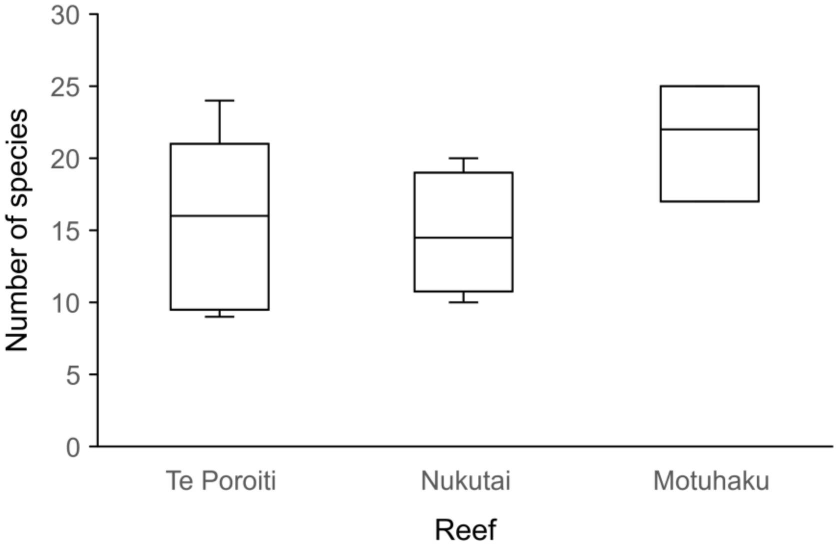


Figure 7. Average sponge species richness per transect at Te Poroiti, Nukutai and Motuhaku reefs. The lower and upper box boundaries show the 25th and 75th percentiles, respectively, the line inside the box shows the median, and the upper and lower whiskers show the minimum and maximum.

2.3.1 Diversity measures

Analysis of ROV footage revealed highly biodiverse sponge communities inhabiting all three of the surveyed mesophotic reefs (Table 4 & Appendix C: Table 1). A total of 53 different sponge species were identified from ROV footage, this being a conservative number to ensure certainty of classifications as discussed earlier. Sponges were predominantly from class Demospongiae, but some calcareous sponges were also seen (Table 4). Of those identified in ROV footage, 11.3% were possibly new or undescribed species (Table 4). Species accumulation curves were still increasing at the maximum number of transects carried out on each reef and overall (transects of all three reefs combined), suggesting that greater sampling effort in future would enable a recording closer to the true species richness present, which is undoubtedly much higher than was able to be recorded in this study (Figure 8). Hence, findings presented here represent a conservative estimate of diversity.

Table 4. Total list of all species and OTUs from Te Poroiti, Nukutai and Motuhaku reefs. Includes those recorded from both ROV footage in August 2022 and samples collected by diving in March 2023, ordered alphabetically. For images of example OTUs, see Appendix D.

Class	Order	Family	Genus	Species/OTU
Calcarea	**Clathrinida**	Leucettidae	*Rowella*	*Rowella* spp.
	Leucosolenida	Leucosoleniidae	*Leucosolenia*	*Leucosolenia rosea*
	Unknown			Calcarea n. sp. 1
Demospongiae	**Axinellida**	Axinellidae	*Pararhaphoxya*	⁺*Pararhaphoxya* cf. *pulchra*
				**Pararhaphoxya sinclairi*
		Raspailiidae	*Raspailia*	^⁺*Raspailia* sp. nov. 1 (spathulate, Motiti Island, Donald)
				**Raspailia* (*Raspaxilla*) *topsenti*
	Biemnida	Biemnidae	*Biemna*	*Biemna rufescens*
	Bubarida	Desmanthidae	*Petromica*	*Petromica* sp.
	Clionaida	Clionaidae	*Cliona*	*Cliona* sp.

		Spirastrellidae	*Spirastrella*	^+*Spirastrella* sp. 01 (0CDN6683-X, Three Kings)
	Dendroceratida	Darwinellidae	*Darwinella*	*Darwinella* cf. *gardineri*
				Darwinella oxeata
			Dendrilla	*Dendrilla* cf. *rosea*
	Dictyoceratida	Irciniidae	*Psammocinia*	#*Psammocinia* spp.
				+*Psammocinia beresfordae*
		Spongiidae	*Spongia*	+*Spongia* (*Heterofibria*) cf. *manipulatus*
		Thorectidae	*Taonura*	*Taonura* cf. *marginalis*
			Thorecta	*Thorecta* cf. *reticulatus*
	Haplosclerida	Callyspongiidae	*Callyspongia*	*Callyspongia* (*Callyspongia*) *nuda*
			Unknown	Callyspongiidae n. sp. 1
		Chalinidae	*Haliclona*	*Haliclona* sp.
		Petrosiidae	*Neopetrosia*	+*Neopetrosia* sp. 1 (spicules 152 – 183 µm, Astrolabe Reef, Donald)
			Petrosia	**Petrosia* (*Petrosia*) *hebes*
			Xestospongia	#*Xestospongia* spp.
				+*Xestospongia* cf. *novaezealandiae*
	Poecilosclerida	Acarnidae	*Iophon*	*Iophon laevistylus*
		Chondropsidae	*Chondropsis*	cf. *Chondropsis* sp.
		Crambeidae	*Crambe*	+*Crambe* sp. 01 (NIWA 51235, Spirits Bay, Kelly)
		Desmacididae	*Desmacidon*	*Desmacidon mamillatum*
		Latrunculiidae	*Latrunculia* (*Biannulata*)	+*Latrunculia* (*Biannulata*) *procumbens*
		Tedaniidae	*Tedania* (*Tedania*)	+*Tedania* (*Tedania*) *battershilli*

		Unknown		Thin encrusting red Poecilosclerid
				^Yellow thick encrusting Poecilosclerid
	Polymastiida	Polymastiidae	*Polymastia*	*Polymastia* cf. *massalis*
				Polymastia crocea
				Polymastia hirsuta
	Suberitida	Halichondriidae	*Ciocalypta*	*Ciocalypta* cf. *penicillus*
			Halichondria	*Halichondria* (*Halichondria*) *moorei*
			Hymeniacidon	*Hymeniacidon* cf. *perlevis*
		Suberitidae	*Aaptos*	+*Aaptos conferta*
				+*Aaptos globosa*
				#*Aaptos* spp.
			Homaxinella	*Homaxinella* cf. *erecta*
			Suberites	+*Suberites* sp. (cf. big cheese sponge)
				#*Suberites* spp.
	Tethyida	Tethyidae	*Tethya*	*Tethya* cf. *bergquistae*
				Tethya spp.
	Tetractinellida	Ancorinidae	*Ecionemia*	*Ecionemia alata*
			Jaspis	+*Jaspis novaezealandiae*
			Stelletta	*Stelletta conulosa*
				Stelletta crater
				Stelletta maori
				Stelletta sandalinum
		Geodiidae	*Geodia*	*Geodia regina*
		Scleritodermidae	*Aciculites*	*Aciculites pulchra*
		Tetillidae	*Cinachyrella*	*Cinachyrella* spp.

	Trachycladida	Trachycladidae	*Trachycladus*	*Trachycladus stylifer*
	Desmacellida	Desmacellidae	*Desmacella*	*Desmacella dendyi*
Demospongiae (Subclass Heterosclero-morpha)	**Unknown**			Heteroscleromorpha n. sp. 1
Unknown				^Black & orange cup
				Dark encrusting sponge
				^Fluffy cluster sponge
				^Orange meandering sponge
				^Oyster mushroom sponge
				^Possibly tumbleweed sponge
				Yellow smooth massive sponge

*Indicates species identified in ROV footage and with samples.

^New or undescribed species (full assignment of ‘Unknown’ OTUs pending a sample and workshop with Prof. Michelle Kelly, NIWA).

$^{+}$Indicates species only identified in samples, not identified in ROV footage and thus not included in statistical analysis.

$^{\#}$Indicates those identified as ‘spp.’ in ROV footage which were included in statistical analysis, but not in the combined total species richness calculation as they are not certainly different to the species identified from samples.

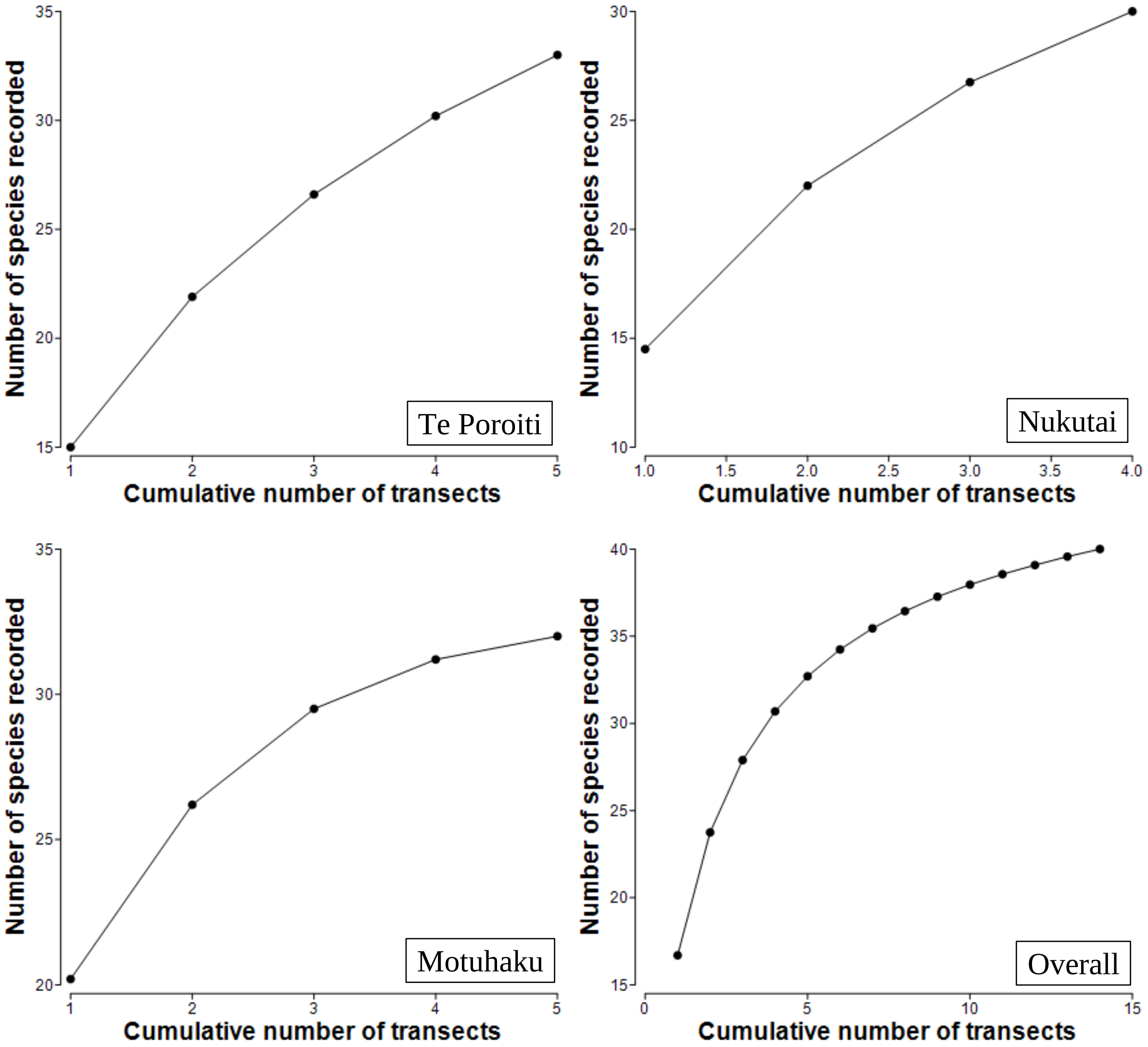


Figure 8. Sponge species accumulation curves across cumulative number of transects, based on ROV footage of Motiti's mesophotic reefs: Top left - Te Poroiti Reef; Top right - Nukutai Reef; Bottom left - Motuhaku Reef; Bottom right - overall. Note that axis scales are different for each graph.

Most transects fell within the 95% confidence limits of the funnel applied to average taxonomic distinctness (Δ+), except for transects B01 North and N02 West which both fell below the lower confidence limit (Figure 9) (Appendix C: Table 2). This implies that the two aforementioned transects had 'lower than expected' Δ+, while the rest were not found to be significantly different from the 'expected' Δ+ value for these sponge communities, which was derived from the total species list given in Table 4. Transect B01 South also fell on the edge of the lower confidence limit (Figure 9), perhaps showing an overall lower Δ+ at the southern tip of Te Poroiti Reef where B01 North and B01 South were in close proximity (Figure 5). Conversely, the mean values of variation in taxonomic distinctness (Λ+) for all transects fell within the confidence funnel, implying that the mesophotic sponge communities inhabiting Te Poroiti, Nukutai and Motuhaku reefs all vary in taxonomic distinctness within the ‘expected’ range (Figure 9).

Interestingly, the majority of transects on Te Poroiti Reef fell below the mean Δ+ value, whereas all Motuhaku transects had high Δ+ values, above the mean. Despite this, neither mean Δ+ nor mean Λ+ were significantly different amongst reefs (PERMANOVA, psuedo-F = 3.34 and 2.003, respectively, and *p* >0.05 for both) (Appendix C: Table 3). This shows that, overall, the sponge communities within the MNEMA were not taxonomically distinct from one another at the time of surveying, despite some differences among transects. Aspect was not detected to have any correlation with TD indices, likely due to the prevailing ocean current swinging in opposite directions between summer and winter (Montaño et al., 2023).

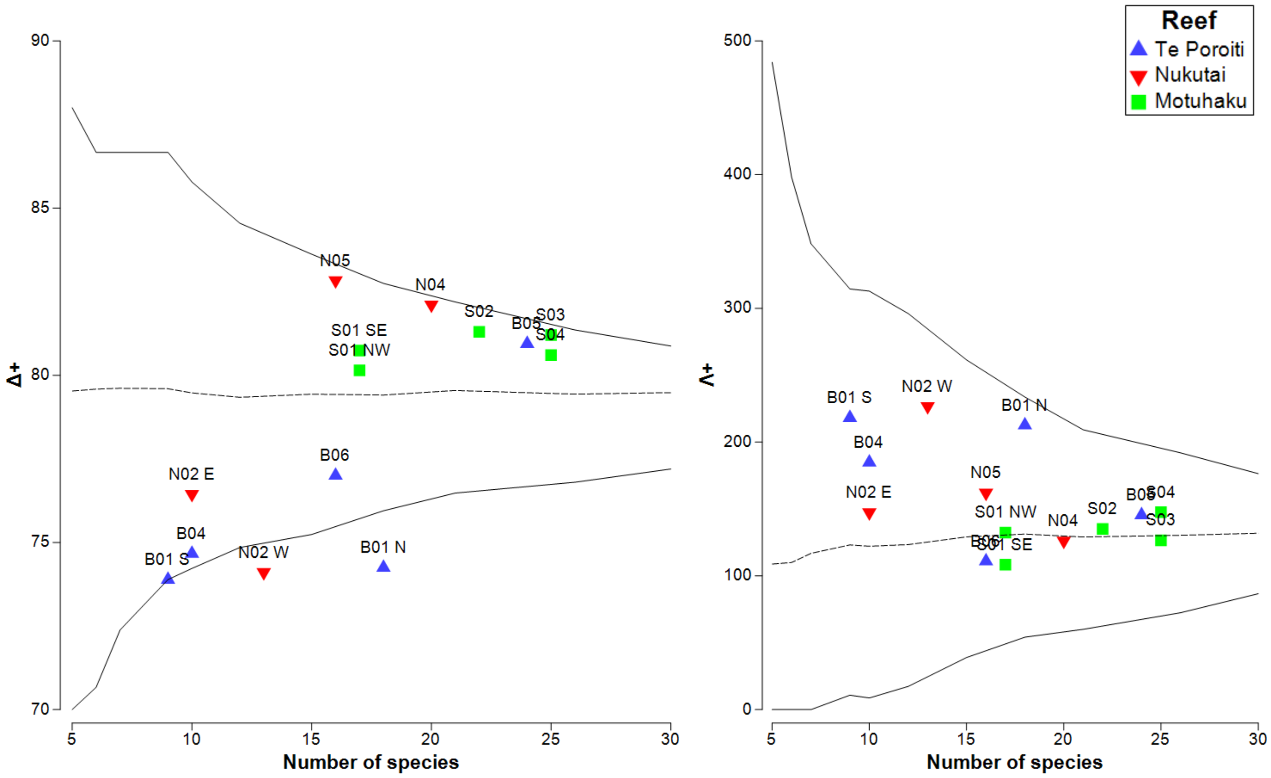


Figure 9. Funnel plots showing (left) average TD (Δ+) and (right) variation in TD (Λ+) of transects across cumulative number of species recorded in the mesophotic zone on Te Poroiti, Nukutai and Motuhaku reefs. The solid funnel lines represent 95% confidence limits (shows the ‘expected’ range of Δ+ and Λ+), while the dashed lines represent the mean values, based on the total species list (Table 4).

2.3.2 Species descriptions

Sample analysis identified a further 13 species and identified 3 already seen in ROV footage, bringing the total species recorded from both ROV footage and samples combined to 63 (Table 4). Two new species were confirmed under the supervision of Prof. Michelle Kelly (NIWA), one from the genus *Raspailia* and one from the genus *Neopetrosia*. Their identification contains a description in brackets following this format: ('descriptive characteristic', 'location where type specimen was found', 'who identified the type specimen').

All species described from samples are of the class Demospongiae and Orders are listed alphabetically. For descriptions of order, family and genus, refer to the primary literature (Bergquist, 1961a, 1961b, 1968, 1970; Bergquist & Warne, 1980; Bergquist & Fromont, 1988). For descriptions of morphological growth forms, refer to Schönberg (2021).

ORDER AXINELLIDA

FAMILY AXINELLIDAE

Genus *Pararhaphoxya*

Pararhaphoxya* cf. *pulchra (Brøndsted, 1924)
23MOT1-10 (Figure 10)

Material examined: 23MOT1-10, Motiti Island, Bay of Plenty, 20-25 m depth.
Description: Fistular. Corrugated fingers projecting from a base, fingers are thicker, with a thinner stem.
Colour: In spirit, white to cream. Turned isopropanol bright orange.
Surface: Corrugated, deeply curved surface on finger-like projections. Hispidity can be seen with the naked eye and some thick spicule brushes are visible under 4x magnification.
Texture: Easily compressible, feels velvety stroking it one way and scratchy stroking the opposite way.

Skeleton: Large spicules at the surface project out of the ectosome, sometimes individually and sometimes in spicule brushes. In comparison, spicules throughout the choanosome appear to be smaller and not as highly condensed, but still packed full. Spicule orientation in the choanosome is confused and no clear choanocyte chambers or other structures are visible. However, some organisation of spicules can be seen just underneath the spicule brushes, where spicules are mostly uniform in direction, perpendicular to the pinacoderm.

Spicules:

Megascleres:

Styles, varying in width, usually evenly curved, sometimes curved a third of the way down from the head. Smaller sized styles are less abundant, while the larger are the predominant spicule of this specimen.

I Mean: 535.3 µm, n=10
Range: 475 – 596 µm
II Mean: 730.4 µm, n=10
Range: 646 – 839 µm

Strongyles, even in width and curvature. Less common than the large styles, but more common than the small styles.

Mean: 596.1 µm, n=10
Range: 429 – 729 µm

Remarks: The enormous, curved styles are characteristic of family Axinellidae and the surface of this specimen matches that described for *Pararhaphoxya* cf. *pulchra* in the primary literature (Bergquist, 1970). However, the spiculation is not entirely consistent with *P. pulchra,* due to the lack of oxea (Bergquist, 1970), hence this is a cautious assignment.

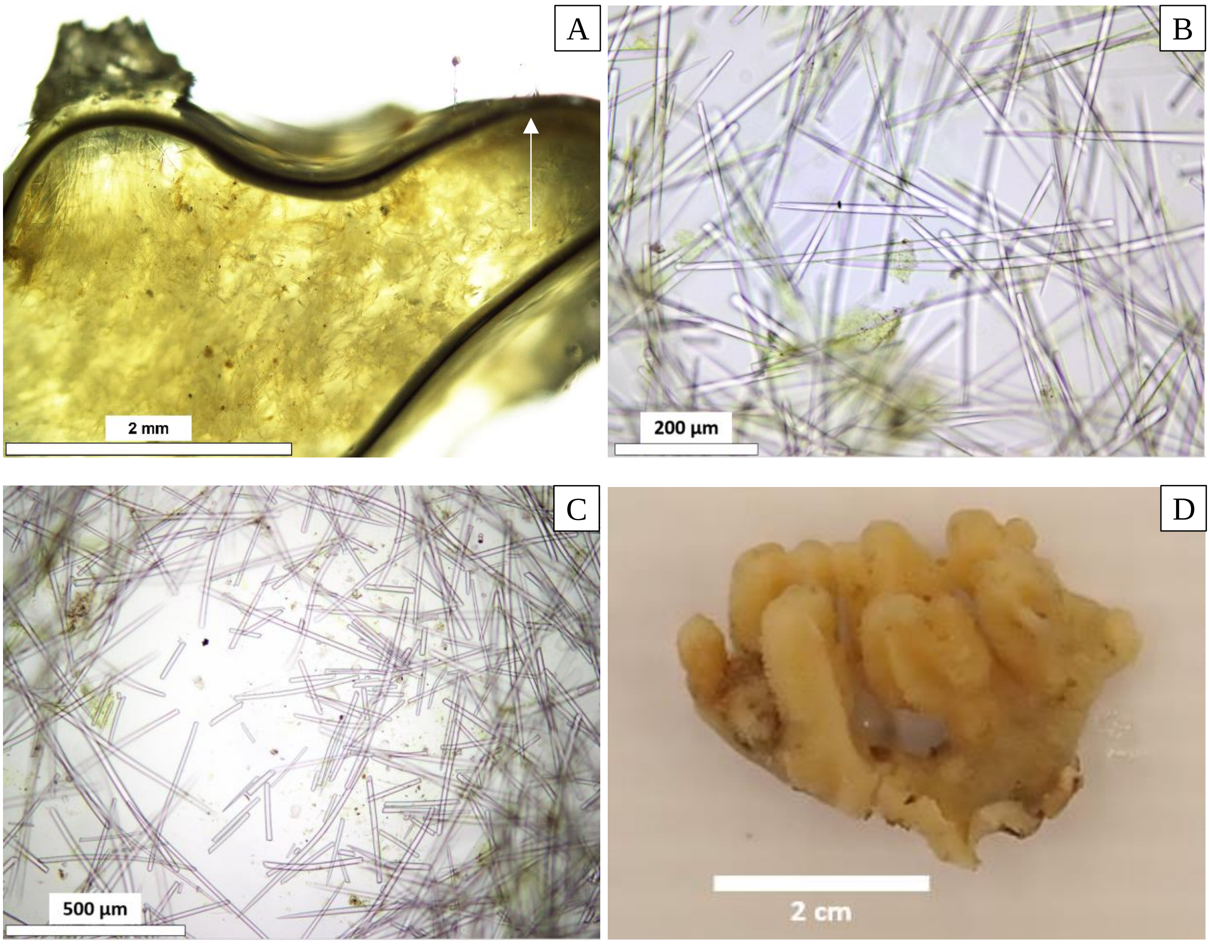


Figure 10. A-D, *Pararhaphoxya* cf. *pulchra* (23MOT1-10): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules showing strongyle in centre; C, spicules showing strongyles and styles; D, desktop photo at a side-on angle.

Pararhaphoxya sinclairi (Gray, 1843)
23MOT1-1 (Figure 11)

Material examined: 23MOT1-1, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: This sponge is three-dimensionally erect, branching with cylindrical branches. Branches are frequently forked into two and have pointed tips.

Colour: In spirit, dull yellow. Turned isopropanol bright orange.

Surface: Star shaped creases along the sides of its circular branches.

Texture: Soft, velvety and compressible.

Skeleton: Radiate and hispid with a very thin surface layer. Confused spicular arrangement deeper into the choanosome, but most sit perpendicular to the surface near the ectosome.

Spicules:

Megascleres:

Oxea, stout, evenly curved.

I Mean: 136.3 µm, n=10
Range: 105 – 148 µm
II Mean: 199.3 µm, n=10
Range: 166 – 223 µm
III Mean: 289.2 µm, n=10
Range: 240 – 383 µm

Styles of two to three size classes. Quite fine and slightly curved.

I Mean: 135.1 µm, n=10
Range: 96 – 175 µm
II Mean: 272.6 µm, n=10
Range: 216 – 318 µm

Strongyles, class I are stout, class II are fine, class III are very sinuous, varying in width but usually fine.

I Mean: 65.8 µm, n=10
Range: 25 – 125 µm
II Mean: 275 µm, n=10
Range: 162 – 340 µm
III Mean: 816.9 µm, n=10
Range: 740 – 886 µm

Remarks: This specimen fits *Pararhaphoxya sinclairi*, although the strongyles are much smaller than those described in Battershill et al. (2010).

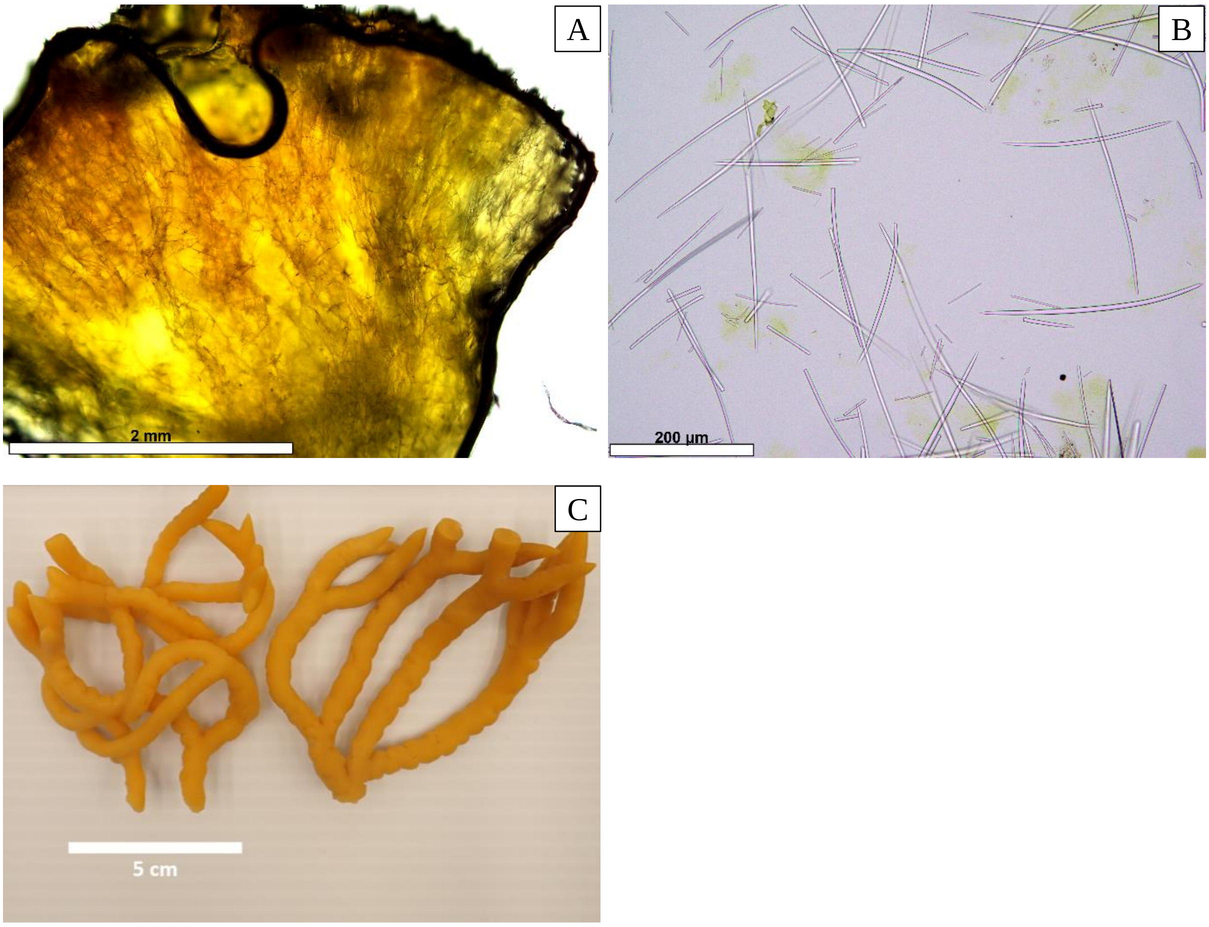


Figure 11. A-C, *Pararhaphoxya sinclairi* (23MOT1-1): A, thick section showing skeletal structure; B, spicules; C, desktop photo at a side-on angle.

FAMILY RASPAILIIDAE

SUBFAMILY RASPAILIINAE

Genus *Raspailia*

***Raspailia* sp. nov. 1 (spathulate, Motiti Island, Donald)**

23MOT1-3 (Figure 12)

Material examined: 23MOT1-3, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Short, bushy and three-dimensionally erect, branching. Branches are bilaterally flattened, spathulate. This thick section is a cross-section of a bilaterally flattened finger-like projection.

Colour: In spirit, dull yellow. Turned isopropanol bright orange.

Surface: Granulose with tiny, short hispidity that can be seen with the naked eye.

Texture: Velvety and smooth.

Skeleton: This specimen has a central core of interweaving spicules in confused orientations, known as axial condensation. Bands of spicules shoot out from the core to the ectosome like pillars with spaces in between. The surface layer is cluttered full of sand, detritus and a mat of spicules. Some spicules echinate through the ectosome.

Spicules:

Megascleres:

Styles, slightly bent, larger ones often with strongylote distal ends. Class I have a proximal kink. Class III are less common.

I Mean: 238.5 µm, n=10
Range: 172 – 407 µm
II Mean: 731 µm, n=10
Range: 637 – 870 µm

Acanthostyles with a proximal kink, same form as class I styles.
Mean: 185.9 µm, n=10
Range: 148 – 211 µm

Oxea, very fine.
Mean: 248.5 µm, n=10
Range: 178 – 282 µm

Remarks: The morphology of this specimen is typical of family Axinellidae and the acanthostyles and axial condensation are characteristic of the genus *Raspailia* (Bergquist, 1970). This has been compared with all currently known OTUs from the genus *Raspailia* in New Zealand and identified as a new species under the guidance of Prof. Michelle Kelly (NIWA).

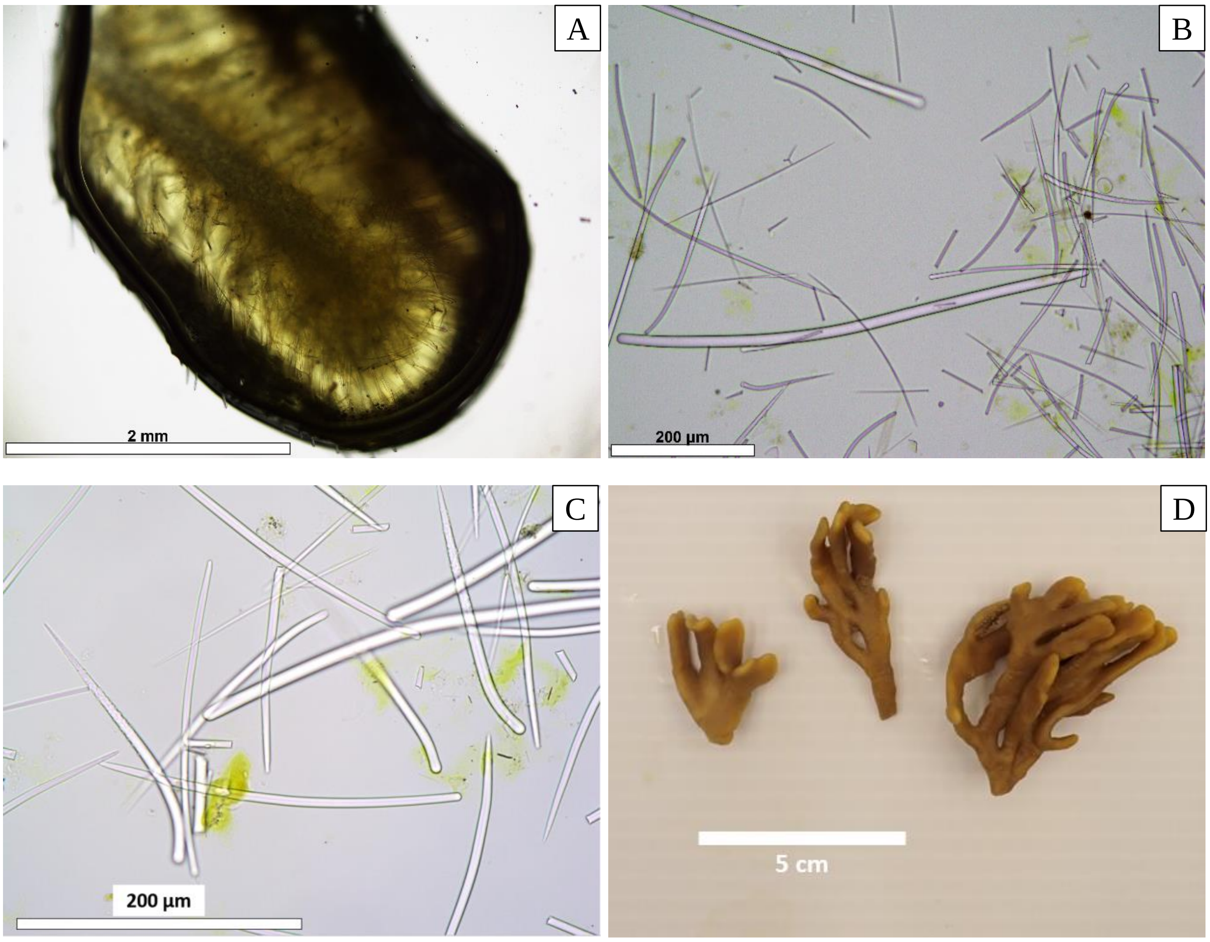


Figure 12. A-D, *Raspailia* sp. nov. 1 (spathulate, Motiti Island, Donald) (23MOT1-3): A, thick section showing skeletal structure; B, spicules; C, spicules showing acanthostyles; D, desktop photo at a side-on angle.

Subgenus *Raspailia* (*Raspaxilla*)

Raspailia* (*Raspaxilla*) *topsenti (Dendy, 1924)
23MOT1-2 (Figure 13)

Material examined: 23MOT1-2, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: This sponge is three-dimensionally erect, branching with cylindrical branches. Branches are frequently forked, often unevenly and have rounded tips. The thick section examined is a cross-section of a branching finger of this specimen.

Colour: In spirit, dull yellow. Turned isopropanol bright orange.

Surface: Looks fluffy with star shaped creases along opposite sides of every branch. Under 4x magnification, hispidity is clear.

Texture: Velvety and easily compressible.

Skeleton: Highly structured bundles of spicules in a reticulate fashion, outlining approximately triangular choanocyte chambers through the choanosome all the way to the ectosome where the surface layer is thin. This pattern radiates out from the centre of the branch.

Spicules:

Megascleres:

Styles, stout, slightly curved.
Mean: 305.9 µm, n=10
Range: 275 – 342 µm

Acanthostyles, strong proximal kink, spines present on posterior end.
Mean: 85.4 µm, n=10
Range: 65 – 104 µm

Raphides or fine styles, long and slender. Some almost straight, some sinuous.
wavy.
Mean: 300.6 µm, n=10
Range: 226 – 355 µm

Remarks: Spiculation, surface, and morphology are all consistent with *Raspailia* (*Raspaxilla*) *topsenti* (Bergquist, 1970).

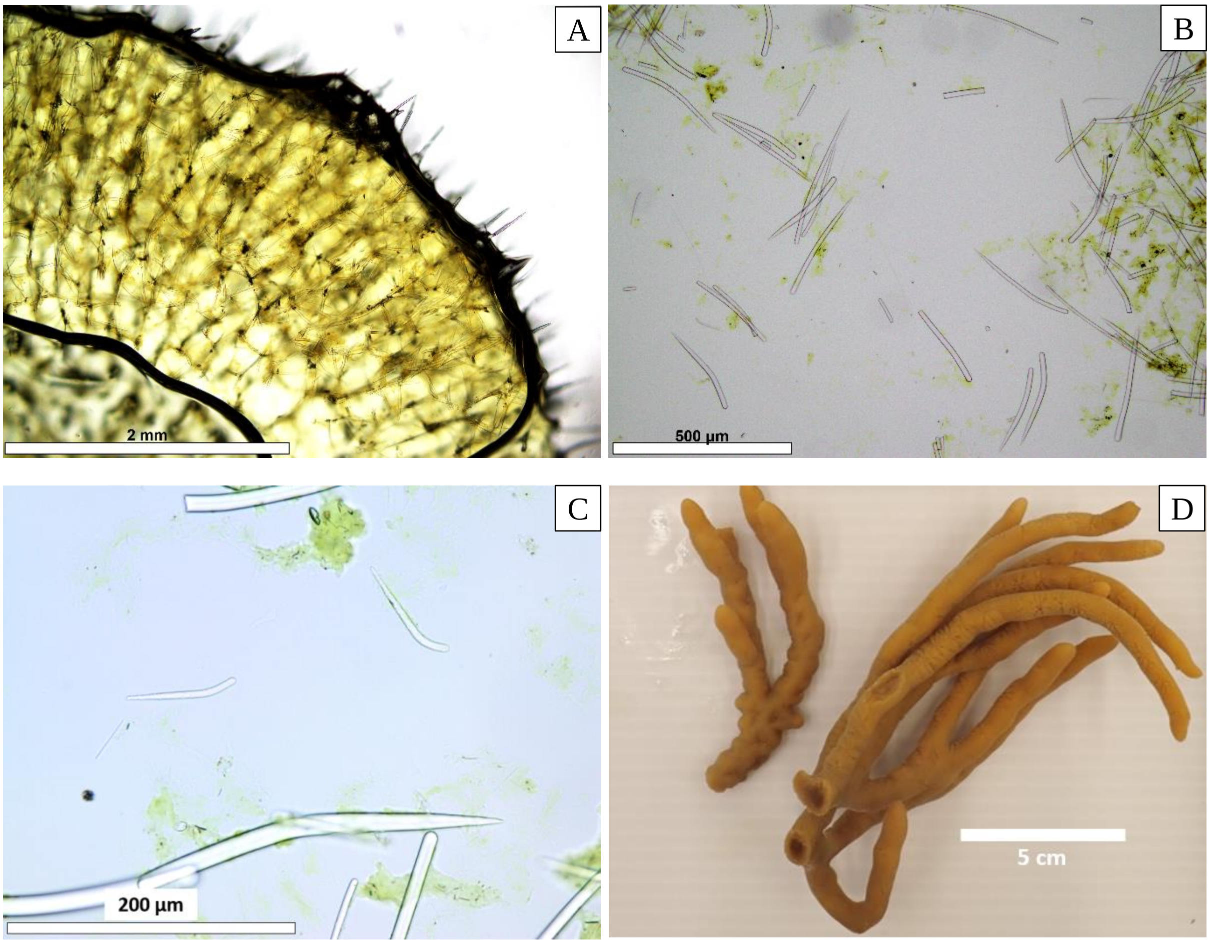


Figure 13. A-D, *Raspailia* (*Raspaxilla*) *topsenti* (23MOT1-2): A, thick section showing skeletal structure; B, spicules; C, spicules showing two acanthostyles in the centre; D, desktop photo at a side-on angle.

ORDER CLIONAIDA

FAMILY SPIRASTRELLIDAE

Genus *Spirastrella*

***Spirastrella* sp. 01 (0CDN6683-X, Three Kings)** (Kelly & Sim-Smith, in press 2023)
23MOT1-4 (Figure 14)

Material examined: 23MOT1-4, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Thick encrusting to massive with many ridges which, in places, give parts of this specimen a two-dimensional erect morphology.

Colour: In spirit, creamy brown to grey. Turned isopropanol dull orange.

Surface: Smooth but highly irregular and bumpy in places. Inclusion of shells and algae, with some growths through the surface.

Texture: Dense cork, characteristic of *Spirastrella* spp. Firm, only slightly compressible.

Skeleton: Choanosome is a confused, condensed mass of spicules. Under 4x magnification the surface is not easily discernible from the choanosome, but it does have slightly more condensed spicules and thus looks thicker than the choanosome.

Spicules:

Megascleres:

Tylostyles.
Mean: 490.9 µm, n=10
Range: 406 – 558 µm

Microscleres:

Amphiasters of two size classes.
I Mean: 21.8 µm, n=10
Range: 12 – 29 µm
II Mean: 39.5 µm, n=10
Range: 34 – 42 µm

Spirasters of two size classes, both of which are smaller than the amphiasters.
I Mean: 10.7 µm, n=10
Range:7 – 16 µm
II Mean: 20.4 µm, n=10
Range: 18 – 22 µm

Remarks: Surface like dense cork is characteristic of the genus *Spirastrella* (Bergquist, 1968). This specimen is consistent with that identified as an OTU in Kelly & Sim-Smith (in press 2023).

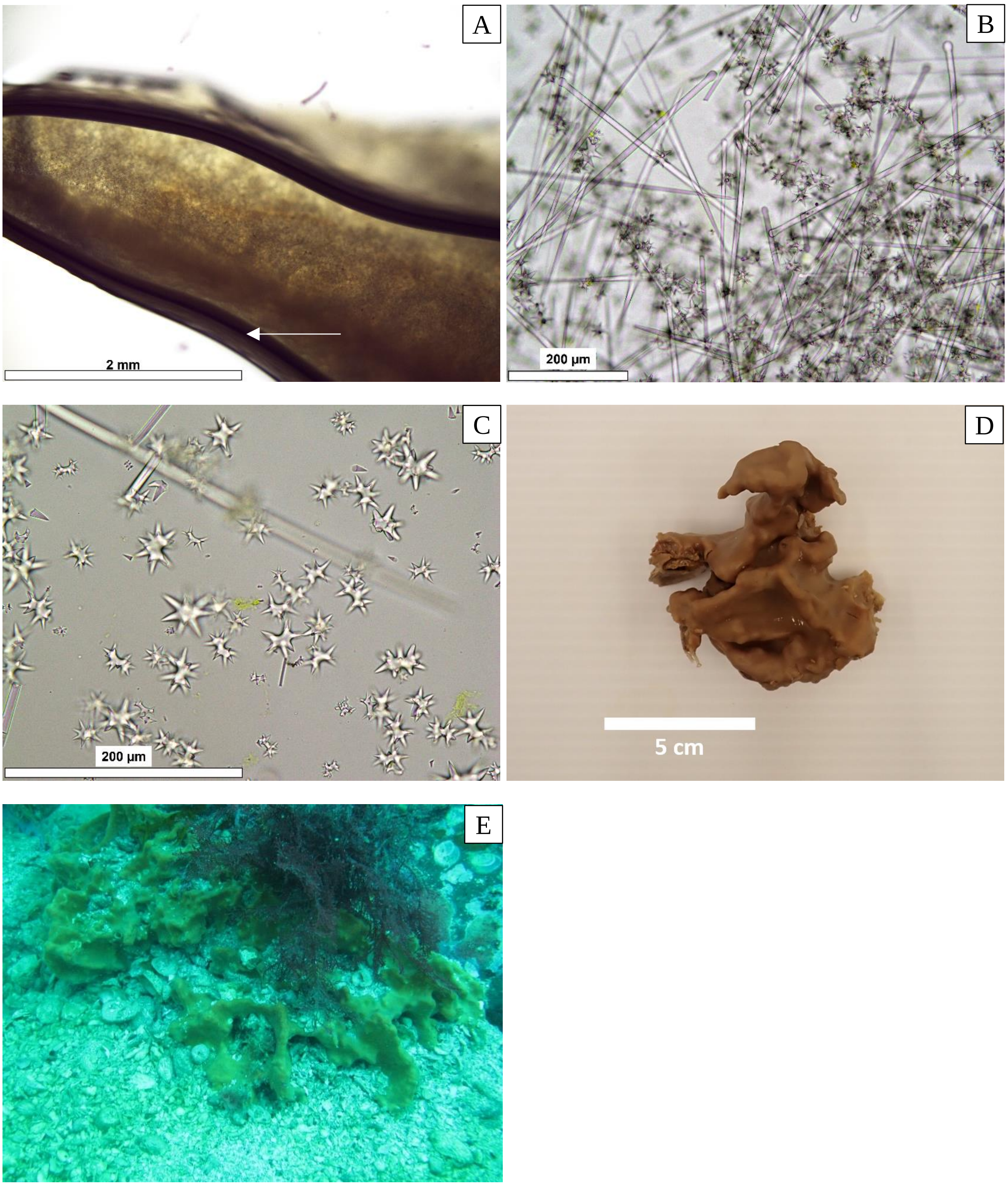


Figure 14. A-E, *Spirastrella* sp. 01 (0CDN6683-X, Three Kings) (23MOT1-4): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, microscleres; D, desktop photo at a top-down angle; E, *in situ* photo.

ORDER DICTYOCERATIDA

FAMILY IRCINIIDAE

Genus *Psammocinia*

***Psammocinia beresfordae* (Cook & Bergquist, 1996)**
23OR1-2 (Figure 15)
23OR1-3 (Figure 16)
23MOT1-7 (Figure 17)

Material examined: 23OR1-2, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: Tube-like forms, made up of rounded, cone shaped oscular chimneys clustered together and arising from a joined base.

Colour: In spirit, dark grey externally and cream to brown internally. Turned isopropanol light yellow-brown.

Surface: Minutely conulose like gooseflesh, has oscular chimneys.

Texture: Rough, easily compressible.

Skeleton: Thick surface layer with lots of turrets projecting out as pictured below. The choanosome and surface layer (excluding turrets) look to have anastomosing reticulate spongin fibres with some coring of detritus.

Spicules: Spicules are absent in Order Dictyoceratida. However, this specimen has many inclusions of foreign spicules as artefacts.

Remarks: This specimen fits *Psammocinia beresfordae*, however not all primary fibres appear to be cored as suggested by Battershill et al. (2010).

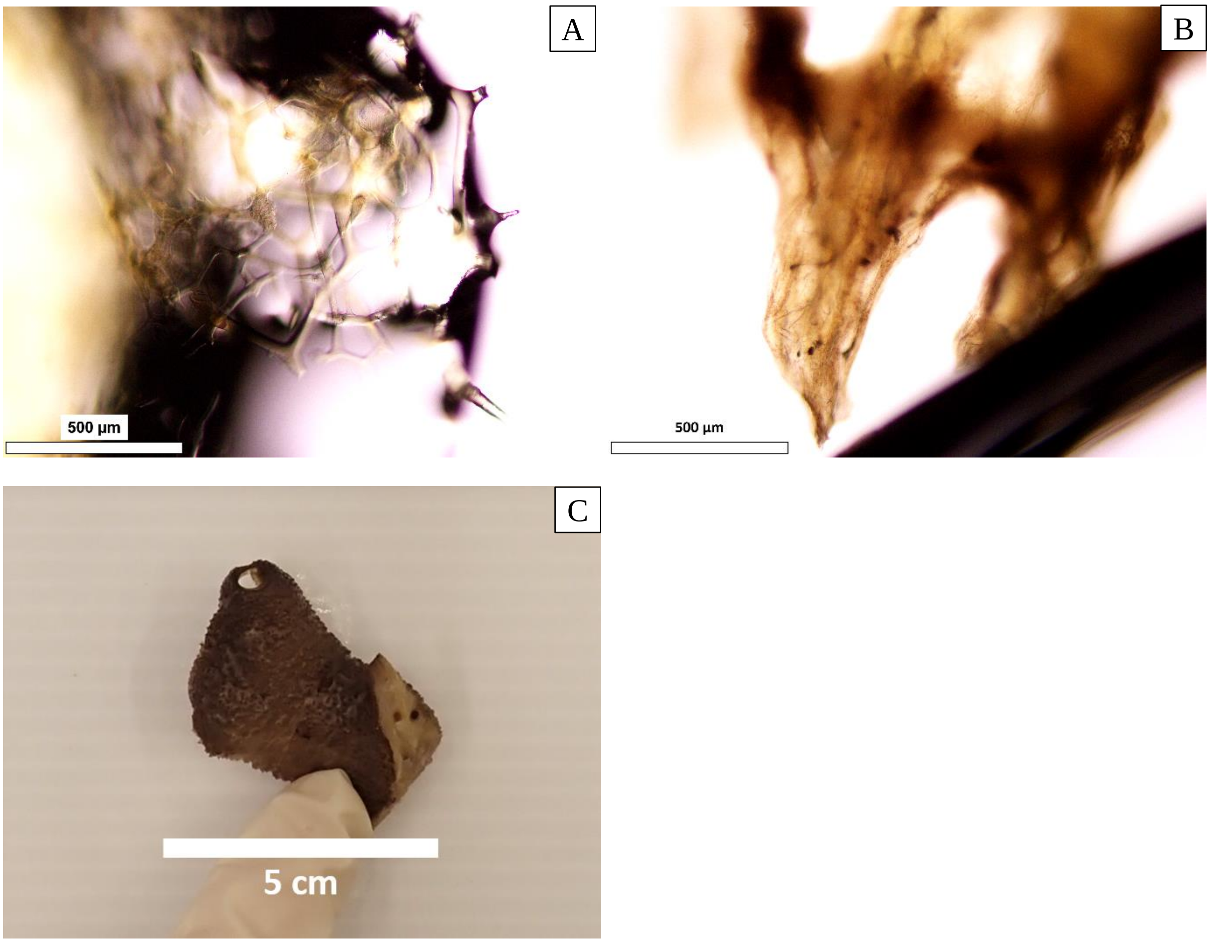


Figure 15. A-C, *Psammocinia beresfordae* (23OR1-2): A, thick section showing skeletal structure; B, thick section showing skeletal structure of a projecting turret; C, desktop photo at a top-down angle with slight sideways lean.

Material examined: 23OR1-3, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: Tube-like forms, made up of rounded, cone shaped oscular chimneys clustered together and arising from a joined base. Some chimneys are fused together.

Colour: In spirit, dark grey externally and cream to brown internally. Turned isopropanol light yellow-brown.

Surface: Same as 23OR1-2 but the spongin fibres in this specimen are more condensed.

Texture: Rough, easily compressible.

Skeleton: General radial flow into choanosome is present. Spongin fibres are amber, some cored and some not. Fibres are not very condensed in the choanosome but denser in the surface layer.

Spicules: None of its own.

Remarks: This specimen and the previous one, 23OR1-2, show two extremes of a microhabitat range.

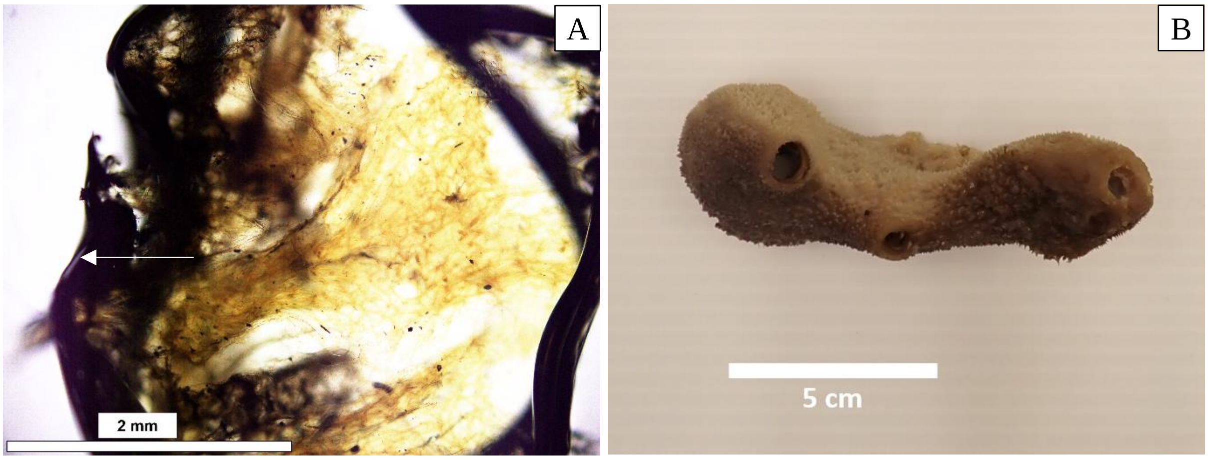


Figure 16. A-B, *Psammocinia beresfordae* (23OR1-3): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, desktop photo at a top-down angle.

Material examined: 23MOT1-7, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Creeping. Branches are thick and knobbly with globular ends. Sunken, translucent membrane that would have been raised oscula when alive.

Colour: In spirit, dark grey to cream in places and internally it is mostly cream but has some orange in places. Turned isopropanol a clear, light green.

Surface: Gooseflesh, feels slightly bumpy but not spiky. Apart from the tiny bumps, it looks generally smooth and rounded but irregular.

Texture: Easily compressible.

Skeleton: Unorganised but reticulate with large choanocyte chambers. Thick, arenaceous surface layer. Under 4x magnification many broken spicules, detritus and sand grains can be seen embedded throughout the surface and choanosome. Large anastomosing amber coloured fibres are present, cored with detritus and broken spicules. Has spongin fibrils with little ball on the ends of them. Dense bundles of filaments cross brace the primary and secondary fibres.

Spicules: None of its own.

Remarks: This specimen fits *Psammocinia beresfordae*, despite its unusual creeping morphology. Also, the sunken translucent membranes contrast with the large, obvious oscular chimneys present in the other specimens collected of this species.

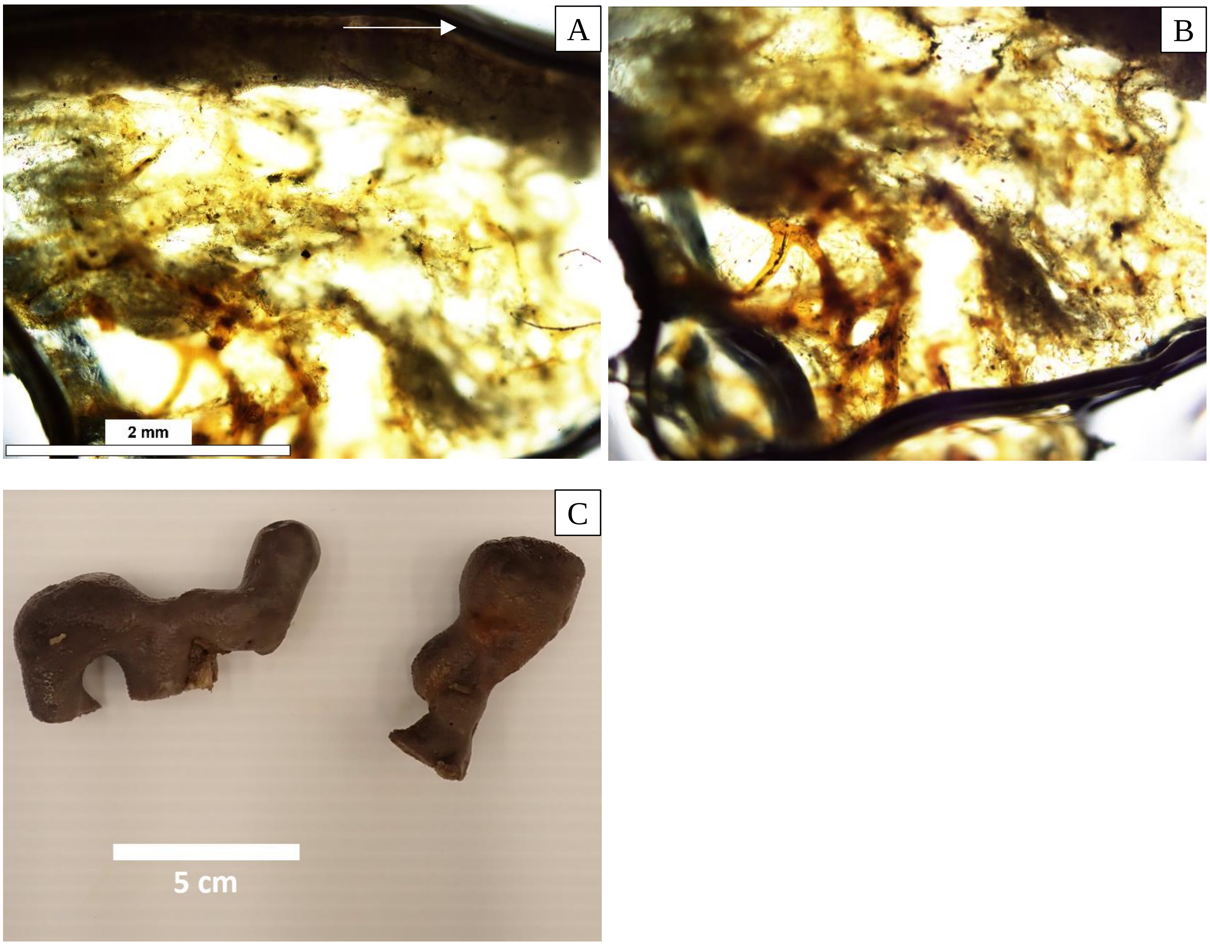


Figure 17. A-C, *Psammocinia beresfordae* (23MOT1-7): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, thick section showing cored fibres; C, desktop photo.

FAMILY SPONGIIDAE

Genus *Spongia*

Subgenus *Spongia (Heterofibria)*

Spongia* (*Heterofibria*) cf. *manipulatus (Cook & Bergquist, 2001)
23OR1-1 (Figure 18)

Material examined: 23OR1-1, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: Thickly encrusting, lobate to mounded. Raised oscules are situated on top of ridges and mounds.

Colour: In situ, grey. In spirit, cream to brown. Turned isopropanol gold-yellow.

Surface: Regularly conulose surface, looks stretched in places with abundant collagen. Attachment points to substrate are fairly rare and relatively small compared to the whole sponge.

Texture: Tough, mildly compressible.

Skeleton: Reticulate with sand embedded throughout. Ectosome is thicker and more condensed than the choanosome. Primary fibres are anastomosed and sand and spicule debris are collected outside of them. Primary fibres are lightly cored and pseudo-tertiary fibres are evident in places.

Spicules: Many inclusions of foreign spicules as artefacts.

Remarks: Spongin fibres are not laminated, characteristic of the family Spongiidae (Battershill et al., 2010).

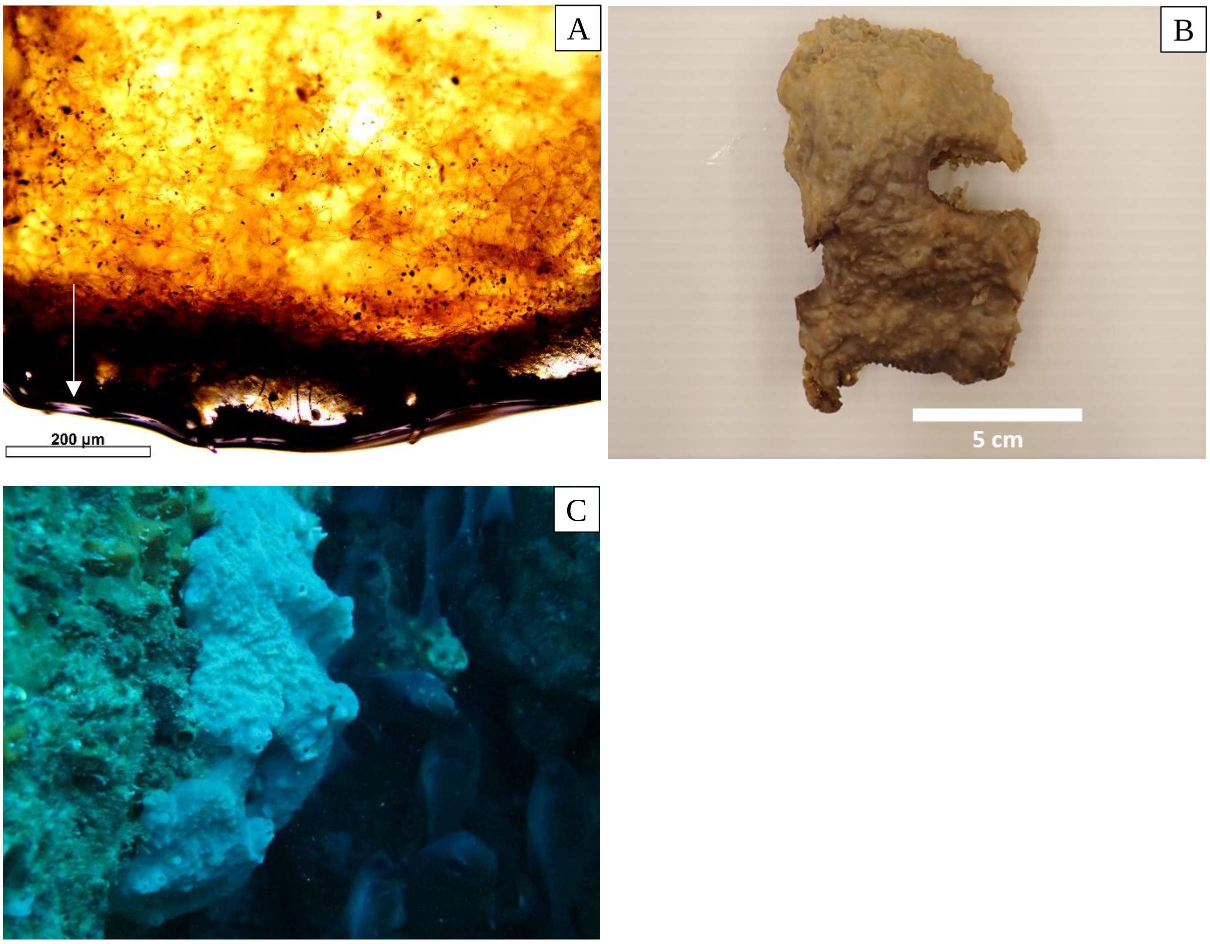


Figure 18. A-C, *Spongia* (*Heterofibria*) cf. *manipulatus* (23OR1-1): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, desktop photo at a side-on angle; C, *in situ* photo.

ORDER HAPLOSCLERIDA

FAMILY PETROSIIDAE

Genus *Neopetrosia*

***Neopetrosia* sp. 1 (spicules 152 – 183 µm, Astrolabe Reef, Donald)**

23AR1-3 (Figure 19)

Material examined: 23AR1-3, Astrolabe Reef, Bay of Plenty, 20-25 m depth.

Description: Thickly encrusting with thick, rounded edges.

Colour: In spirit, grey. Turned isopropanol dark gold-yellow.

Surface: Large oscula (4 mm diameter), under 4x magnification there is no visible differentiation between the surface and choanosome.

Texture: Smooth and velvety to the touch, not easily compressible, crumbly inside.

Skeleton: Reticulate with confused spicule direction and choanocyte chambers.

Spicules:

Megascleres:

Oxea, slightly curved.

Mean: 164.5 µm, n=10

Range: 152 – 183 µm

Remarks: Spicule sizes <200 µm in one size class place it within the genus *Neopetrosia*. This specimen has been compared with all currently known OTUs from the genus *Neopetrosia* in New Zealand and identified as a new species under the guidance of Prof. Michelle Kelly (NIWA).

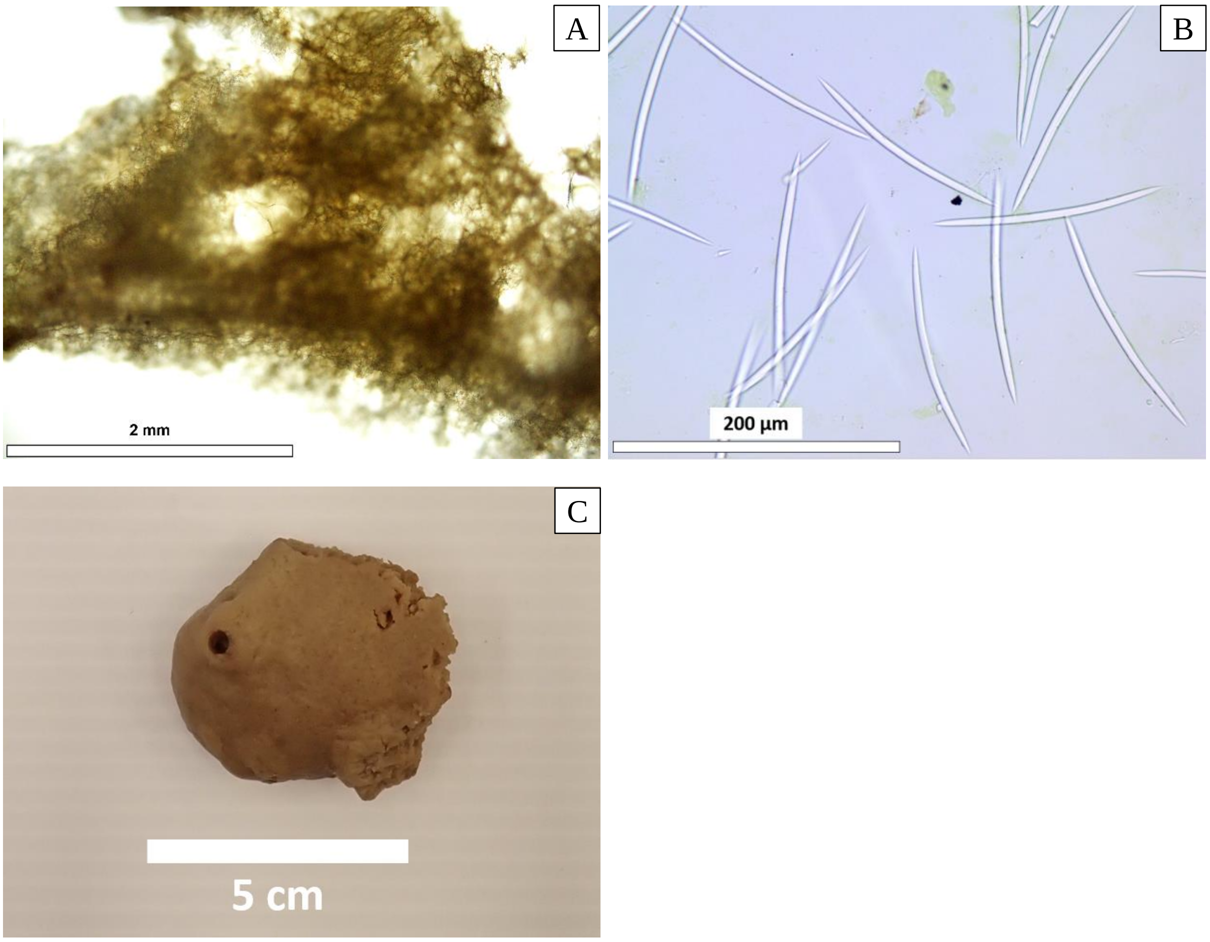


Figure 19. A-C, *Neopetrosia* sp. 1 (spicules 152 – 183 µm, Astrolabe Reef, Donald) (23AR1-3): A, thick section showing skeletal structure; B, spicules; C, desktop photo at a top-down angle.

Genus *Petrosia*

Subgenus *Petrosia* (*Petrosia*)

Petrosia* (*Petrosia*) *hebes (von Lendenfeld, 1888)
23OR1-5 (Figure 20)
23MOT1-5 (Figure 21)

Material examined: 23OR1-5, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: Tabular “cup” with irregular upper surface that has ridges and troughs. Rim is thin, rounded and irregular.

Colour: In spirit, dull yellow to cream on one side with pink-brown in places. Grey on the other side. Turned isopropanol gold-yellow.

Surface: Very smooth, irregular surface. Under 4x magnification it is mostly smooth with slight spicular echination through the ectosome.

Texture: External is velvety to the touch, internal is crumbly. Not compressible at all, hard like stone.

Skeleton: Anastomosing, haphazard, reticulate structure. Quite condensed spicules.

Spicules:

Megascleres:

Oxea, evenly curved, classes I are of varying width, class II are fine, class III are stout.

I Mean: 65.2 µm, n=10
Range: 45 – 89 µm
II Mean: 150.1 µm, n=10
Range: 103 – 183 µm
III Mean: 266.7 µm, n=10
Range: 239 – 303 µm

Strongyles, stout, class I are abundant, class III are very rare and often have pinched ends.

I Mean: 42.3 µm, n=10
Range: 31 – 56 µm
II Mean: 109.8 µm, n=10
Range: 64 – 174 µm
III Mean: 267.6 µm, n=5
Range: 238 – 300 µm

Styles, often with a pinched head, same form as the oxeas.

Mean: 251.4 µm, n=10
Range: 214 – 266 µm

Remarks: Morphology, surface, texture, and spicules are consistent with the description of *Petrosia hebes* given by Bergquist & Warne (1980). However, large strongyles (class III) are very rare in this specimen but were abundant in Bergquist & Warne (1980).

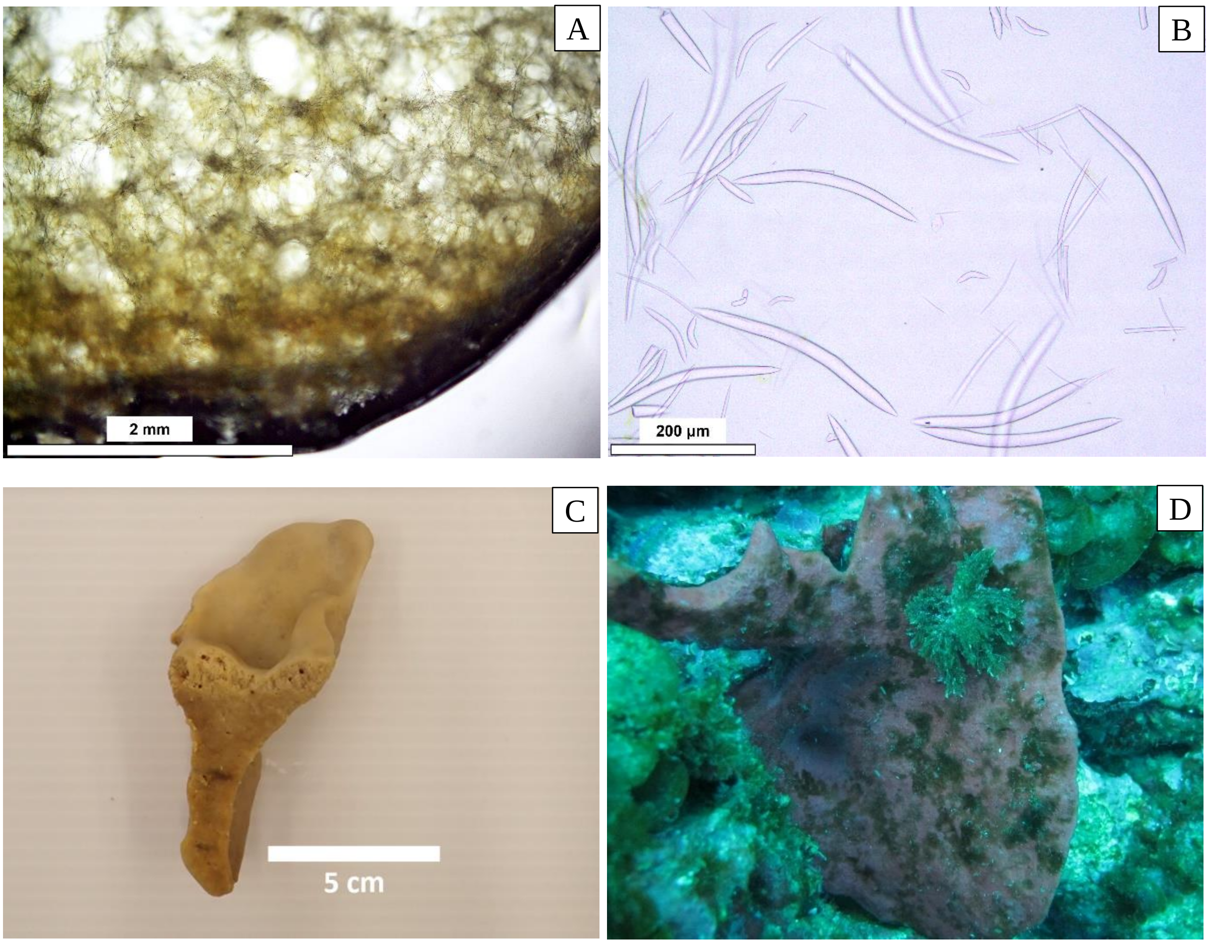


Figure 20. A-D, *Petrosia* (*Petrosia*) *hebes* (23OR1-5): A, thick section showing skeletal structure; B, spicules; C, desktop photo at side-on angle; D, *in situ* photo.

Material examined: 23MOT1-5, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Tabular “cup” with irregular upper surface that has ridges and troughs. Rim is thick and rounded. Hard to tell if it is irregular or not as this specimen is a small section cut off a seemingly very large sponge.

Colour: In spirit, creamy grey on one side to mauve on the other side. Turned isopropanol yellow-brown.

Surface:, Smooth and irregular. Looks the same under 4x magnification as it does to the naked eye.

Texture: Noticeably velvety to the touch externally, rock solid, not compressible. Internal is crumbly.

Skeleton: Anastomosing, haphazard, reticulate structure. The spicules are quite condensed and a thick mat of spicules lies at the ectosome parallel to the surface.

Spicules:

Megascleres:

Oxea, evenly curved, classes I are of varying width, class II are fine, class III are stout.

I Mean: 55.6 µm, n=10
Range: 51 – 62 µm
II Mean: 162.5 µm, n=10
Range: 134 – 191 µm
III Mean: 308.1 µm, n=10
Range: 291 – 326 µm

Strongyles, stout, class I are abundant, class III are relatively rare.

I Mean: 47.3 µm, n=10
Range: 41 – 60 µm
II Mean: 77.4 µm, n=10
Range: 65 – 93 µm
III Mean: 293 µm, n=10
Range: 267 – 326 µm

Styles, some with a pinched head, same form as the oxeas.

Mean: 292.1 µm, n=10
Range: 249 – 326 µm

Remarks: Consistent with description of *Petrosia hebes* by Bergquist & Warne (1980). Large (class III) strongyles are relatively rare in this sample, but not as rare as in 23OR1-5.

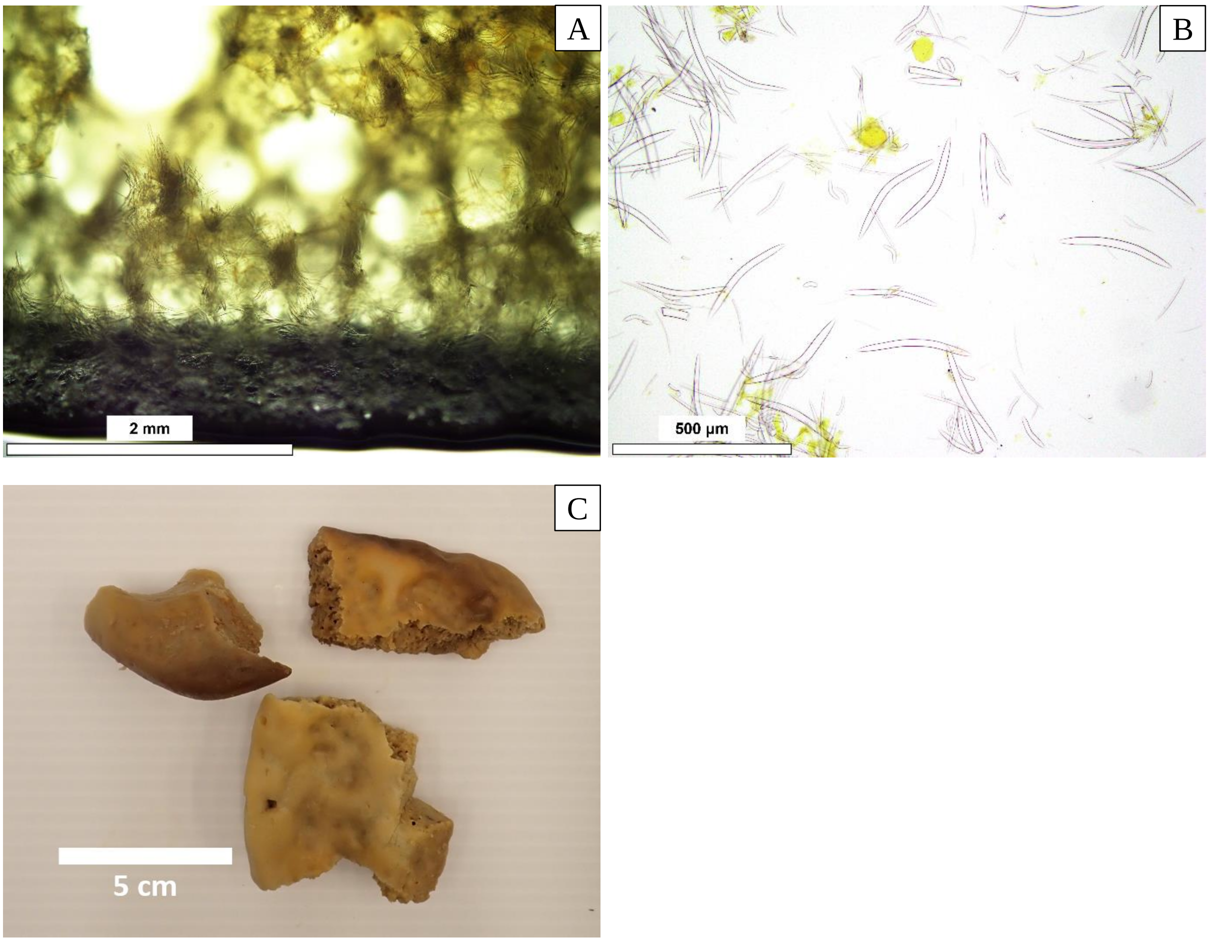


Figure 21. A-C, *Petrosia* (*Petrosia*) *hebes* (23MOT1-5): A, thick section showing skeletal structure; B, spicules; C, desktop photo, the specimen sample on the left is at a bottom-up angle while the two on the right are at a top-down angle.

Petrosia* (*Petrosia*) cf. *hebes (von Lendenfeld, 1888)

23OR1-6 (Figure 22)

Material examined: 23OR1-6, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: This specimen is a thick, rounded, finger-like projection.

Colour: In spirit, creamy grey to mauve. Turned isopropanol gold-yellow.

Surface: Oscula are 2 mm in diameter and are situated upon raised conical projections which occur approximately every 2 cm. Morphology has finger-like projections, rounded and smooth.

Texture: Noticeably velvety to the touch and firm, not compressible. Brittle and crumbly internally but smooth dermal layer externally.

Skeleton: Highly structured skeleton with a condensed mat of spicules at the surface layer and square choanocyte chambers throughout the choanosome. Lots of compact spicules, with smaller spicules being matted at the surface while larger spicules and strongyles form the choanosome.

Spicules:

Megascleres:

Oxea, evenly curved, blunt ends, class I and II are fine, class III are stout.

I Mean: 66.4 µm, n=10
Range: 46 – 92 µm
II Mean: 168.2 µm, n=10
Range: 143 – 196 µm
III Mean: 301.6 µm, n=10
Range: 267 – 320 µm

Strongyles, stout, class I are very abundant, class III are uncommon.

I Mean: 36.7 µm, n=10
Range: 31 – 46 µm
II Mean: 87.3 µm, n=10
Range: 62 – 123 µm
III Mean: 309 µm, n=10
Range: 279 – 338 µm

Styles, evenly curved with blunt point.
Mean: 283.9 µm, n=10
Range: 255 – 327 µm

Remarks: Cautious assignment is *Petrosia* cf. *hebes* (Bergquist & Warne, 1980), as it has features such as the clearly visible oscula, raised conical projections with oscula on ends and blunt oxea compared to 23OR1-5 and 23MOT1-5. These differences could potentially just be a function of its microhabitat. It is also not the typical vase shape for this species.

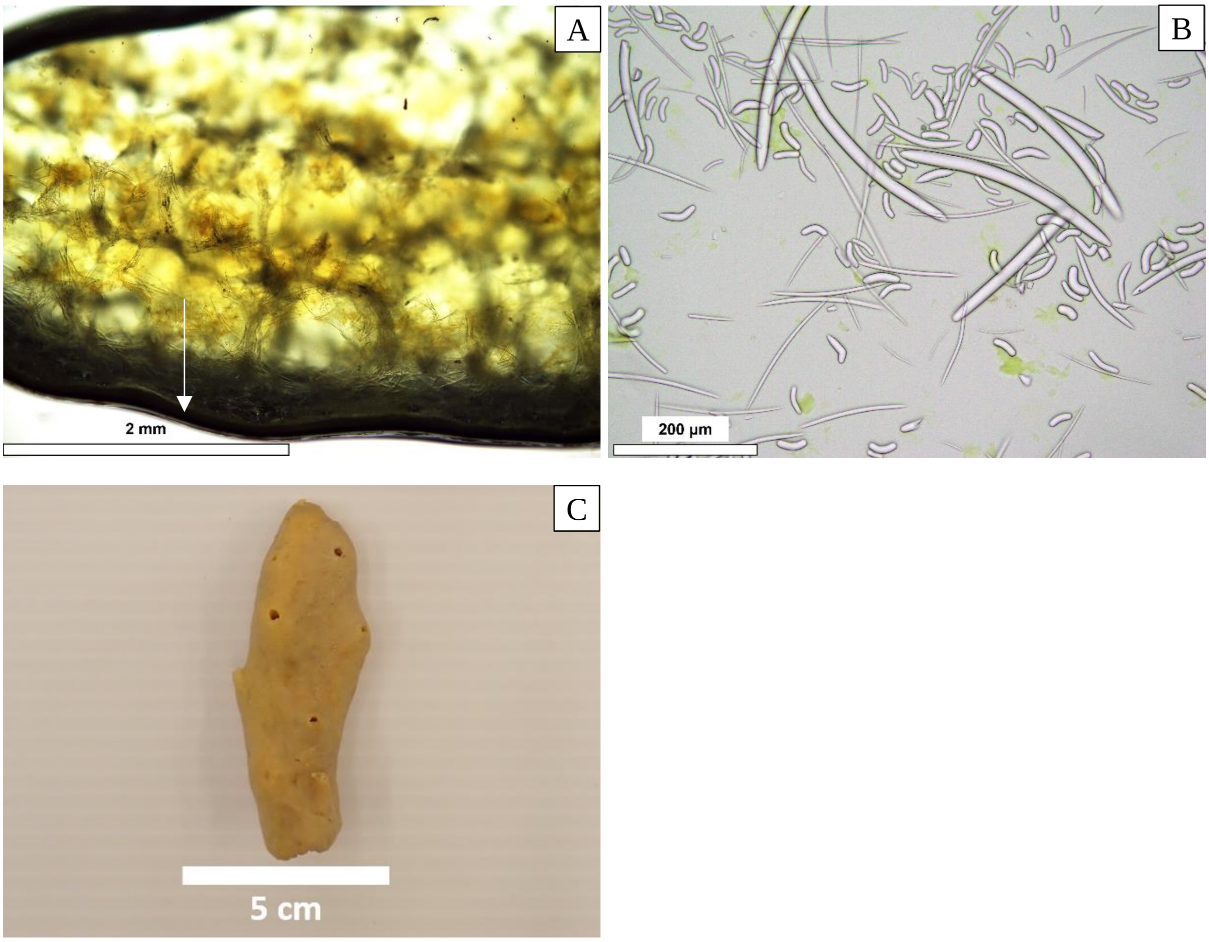


Figure 22. A-C, *Petrosia* (*Petrosia*) cf. *hebes* (23OR1-6): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, desktop photo at a side-on angle.

Genus *Xestospongia*

Xestospongia* cf. *novaezealandiae (Bergquist & Warne, 1980)
23KR1-2 (Figure 23)

Material examined: 23KR1-2, Karewa Reef, Bay of Plenty, 20-25 m depth.

Description: Tabular "cup" with a rounded rim.

Colour: In spirit, cream. Turned isopropanol dull orange.

Surface: Smooth but with raised oscula edges. Oscula are more frequent on one side and are also concentrated along the rounded rim of the plate-like specimen. The surface is densely covered in tiny ostia pores, giving it a slightly translucent appearance. Under 4x magnification, one can see spicules echinating through the ectosome creating relatively even hispidity across the surface.

Texture: Incompressible, brittle and crumbly.

Skeleton: Regular, multispicular fibre reticulation. Choanocyte chambers are roughly circular to square in shape.

Spicules:

Megascleres:

Oxeas, stout, slightly curved.
Mean: 217.6 µm, n=10
Range: 206 – 229 µm

Remarks: It is not *Xestospongia coralloides* because it doesn’t have the distinctive surface of visible pores on both sides, pores are only visible on the upper side in this specimen (Bergquist & Warne, 1980). It is most closely comparable to *Xestospongia novaezealandiae* because the surface is very similar to what is illustrated in Bergquist & Warne (1980), although the spicules are slightly smaller.

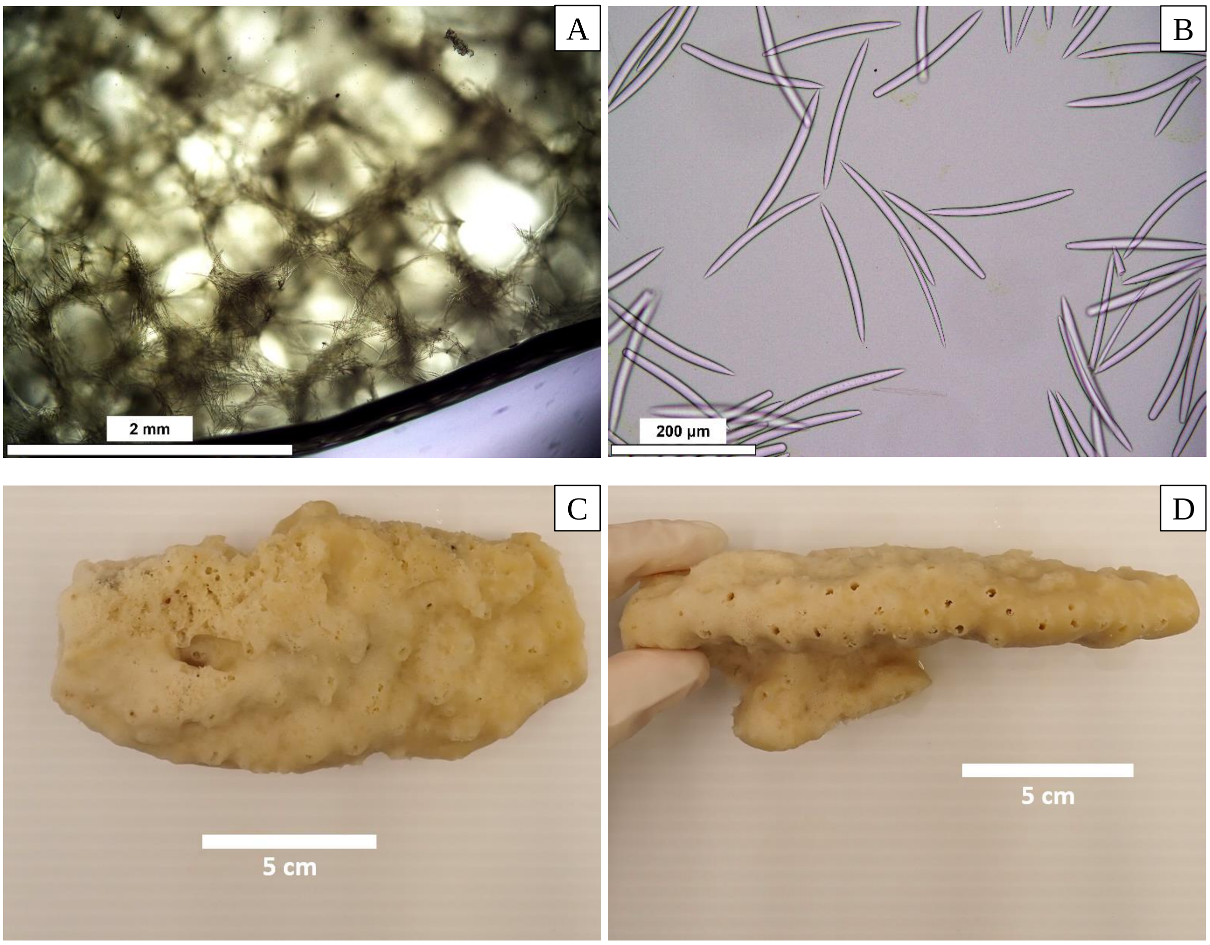


Figure 23. A-D, *Xestospongia* cf. *novaezealandiae* (23KR1-2): A, thick section showing skeletal structure; B, spicules; C, desktop photo at a top-down angle; D, desktop photo at a side-on angle.

ORDER POECILOSCLERIDA

FAMILY CRAMBEIDAE

Genus *Crambe*

***Crambe* sp. 01 (NIWA 51235, Spirits Bay, Kelly)** (Kelly & Sim-Smith, in press 2023) 23OR1-7 (Figure 24)

Material examined: 23OR1-7, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: Thinly encrusting over a pebble.

Colour: In spirit, cream. Turned isopropanol bright orange.

Surface: This specimen has an extremely thin encrusting morphology, so no thick section was able to be cut. A dense scattering of oscula or ostia pores can be seen with the naked eye, giving it a lacey, translucent appearance.

Texture: Scratchy, minutely rough.

Spicules:

Megascleres:

Styles to subtylostyles, irregular, lumpy, abundant.
Mean: 214.8 µm, n=10
Range:190 – 249 µm

Polyaxonic sphaeroclone desmas.
Mean: 115.1 µm, n=10
Range: 74 – 142 µm

Microscleres:

Unguiferate isochelae, class I are abundant, class II are less common.
I Mean: 9.2 µm, n=10
Range: 8 – 10 µm
II Mean: 24.5 µm, n=10
Range: 21 – 29 µm

Remarks: Needs to be compared to the fossil sponge that is represented by *Crambe oamaruensis* (Hinde & Holmes, 1892; Kelly et al., 2003).

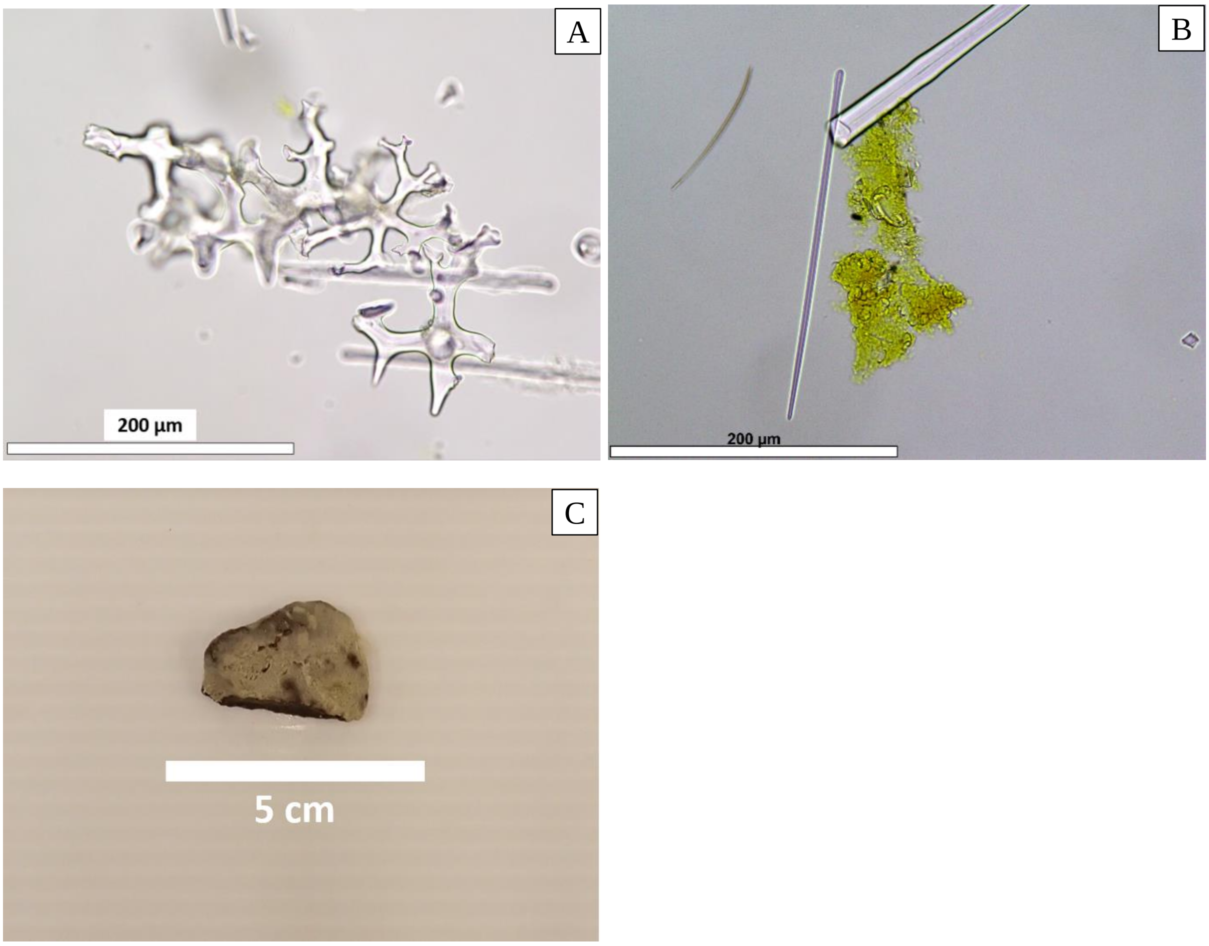


Figure 24. A-C, *Crambe* sp. 01 (NIWA 51235, Spirits Bay, Kelly) (23OR1-7): A, spicules - desmas; B, megascleres and isochelae spicules; C, desktop photo, note that the sponge is thinly encrusting a broken piece of rock.

FAMILY LATRUNCULIIDAE

Genus *Latrunculia*

Subgenus *Latrunculia* (*Biannulata*)

Latrunculia* (*Biannulata*) *procumbens (Alvarez, Bergquist & Battershill, 2002)
23OR1-4 (Figure 25)
23MOT1-11 (Figure 26)
23KR1-1 (Figure 27)

Material examined: 23OR1-4, Okarapu Reef, Bay of Plenty, 20-25 m depth.

Description: Thickly encrusting with large oscula and flat-topped, mushroom-like or pustule-like ostia projecting in a fistular fashion.

Colour: In situ, dark green and in spirit, black. Turned isopropanol dark brown.

Surface: 'Hairy', very irregular and has shell, algae and rock shards embedded in it. Under 4x magnification it is smooth but tented with spicule brushes projecting through the ectosome approximately every 230-330 µm.

Texture: Firm to the touch.

Skeleton: Spicules are very densely packed, forming choanocyte chambers throughout the choanosome.

Spicules:

Megascleres:

Anisostyles, fusiform and slightly sinuous.
Mean:327.9 µm, n=10
Range: 296 – 348 µm

Microscleres:

Discorhabds with four whorls, three of which are in the top half of the spicule.
Mean: 32.9 µm, n=10
Range: 27 – 36 µm

Remarks: Consistent with illustrations and description by Sim-Smith et al. (2022).

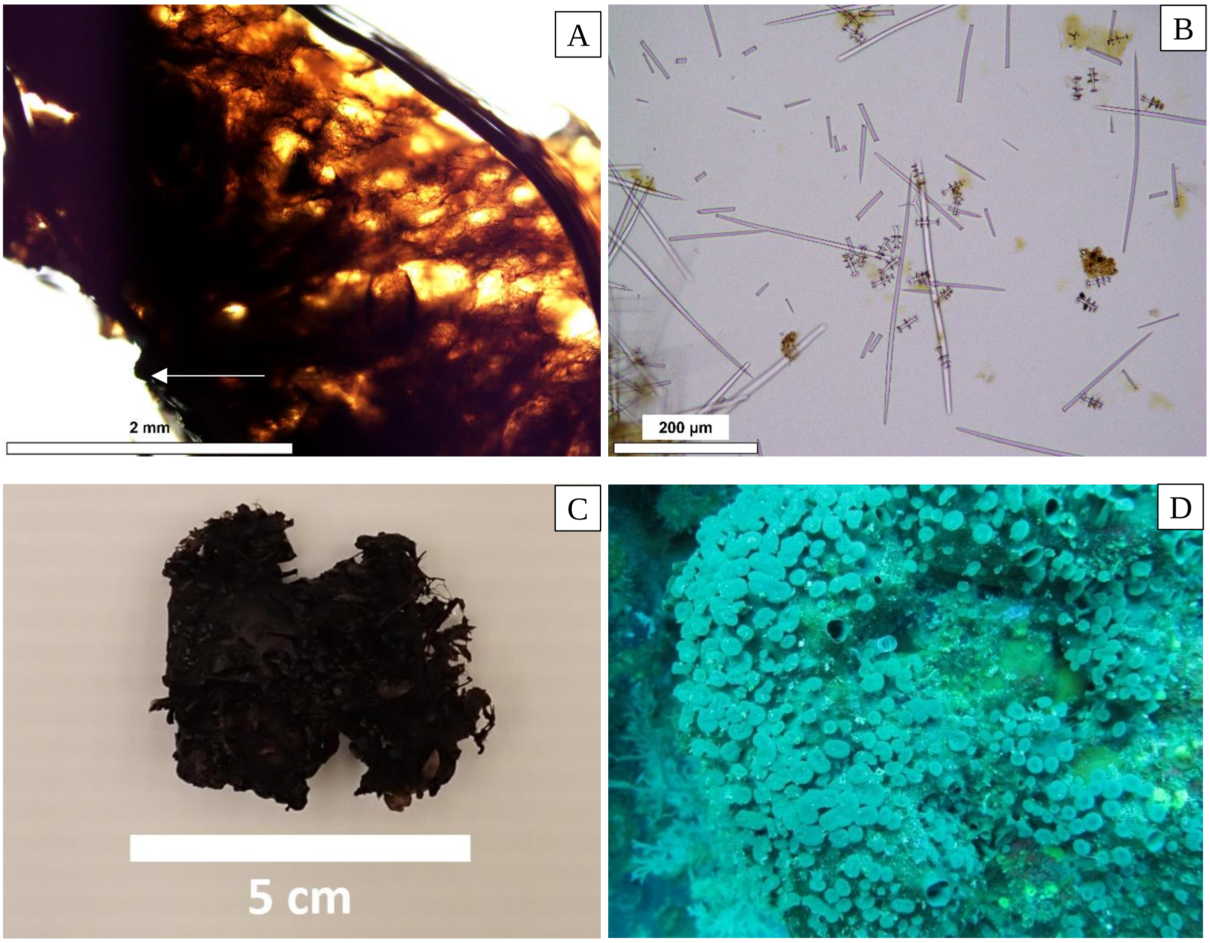


Figure 25. A-D, *Latrunculia* (*Biannulata*) *procumbens* (23OR1-4): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, desktop photo at a top-down angle; D, *in situ* photo.

Material examined: 23MOT1-11, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Thinly encrusting.

Colour: In spirit, black. Turned isopropanol dark green.

Surface: Almost completely embedded with shell, rock and other organisms. Where the sponge surface can be seen, it is smooth with fistular projections. The fistula ends are flat, like mushrooms with very thin stalks.

Texture: Easily compressible in the parts not embedded with shell and rock.

Skeleton: Anastomosing reticulate. The surface layer consists of a mat of spicules laid parallel to the surface. In projections and at the area of surface layer near to the beginning of a projection, spicule orientation gradually turns to be pointing directly outward and then they flow in one direction through the projection. In these areas are also an abundance of microscleres.

Spicules:

Megascleres:

Anisostyles, fusiform and slightly sinuous.
Mean: 324 µm, n=10
Range: 300 – 346 µm

Microscleres:

Discorhabds with four whorls, three of which are in the top half of the spicule.
Mean: 33.8 µm, n=10
Range: 31 – 36 µm

Remarks: Fits with description and illustrations of *Latrunculia* (*Biannulata*) *procumbens* (Sim-Smith et al., 2022). However, a difference to note is that this specimen has skinner projecting fistulas than those described by Battershill et al. (2010).

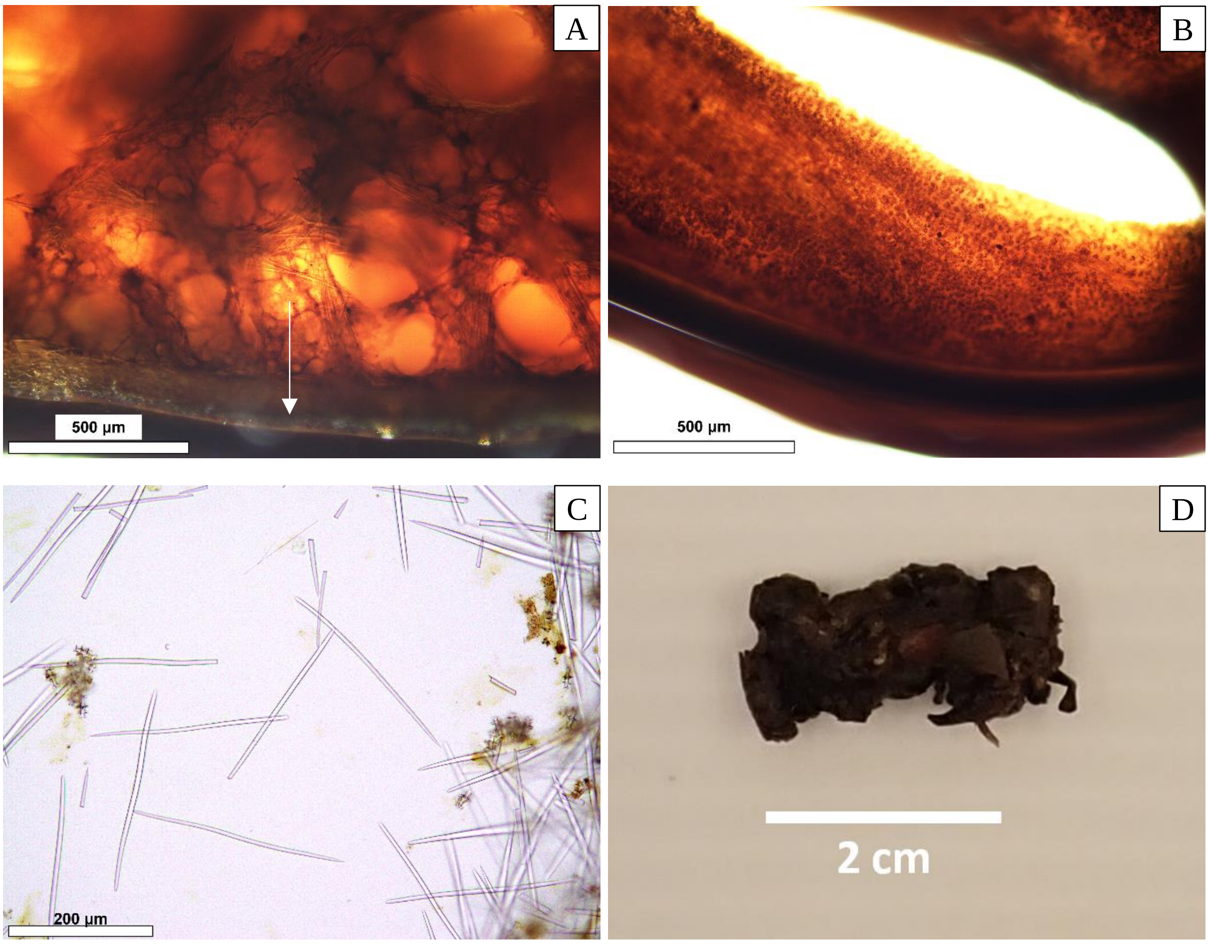


Figure 26. A-D, *Latrunculia* (*Biannulata*) *procumbens* (23MOT1-11): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, thick section showing concentration of microscleres in fistular projection; C, spicules; D, desktop photo at a top-down angle.

Material examined: 23KR1-1, Karewa Reef, Bay of Plenty, 20-25 m depth.

Description: Simple-massive.

Colour: In spirit, black. Turned isopropanol dark green.

Surface: Smooth but covered in pustules. Specimen has invertebrates growing in and through it. Under 4x magnification one can see a little echination of spicules through the ectosome, but it is not consistent over the whole surface.

Texture: Easily compressible.

Skeleton: Anastomosing reticulate. Irregular occurrence of circular to oval shaped choanocyte chambers. No clear demarcation of the surface layer and choanosome is visible.

Spicules:

Megascleres:

Anisostyles, fusiform and slightly sinuous.

Mean: 381 µm, n=10

Range: 326 – 423 µm

Microscleres:

Discorhabds with four whorls, three of which are in the top half of the spicule.

Mean: 32.4 µm, n=10

Range: 29 – 36 µm

Remarks: It is worth noting that this specimen has a massive morphology whereas the description by Sim-Smith et al. (2022) states that is a thinly to thickly encrusting species. High abundance of these species with massive growth forms was noted on the sample collection dive by Prof. Christopher Battershill.

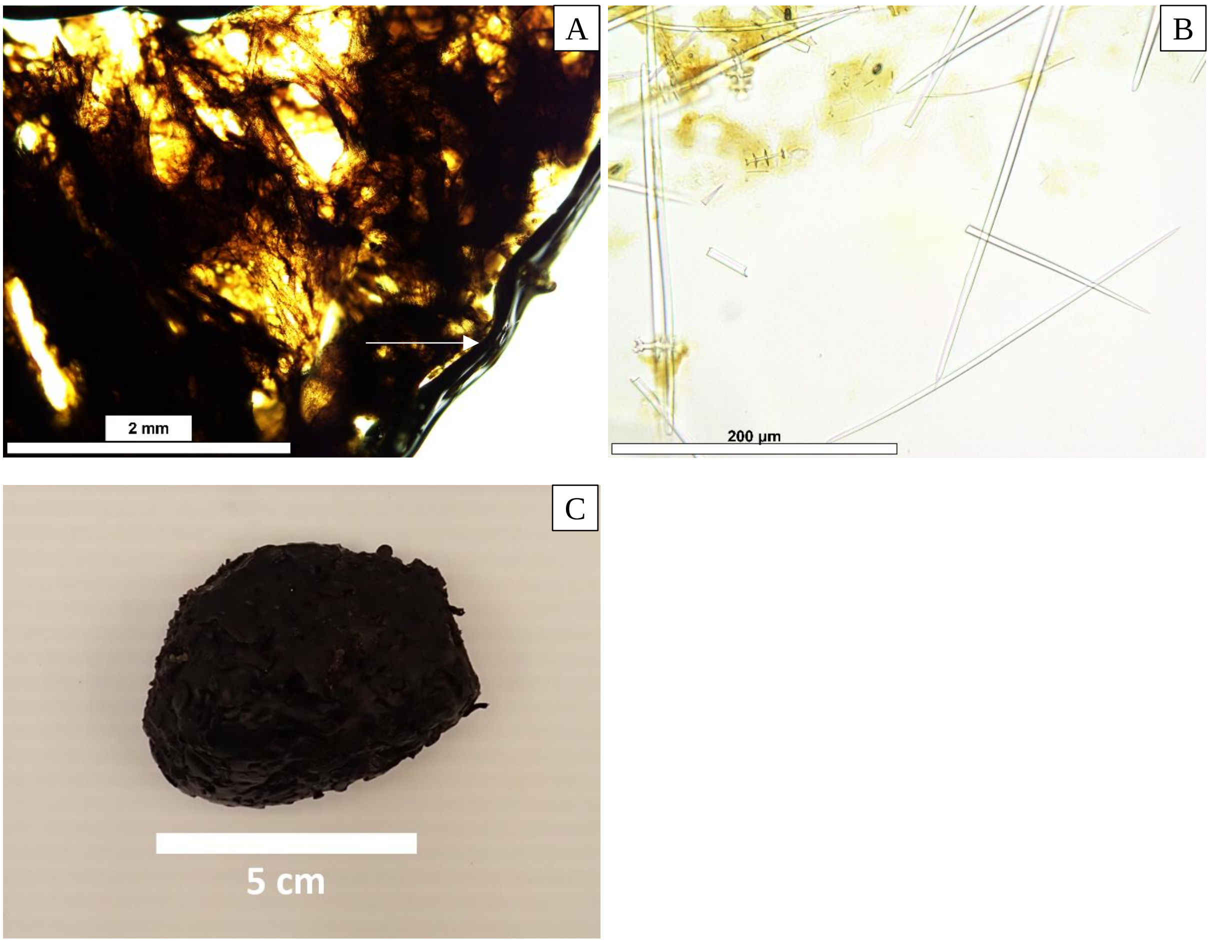


Figure 27. A-C, *Latrunculia* (*Biannulata*) *procumbens* (23KR1-1): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, desktop photo at a top-down angle.

FAMILY TEDANIIDAE

Genus *Tedania*

Subgenus *Tedania (Tedania)*

Tedania* (*Tedania*) *battershilli (Bergquist & Fromont, 1988)
23MOT1-8 (Figure 28)

Material examined: 23MOT1-8, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Thinly encrusting.

Colour: In spirit, cream. Turned isopropanol bright orange.

Surface: Very uneven with algae and other organisms growing in and through it. Under 4x magnification the surface is highly uneven with some very small spicule brushes.

Texture: **S**oft and easily compressible.

Skeleton: Stands of spicules in the choanosome are all generally perpendicular to the surface and flow down in a wavy nature akin to flowy moss. Spicules becomes slightly matted at the surface, but the surface layer is thin. Detritus is incorporated throughout the surface and choanosome.

Spicules:

Megascleres:

Styles, smooth, slightly curved to straight, some with elongated heads and some with small, rounded heads.
Mean: 267.4 µm, n=10
Range: 247 – 286 µm

Tylotes, slender, large size range.
Mean: 265.3 µm, n=10
Range: 206 – 313 µm

Microscleres:

Onychaetes, evenly spined.
Mean: 122 µm, n=10
Range: 105 – 132 µm

Remarks: Fits the description of *Tedania* (*Tedania*) *battershilli* given by Bergquist & Fromont (1988). Many inclusions of foreign spicules as artefacts.

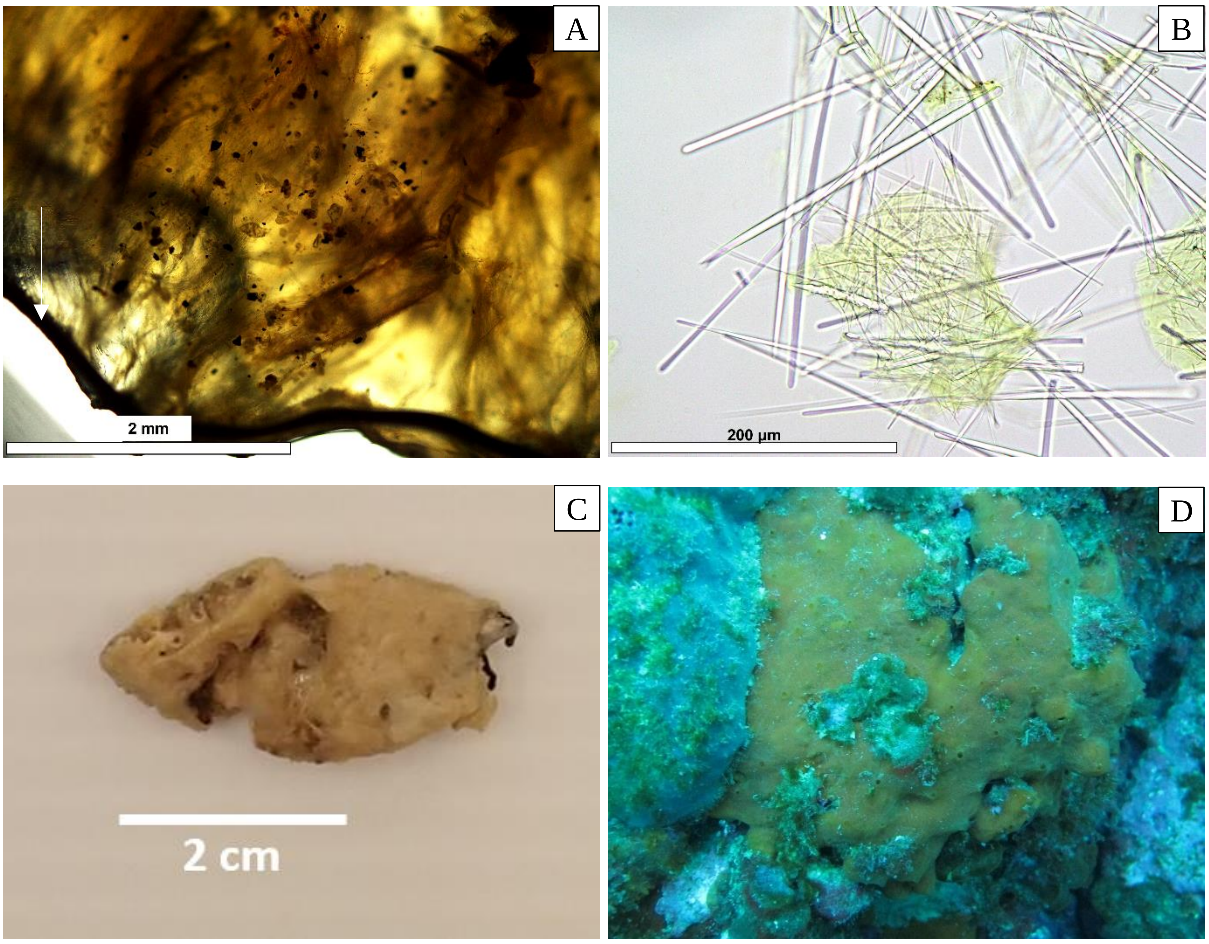


Figure 28. A-D, *Tedania* (*Tedania*) *battershilli* (23MOT1-8): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, desktop photo at a top-down angle; D, *in situ* photo.

ORDER SUBERITIDA

FAMILY SUBERITIDAE

Genus *Aaptos*

Aaptos conferta (Kelly-Borges & Bergquist, 1994)
23AR1-4 (Figure 29)

Material examined: 23AR1-4, Astrolabe Reef, Bay of Plenty, 20-25 m depth.

Description: Composite-massive.

Colour: In situ, clack with some gold peeking through, giving the black outer colour a thin, semi-translucent appearance. In spirit, black. Turned isopropanol orange-brown.

Surface: Looks relatively smooth but very irregular and can see spicules echinating through the ectosome.

Texture: Feels minutely spiky, like freshly shaved stubble.

Skeleton: All spicules in choanosome are perpendicular to the surface and highly structured. Surface layer is a mat of spicules that echinate through the ectosome.

Spicules:

Megascleres:

Strongyleoxeas, slightly curved, uncommon.
Mean: 1245.5 µm, n=10
Range: 789 – 1545 µm

Styles, centrally thickened, slightly curved, some with subtylote heads.
I Mean: 167.4 µm, n=10
Range: 138 – 180 µm
II Mean: 246.4 µm, n=10
Range: 211 – 271 µm
III Mean: 414.4 µm, n=10
Range: 331 – 546 µm

Oxeas, less common, straight to slightly curved.
Mean: 154 µm, n=10
Range: 101 – 208 µm

Inclusion of many other foreign mega- and microscleres.

Remarks: Morphology, colour, surface and spiculation are all consistent with *Aaptos conferta* Battershill et al. (2010). However, class I styles are only slightly curved, not abruptly curved as described in Battershill et al. (2010).

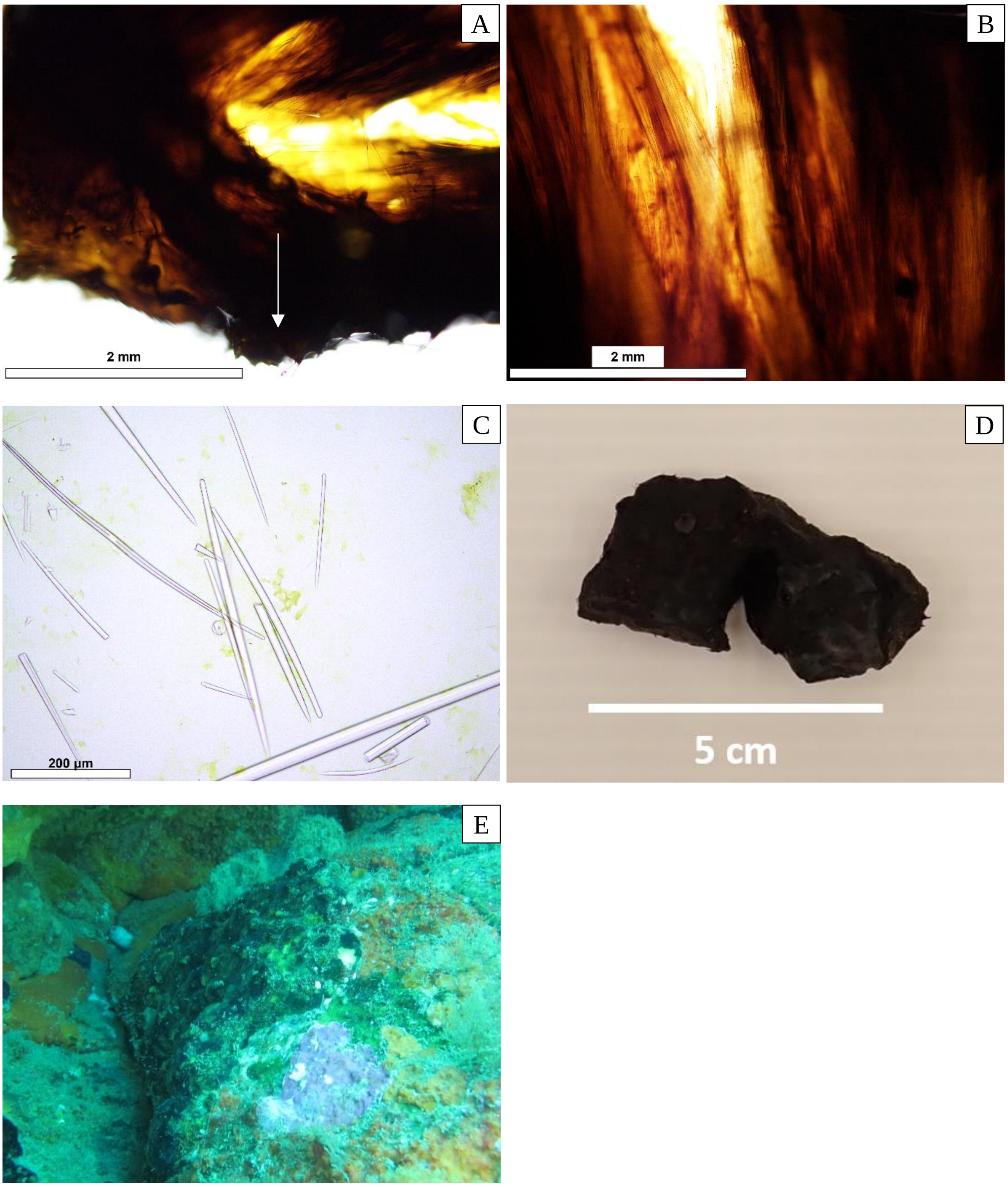


Figure 29. A-E, *Aaptos conferta* (23AR1-4): A, thick section showing skeletal structure at the surface with arrow pointing to the ectosome; B, thick section showing skeletal structure in the choanosome; C, spicules; D, desktop photo at a top-down angle; E, *in situ* photo.

Aaptos globosa (Kelly-Borges & Bergquist, 1994)
23MOT1-12 (Figure 30)

Material examined: 23MOT1-12, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Globular massive.

Colour: In spirit, grey. Turned isopropanol dull red-brown.

Surface: Bumpy and irregular with no oscula visible to the naked eye. Texture is very firm, hardly compressible. Hispidity is clear under 4x magnification.

Texture: Very firm, hardly compressible.

Skeleton: Dense, highly structured radial skeleton. No demarcation of the surface layer and choanosome.

Spicules:

Megascleres:

Strongyleoxeas, slightly curved, uncommon.

I Mean: 1042.6 µm, n=10
Range: 721 – 1309 µm
II Mean: 1832.4 µm, n=10
Range: 1460 – 2685 µm

Tylostyles, definite tylote heads, large variations in size.
Mean: 233.5 µm, n=10
Range: 165 – 390 µm

Styles to subtylostyles, subtylote head is very faint, large variations in size.
Mean: 501.9 µm, n=10
Range: 283 – 768 µm

Remarks: It is hard to determine the sizes of strongyleoxeas due to most of the large spicules being broken in the spicule mount. This specimen fits the description of *Aaptos globosa* given by Battershill et al. (2010).

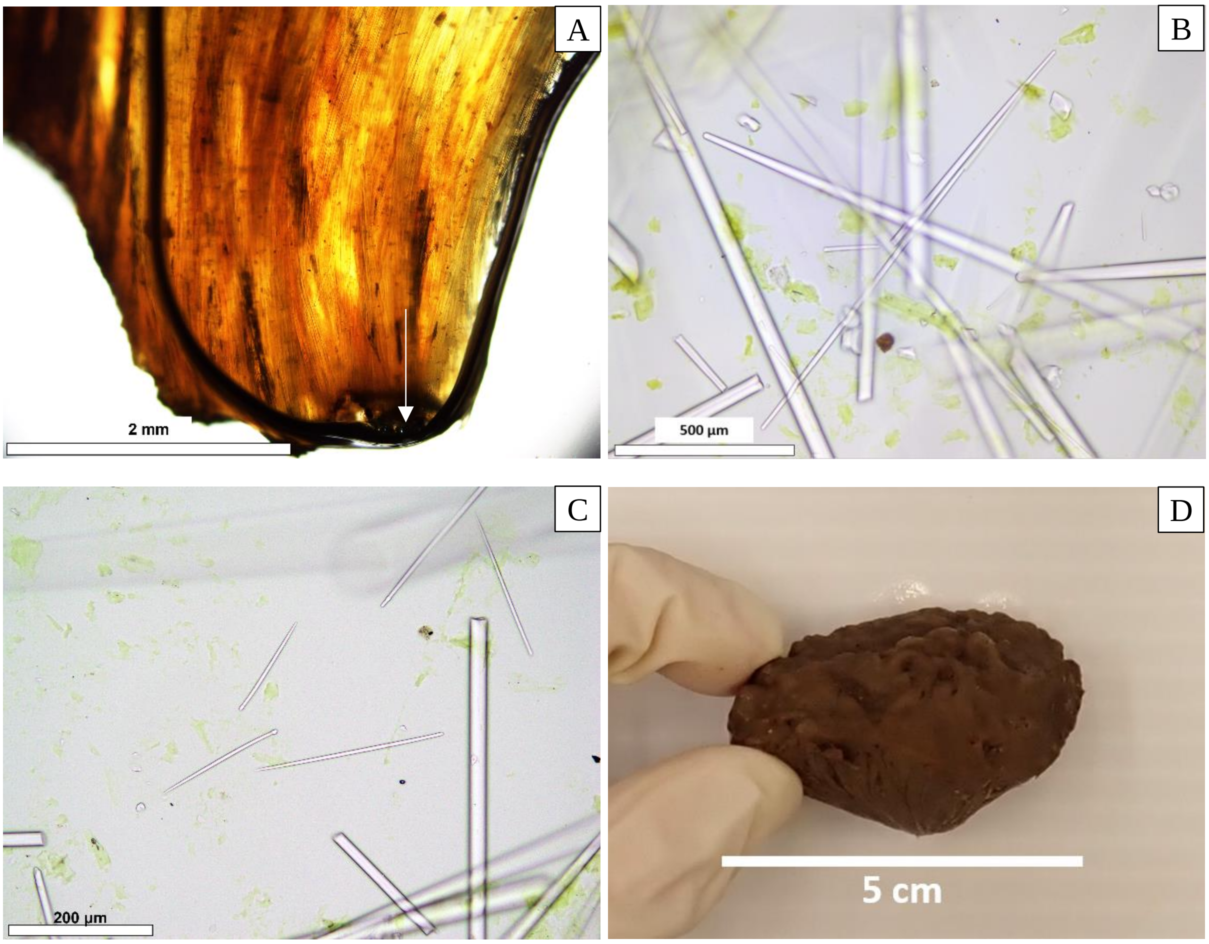


Figure 30. A-D, *Aaptos globosa* (23MOT1-12): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, tylostyles; D, desktop photo at a side-on angle with a slight lean towards the top.

Genus *Suberites*

***Suberites* sp. (cf. big cheese sponge)** (Kelly, 2022)
23AR1-1 (Figure 31)
23AR1-2 (Figure 32)

Material examined: 23AR1-1, Astrolabe Reef, Bay of Plenty, 20-25 m depth.

Description: Thickly encrusting, tending toward simple-massive, with turned up edges and a thin rim.

Colour: In situ, pale grey. In spirit, cream to light brown in places. Turned isopropanol light yellow-orange.

Surface: Smooth, irregular. Under 4x magnification, smooth but with spicule brushes projecting through ectosome.

Texture: Easily compressible and velvety to the touch.

Skeleton: No clear demarcation between the surface and choanosome. Ectosome is very thin. Skeleton structure is plumose, tending plumose-reticulate and looks like flowy moss.

Spicules:

Megascleres:

Subtylostyles to styles, well-rounded heads, some sinuous and some curved.

I Mean: 261.1 µm, n=10
Range: 222 – 286 µm

II Mean: 515.7 µm, n=10
Range: 454 – 571 µm

Many inclusions of foreign spicules as artefacts, especially acanthostyles.

Remarks: This specimen has subtylostyles typical of the genus *Suberites* and the morphology and surface are also typical for this genus. However, it does not fit any of the described species (Bergquist, 1968; Battershill et al., 2010). It is most closely comparable and needs to be checked against the *Suberites* sp. identified as the ‘big cheese sponge’, described by Kelly (2022).

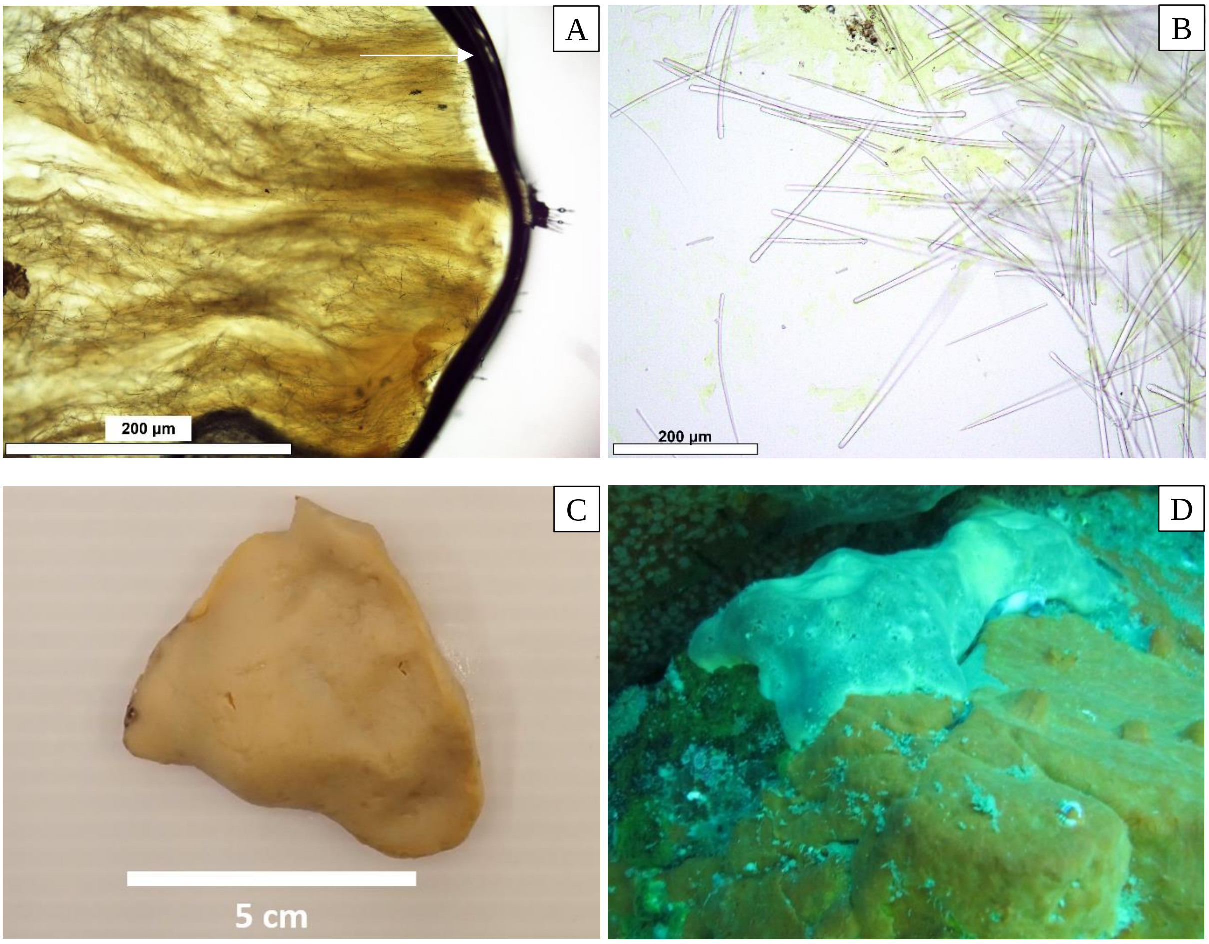


Figure 31. A-D, *Suberites* sp. (cf. big cheese sponge) (23AR1-1): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, desktop photo at a top-down angle; D, *in situ* photo.

Material examined: 23AR1-2, Astrolabe Reef, Bay of Plenty, 20-25 m depth.

Description: Thickly encrusting with a thick, rounded rim tending simple-massive.

Colour: In situ, pale grey to orange. In spirit, cream and grey. Turned isopropanol orange-yellow.

Surface: Smooth but with minute conical bumps visible under 4x magnification.

Texture: Smooth, easily compressible, velvety to the touch.

Skeleton: Radial near the surface with a thick surface layer. Deeper into the choanosome although still looking overall like a radial structure, the spicules become irregularly matted in confused orientations.

Spicules:

Megascleres

Subtylostyles to styles, well-rounded heads, some sinuous and some curved.

I Mean: 241.8 µm, n=10
Range: 131 – 295 µm

II Mean: 490.9 µm, n=10
Range: 461 – 571 µm

Many inclusions of foreign spicules as artefacts, especially acanthostyles.

Remarks: Same as 23AR1-1, this specimen is most closely comparable and needs to be checked against the *Suberites* sp. identified as the 'big cheese sponge', described by Kelly (2022).

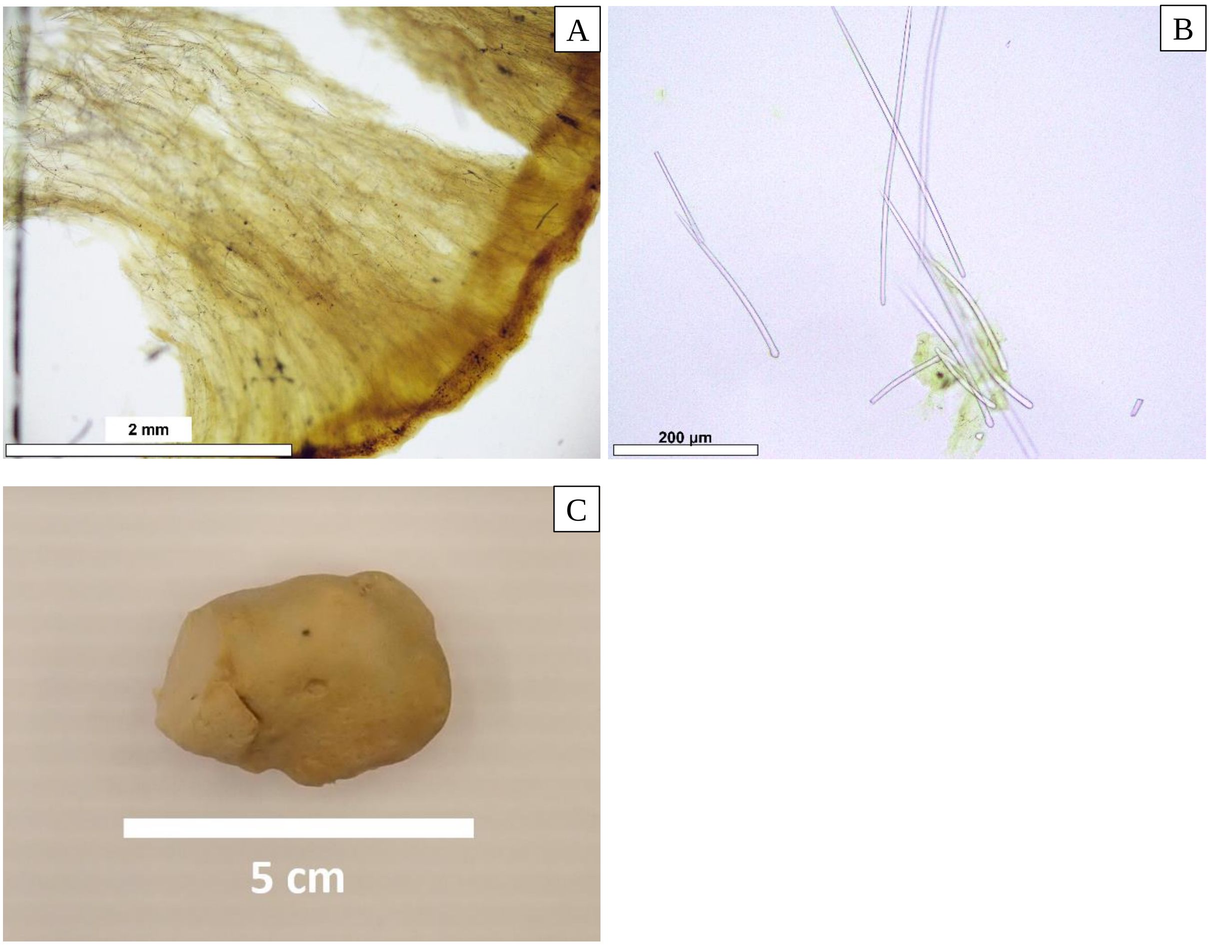


Figure 32. A-C, *Suberites* sp. (cf. big cheese sponge) (23AR1-2): A, thick section showing skeletal structure; B, spicules; C, desktop photo at a top-down angle with a slight lean to the side due to an uneven lower surface.

ORDER TETRACTINELLIDA

SUBORDER ASTROPHORINA

FAMILY ANCORINIDAE

Genus *Jaspis*

Jaspis novaezealandiae (Dendy, 1924)
23MOT1-6 (Figure 33)
23MOT1-9 (Figure 34)

Material examined: 23MOT1-6, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Thickly encrusting.

Colour: In spirit, dark grey with white areas externally and cream to white internally.

Surface: Other organisms growing on it. Small oscula can be seen in clusters. Under 4x magnification the spicules can be seen echinating a short way through the ectosome.

Texture: Firm, mildly compressible and irregular. Smooth when brushed one way but prickly when brushed the other way, suggesting angular echination of spicules.

Skeleton: A thick spicule mat makes up the surface layer with lots of sand and detritus inclusion which carries through the choanosome too. Ectosome is tangential to the skeleton.

Spicules:

Megascleres:

Oxea, slightly and evenly curved.

I Mean: 89.2 µm, n=10
Range: 57 – 118 µm
II Mean: 147.9 µm, n=10
Range: 125 – 210 µm
III Mean: 1198.2 µm, n=10
Range: 938 – 1652 µm

Strongyles, centrally bent.

I Mean: 68.2 µm, n=10

Range: 60 – 83 µm

II Mean: 105.2 µm, n=10

Range: 96 – 121 µm

Microscleres:

Oxyspherasters.

Mean: 16.8 µm, n=10

Range: 13 – 20 µm

Remarks: The key characteristics of this specimen are its encrusting morphology and scalloped surface.

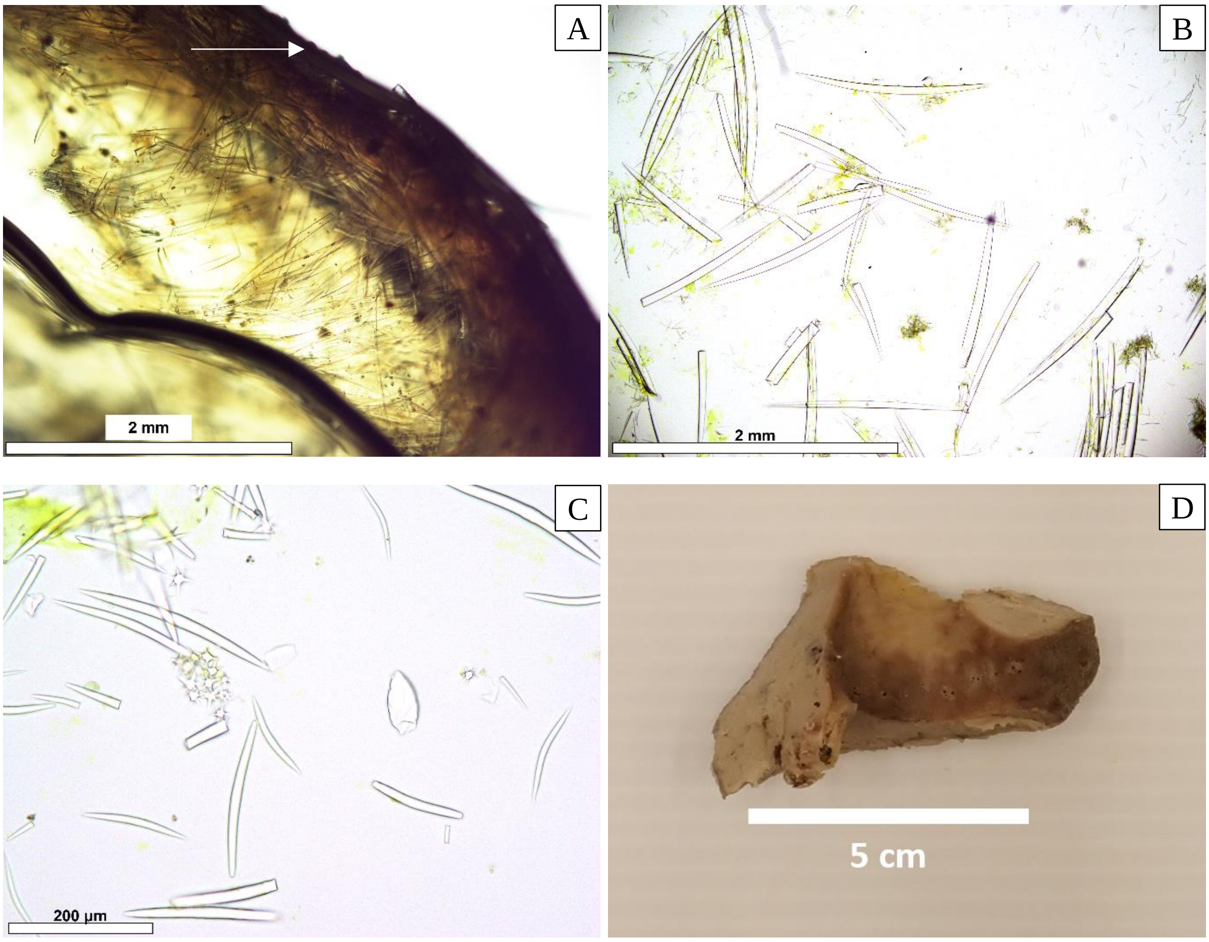


Figure 33. A-D, *Jaspis novaezealandiae* (23MOT1-6): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules – extremely large megascleres; C, spicules – smaller mega- and microscleres; D, desktop photo at a top-down angle.

Material examined: 23MOT1-9, Motiti Island, Bay of Plenty, 20-25 m depth.

Description: Thickly encrusting.

Colour: In spirit, dark grey externally and cream internally.

Surface: On one side it is scratchy and embedded with shells and invertebrates. On the other side it is smooth but still scratchy. It is irregular all over and hispidity is visible under 4x magnification.

Texture: Same as 23MOT1-6.

Skeleton: There is clear demarcation of the surface layer and choanosome which is visible to the naked eye. The surface layer is a confused mat of finer, smaller spicules at the ectosome, with large oxea and broken spicules in a layer beneath this, surrounded by the smaller, finer spicules. The demarcation between surface and choanosome is due to a dark brown line which is followed in the choanosome by densely packed, large oxea in confused orientations. Small brown ball-shaped objects are spread throughout the choanosome but are more concentrated along the brown line of separation between the surface layer and choanosome.

Spicules:

Megascleres:

Oxea, slightly and evenly curved.

I Mean: 61.5 µm, n=10
Range: 56 – 72 µm
II Mean: 127.8 µm, n=10
Range: 90 – 149 µm
III Mean: 1321.5 µm, n=10
Range: 1039 – 1496 µm

Strongyles, centrally bent.

I Mean: 78.7 µm, n=10
Range: 69 – 96 µm
II Mean: 116.8 µm, n=10
Range: 106 – 129 µm

Microscleres:

Oxyspherasters.

Mean: 17.6 µm, n=10

Range: 13 – 22 µm

Remarks: Same as 23MOT1-6.

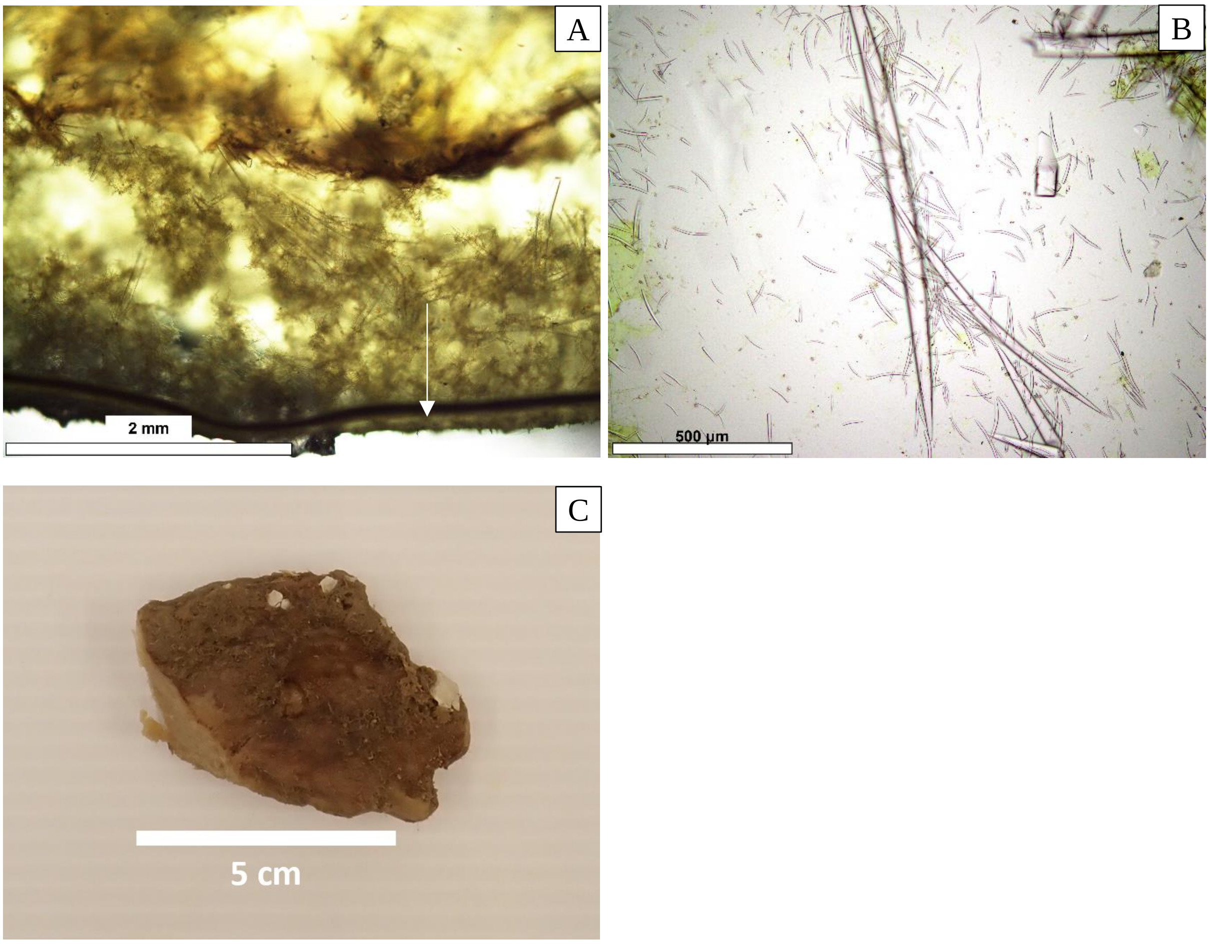


Figure 34. A-C, *Jaspis novaezealandiae* (23MOT1-9): A, thick section showing skeletal structure with arrow pointing to the ectosome; B, spicules; C, desktop photo at a top-down angle.

2.3.3 Biogeographic distributions

This study has updated the current biogeographic knowledge of the Bay of Plenty. Twenty-two sponge species identified from a combination of ROV footage and specimen samples (34.92% of total species list), presented new occurrence records for the Bay of Plenty and some species' known depth ranges were extended (Table 5). The sponges identified in this study represent a highly mixed assemblage made up of multiple well connected and diverse communities (Table 4 & Figure 35). The total species list comprised of species with northern warm-water and southern cold-water affinities relative to the BoP (33% and 16%, respectively), as well as a range of temperate (27%) and cosmopolitan species (24%) (Figure 35 & Appendix E). Temperate represents species found only in temperate waters, both to the North and to the South of the BoP. Cosmopolitan represents species found from the tropics or subtropics through to cold-temperate waters.

Table 5. New species occurrence records for geographic and depth ranges. Previously known distributions informed by Mc Cormack (2015), Donald (2021), Kelly (2022), Kelly & Sim-Smith (2023) and WoRMS Editorial Board (2023).

Species	Previously known distribution	New record of range extension
+***Aaptos conferta***	From the Three Kings Islands down to the Hauraki Gulf along the eastern coast.	Yes.
Black & orange cup		Possibly new species.
***Cinachyrella* sp.**	Undescribed *Cinachyrella* sp. (golden hemisphere sponge) previously known from the Eastern coast of Far North NZ, down to Great Barrier Island (Kelly, 2022). *Cinachyrella* genus generally distributed through circumtropical to warm temperate regions (WoRMS Editorial Board, 2023). Recently also recorded on Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
+***Crambe* sp. 01 (NIWA 51235, Spirits Bay, Kelly)**	Spirits Bay, currently known as endemic to New Zealand.	Yes.
Fluffy cluster sponge		Possibly new species.

Halichondria* (*Halichondria*) *moorei	Down to 15 m (Mc Cormack, 2015).	New depth range extension to approximately 40 m.
Homaxinella* cf. *erecta	West coast of the North Island, East coast from Northland to Auckland, East Cape, and Chatham Islands (Kelly, 2022; WoRMS Editorial Board, 2023). Seen on Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
Hymeniacidon* cf. *perlevis	Mainly temperate (WoRMS Editorial Board, 2023). In NZ, only intertidal on the Eastern coast from the Far North to the Hauraki Gulf as well as around Wellington, Nelson, and the West coast of Auckland (Kelly, 2022).	Yes. Also new depth range extension for NZ to approximately 50 m.
+*Jaspis novaezealandiae*	In NZ, known from the eastern coast of the North Island from the Far North down to around Kawau Island, as well as East Cape, the Bounty Islands (Kelly, 2022). Also recorded in the Ross Sea, Antarctica (WoRMS Editorial Board, 2023).	Yes.
Leucosolenia rosea	Down to 30 m and only from the South Island of NZ (Kelly, 2022; WoRMS Editorial Board, 2023).	Yes. Also new depth range extension – to approximately 70 m.
+*Neopetrosia* sp. 1 (spicules 152 – 183 µm, Astrolabe Reef, Donald)		New species.
Orange meandering sponge		Possibly new species.

Oyster mushroom sponge	Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
***Petromica* sp.**	Undescribed *Petromica* sp. ('witchy' finger sponge) known in NZ from Rodney Coast, Poor Knights Islands (Kelly, 2022). Also Nukutai Reef (Donald, 2021). *Petromica* genus is known to occur in tropical and temperate waters (WoRMS Editorial Board, 2023).	No, but only record in BoP is from unpublished study (Donald, 2021).
Possibly tumbleweed sponge	Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).
+*Raspailia* sp. nov. 1 (spathulate, Motiti Island, Donald)		New species.
+*Spirastrella* sp. 01 (0CDN6683-X, Three Kings)	Three Kings Islands, currently known as endemic to New Zealand.	Yes.
+*Suberites* sp. (cf. big cheese sponge)	Northeastern coast of the North Island from Cape Reinga down to the Rodney Coast.	Yes.
Taonura* cf. *marginalis	Known from northern and southern Australia, and from the North Cape in NZ. Seen on Nukutai Reef (Donald, 2021).	No, but only record in BoP is from unpublished study (Donald, 2021).

Thorecta* cf. *reticulatus	South Island of NZ (Kelly, 2022).	Yes. Similar specimen was recorded in Donald (2021), so may not be a completely new record.
Trachycladus stylifer	Recorded in subtropical New Caledonia and the Far North and Bay of Islands in NZ (Kelly, 2022; WoRMS Editorial Board, 2023). Potentially seen in Donald (2021) but ID was not certain.	Yes.
Yellow thick encrusting Poecilosclerid	Recorded on Nukutai Reef as a ‘possibly new species’ by Donald (2021 - see sponge number 58 in visual ID guide).	No, but only record in BoP is from unpublished study (Donald, 2021).

[+] Species identified from samples but not recorded in ROV footage.

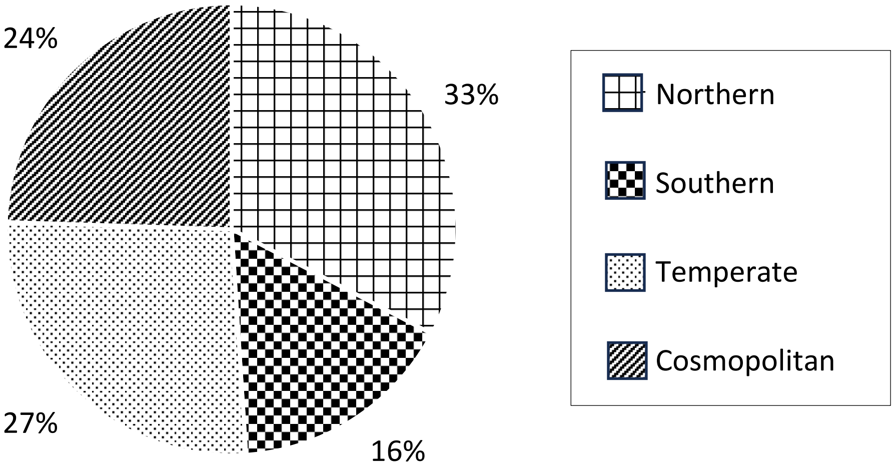


Figure 35. Compositional makeup of sponges identified in this study according to their recorded geographical affinities.

2.4 Discussion

2.4.1 Biodiversity hotspot

Mesophotic rocky reefs are known to be biodiversity hotspots and the Motiti mesophotic archipelago has proven to be no exception, boasting a rich variety of species throughout (Bo et al., 2012; Donald, 2021; Rossi, 2013; Bart et al., 2021; Bell et al., 2022). The conservative identification of fifty-three sponge species from the ROV footage, in conjunction with the still-increasing species accumulation curves (Figure 8), provides a valuable indication as to the probable extent of the true species diversity in these sponge reef communities. This is due to the grouping of species into higher taxonomic levels as needed to attain certain and reliable results, as discussed earlier. Although species richness is difficult to compare between studies (Clarke & Warwick, 1998) it is still valuable information as it has provided a benchmark in an area with little current knowledge. A smaller-scale survey by Donald (2021) recorded a greater number of sponge species (70 species), however, that study was much less conservative and robust in terms of species' assignments. Therefore, the species richness measures herein should be primarily referred to as the benchmark for future research of mesophotic reefs in the Motiti area.

2.4.2 Taxonomic distinctness indices

When average taxonomic distinctness (TD) values are 'lower than expected' (i.e., fall below the confidence funnel in Figure 9), this generally means that the habitat has been degraded in some way by anthropogenic influences (Clarke & Warwick, 1998; Leonard et al., 2006). Although the average TD of sponge communities along most transects were detected to be within the 'expected' range (i.e., values fall within the confidence funnel in Figure 9), the southern tip of Te Poroiti and southwestern area of Nukutai presented lower than expected average TD values (Clarke & Warwick, 1998). On the other hand, variation in TD was within the expected range for all transects. However, those same transects that had low average TD (N02 West, B01 North and B01 South) approached the upper limit of the confidence funnel for variation in TD. This shows that the sponge communities observed along these transects had a more uneven distribution of species across the hierarchical taxonomic tree (Clarke & Warwick, 2001; Hu & Zhang, 2016). The combination of low average TD coupled with high heterogeneity in taxonomic distribution suggests that some groups of species are under- or over-represented compared to others, likely due to certain habitat-types being absent from these transects possibly due to the influence of anthropogenic stressors (Clarke & Warwick, 2001).

2.4.3 Local variability

Despite some transects showing evidence of degradation attributable to anthropogenic stressors (low average TD plus bleaching recovery, recently exposed bare patches and signs of necrosis – see Chapter Three below), overall, no significant local variation was present amongst reefs in either of the TD indices (Clarke & Warwick, 1998). These observations indicate that sponge communities within the MNEMA are taxonomically well-connected and that any stress effects are spread relatively evenly across these reef systems at large spatial scales. Nevertheless, it is worth highlighting that some deviations from the mean were discernible, with grouping below the mean for Te Poroiti and above the mean for Motuhaku. Such deviations not only suggest that subtle alterations in the overall diversity of these reefs have already transpired but also hint at the presence of local, smaller spatial scale variations in biophysical dynamics. This implies that sponge communities at and within each reef have responded dissimilarly, or potentially at different rates, to the impacts of climate and/or more direct or local anthropogenic stressors. Even though the MNEMA is a reasonable distance offshore (approximately 10 km), it is still subject to sedimentation plumes (Crawshaw, 2022). Furthermore, even though these communities are in deep water in the mesophotic zone, marine heat waves can still reach them (Perkins et al., 2022; Bell et al., 2023). This grouping pattern emphasizes the unique character of the Motiti archipelago, as the MNEMA encompasses an expanse likely to exhibit increasing patchiness over time in reflection of a varied physical environment. These findings provide a crucial foundation for the establishment of long-term monitoring initiatives for the Motiti mesophotic reefs. Future assessments of TD indices will facilitate the creation of a temporal record, enabling the tracking of changes in benthic biodiversity over time.

2.4.4 New/undescribed species

Among the 11.3% of new or undescribed species identified from ROV footage, the tumbleweed sponge emerged as an intriguing subject of investigation. Donald (2021) identified the tumbleweed sponge as a 'probably new species', based on its prevalence in their preliminary survey and thriving presence in February 2021, on Nukutai Reef between 40 – 50 m depth. However, this study, conducted only a year and a half later, revealed a starkly contrasting scenario. The tumbleweed sponge was seldom encountered and when it was, specimen appeared markedly degraded (see Appendix D: Figure 3). Sponge reefs are renowned as long-lived communities (Teixidó et al., 2009; Bell et al., 2014, Micaroni, 2022) and the size of the sponges alone, for example the large patches of encrusting sponges, indicates that the individuals observed in this study are likely to be decades old (Ayling, 1983). Consequently, this rapid shift in the tumbleweed sponge population a matter of considerable ecological significance. The precise cause behind this shift is yet unknown, but a key initial observation was that all sightings except one, were exclusively at the deepest depths exceeding 80 m. Intuitively, temperature may be cause for consideration as it is possible that we have captured the remnant population of the tumbleweed sponge where they have disappeared from shallow habitats but some individuals were surviving in deeper, cooler areas on these reefs (Idan et al., 2018). If this is the case, a shift from colder to warmer water species could be occurring on these reefs, as it has done in other areas impacted by increasing temperature with climate change (Wernberg et al., 2016). Although this species is categorized as 'possibly a tumbleweed sponge' in this study due to the absence of physical samples and limited prior records, it is noteworthy that only a single SCUBA dive conducted in comparable habitats identified an additional nine species. This finding strongly implies that many inconspicuous species may have eluded detection in these deeper realms, which were only accessible by ROV. Considering the overall taxonomic similarity between sampled reefs and the conservative nature of our results, it is reasonable to infer that a similar shift has likely unfolded across all mesophotic reefs within the Motiti archipelago, perhaps even the wider BoP. Moreover, the broader implication suggests that this phenomenon might extend beyond the tumbleweed sponge, necessitating an urgent and in-depth investigation to comprehensively assess any rapid alterations in what is typically regarded as a stable benthic community (Teixidó et al., 2009; Bell et al., 2014). This study underscores the urgency of conducting further research at a finer scale to unravel the intricacies of this ecological transformation.

2.4.5 Biogeographic Distributions

Through comprehensive examination of sponge biodiversity on Motiti’s mesophotic reefs, this study identified a total of sixty-three sponge species and revealed that over a third of these (34.92%) constitute novel occurrence records in terms of either their geographical distribution or depth range. Some of these newly documented occurrences, such as *Homaxinella erecta* and *Jaspis novaezealandiae*, bridge previously known distributions situated both to the north and south of the BoP (Kelly, 2022; WoRMS Editorial Board, 2023). Perhaps most notably, though, was the identification of *Crambe* sp. 01 (NIWA 51235, Spirits Bay, Kelly), found on Okarapu Reef. This species has only been found live once before, in Spirits Bay, from which Kelly et al. (2003) discovered that its spicules are indistinguishable from the fossilised spicules originally identified as *Vetulina oamaruensis* (Hinde & Holmes, 1892). These fossilised spicules were found within Oamaru siliceous rock dated from the Upper Eocene or Oligocene (Hinde & Holmes, 1892). The finding of this rare and undescribed species with its linkages back to pre-human times underscores the significance of this region in sponge biogeography.

The diversity in sponge taxa found in this study also provides valuable insights into the influence of currents within the BoP's mesophotic zone. The composition of sponge communities in the Motiti mesophotic reefs and the broader BoP region reflects an amalgamation of warm-water (northern) and cold-water (southern) affinities, indicating the complex interplay of oceanic currents within this area. Intriguingly, the proportion of species with demonstrated warm-water preferences was double that of the species extending into colder regions further south, indicative of the pronounced influence of the East Auckland Current (EAUC) in the BoP. However, it is noteworthy that cold-water currents like the Wairarapa Eddy (WE) also contribute to the sponge community dynamics in this region, corroborating previous findings by Donald (2021). Considering the significant influence of the EAUC in the BoP, as indicated by this study and supported by Donald (2021), it raises the question of how the increasing frequency and intensity of marine heat waves being carried down to New Zealand from the tropics will potentially have repercussions for precious mesophotic ecosystems within the Bay of Plenty (Behrens et al., 2022). These discoveries highlight the existence of a highly mixed sponge assemblage characterized by taxonomically diverse and interconnected communities. In addition, their associations with oceanic currents make them a crucial area for further investigation and conservation efforts.

2.4.6 Limitations & future recommendations

When considering the merits and limitations of the ROV and drop camera surveying methodologies as implemented in this study and by Donald (2021), respectively, it becomes clear that the optimal survey design in future should entail a compromise between the two. The utilization of an ROV afforded significant advantages in terms of manoeuvrability, extended transects length, and enhanced control. Nonetheless, it frequently resulted in blurry images and the omission of inconspicuous species when driven at excessive speed or positioned too far away from the substrate. Conversely, the drop camera yielded high quality, close-up imagery due to slower movement, but came with limitations including shorter transect lengths, reduced manoeuvrability, and, at times, an excessively gradual pace. In light of these factors, it is recommended that future research continues to employ an ROV while adopting a modified approach. Specifically, similar length transects should be conducted but still images should be taken at further time intervals. The ROV should descend gradually toward the benthos at each set interval to capture close-up, high-quality images before ascending and progressing to the next image point. This approach will optimise time efficiency by improving image retention while retaining the benefit of large-scale surveys. More transects should also be carried out at each reef until the species accumulation curve plateaus, to enable a more accurate representation of the species richness present, undoubtedly much higher than we were able to capture (Figure 8). Additionally, another recommendation for future research is to extract diversity data from Donald (2021) using taxonomic distinctness indices to backdate the beginning of a comparable temporal record of biodiversity trends over time on the mesophotic reefs of the Motiti archipelago. However, it is essential that any photographic survey is complemented by the specimen collections linked to their images to ensure accurate taxonomic assignment. Unfortunately, this aspect fell beyond the scope of this thesis, primarily due to the unavailability of suitable deep-water sampling ROVs. Our research group intends to conduct this work in future to validate species descriptions and diversity measures. Acting on these recommendations will provide a more comprehensive context and enhance our understanding of the ongoing ecological processes in the MNEMA.

2.5 Conclusions

Motiti's mesophotic reefs represent a remarkable biodiversity hotspot characterised by interconnected sponge assemblages with a complex blend of geographic affinities. This study serves as a benchmark for future research and monitoring, yet it is clear that our highly conservative identification of sixty-two species has only scratched the surface of these vibrant and rich sponge communities. Evidence of degradation due to anthropogenic stressors hinted at the presence of local variation in biophysical dynamics, imparting a unique, patchy character to the MNEMA. Notably, this study identified several new or undescribed species, including the tumbleweed sponge, which revealed what appears to be rapid shift in the community from cold-water to warm-water species, possibly driven by climate change-induced increasing temperatures. This study has extended geographic and occurrence data, improved knowledge of New Zealand mesophotic sponge diversity and offered valuable insight into the role of oceanic currents within the BoP. The dominance of the EAUC in this region underscores concerns about the escalating frequency and intensity of marine heatwaves transported from the tropics, raising questions about potential repercussions on these precious ecosystems. This study provides the foundation for establishing long-term monitoring and highlights the urgency of conducting more fine-scale research to understand the intricate ecological processes shaping the Motiti mesophotic reefs. Regular monitoring will be instrumental in tracking any temporal changes or patterns on Motiti mesophotic reefs, especially in light of the degradation and community shifts indicated by this study. Future research recommendations include methodology improvements, analysis of historic taxonomic data to backdate the temporal record, and the incorporation of TD indices for comparability. It is our hope that this research will facilitate the preservation and sustainable management of these ecologically invaluable mesophotic reefs.

Chapter 3

Community Ecology & Stressors

3.1 Introduction

3.1.1 Threats to sponge characterised reefs

Sponge-dominated rocky TMEs are under-researched yet widely distributed and highly valued due to the vast array of ecosystem services they provide, as described in Chapter One (see Bell et al., 2022). In light of the mounting pressures of global warming, understanding these precious ecosystems has become a priority. Rapid ecological changes can occur in response to shifting environmental pressures such as alterations in oceanic currents (van Gennip et al., 2017), temperature fluctuations (Bell et al., 2023) or changes in sedimentation regimes (Beets, 2017). In New Zealand, all of these factors are either currently being observed (e.g., increasing temperature and sedimentation (Behrens et al., 2022; Cornwall et al., 2023; Noll & Andrews, 2023)) or are anticipated to occur in the near future (e.g., oceanic currents shifting spatially or in intensity (Boyd & Law, 2011)). Other pressures that can influence sponge communities include food limitation, ocean acidification (for calcareous sponges, e.g., Bell et al., 2018) pollution from fishing gear and chemical waste, eutrophication, invasive species, and bottom-contact fishing methods (see Bell et al., 2022). When stressors such as those outlined above are experienced in combination, they can have a compounding effect, multiplying the stress from each individual physical and/or ecological pressure and potentially causing more damage than these stressors would have done in isolation (Beets, 2017; Scanes et al., 2018; Bell et al., 2022). Following groundbreaking exploratory surveys in 2021 that reported vibrant and biologically diverse sponge gardens inhabiting the mesophotic reefs of the Motiti Island archipelago, Bay of Plenty (BoP), a need has arisen for understanding the system's ecology (Donald, 2021). Prior to this investigation, we have been blind to any biogeographic or ecological shifts on these reefs, underscoring the urgency of this research.

3.1.2 Sedimentation stress

Different sponge species have varying stress tolerance levels to abiotic factors like sedimentation, temperature and pH. While marine sponges naturally encounter sedimentation to some degree, exceeding the levels found in their natural environment typically results in adverse impacts (Bell et al., 2015). These impacts encompass various aspects of sponge biology, including pumping activities, respiration, feeding, reproduction, growth, and symbiotic relationships (as referenced in Beets, 2017, p. 14). In response, sponges exhibit species-specific active and passive responses. Active responses can include changes in respiration and pumping rates (Tompkins-MacDonald & Leys, 2008; Grant et al., 2018) and mucus production (Biggerstaff et al., 2017; Pineda et al., 2017), amongst others, while the main passive responses are functional morphology (Schönberg, 2021) and structural adaptations (Bell et al., 2002; Bell, 2004; Bannister et al., 2012; Bell et al., 2015). Sponge functional morphology is a particularly valuable characteristic to examine during ecological surveys, due to its capacity to serve as a key indicator of prevailing environmental conditions, particularly sedimentation regimes (Battershill & Bergquist, 1990; Bell et al., 2015). With the increasing frequency and severity of weather events amplifying coastal sedimentation concerns (IPCC, 2023; Noll & Andrews, 2023), sponges present an excellent avenue for ongoing monitoring to inform management strategies aimed at reducing the effects of a changing marine climate and enhancing resilience of important subtidal reef systems.

3.1.3 Heat stress

Sponges, as a diverse group of organisms, exhibit varying degrees of resilience to temperature fluctuations. While ocean temperatures have been rising slowly but surely (IPCC, 2023), the increasing frequency and intensity of marine heatwaves poses an immediate and severe threat to TME sponges (Frölicher et al., 2018; Bell et al., 2023). Sponge communities worldwide have been recorded exhibiting signs of heat stress (López-Legentil et al., 2008; Garrabou et al., 2022). Bell et al. (2023) notably provided the first published record in New Zealand of large-scale necrosis and bleaching of sponges in response to a marine heatwave. Furthermore, their research suggested that the devastating effects observed on these sponge communities only represented a fraction of the true extent of damage caused by marine heatwaves in New Zealand (Bell et al., 2023). Their research highlights the potential unseen damage that heat stress has inflicted on sponge communities not only in New Zealand but globally, emphasising the urgency of this research.

3.1.4 Food limitation

The ecological impact of food limitation on the distribution and abundance patterns within sponge communities has been a source of debate in scientific literature, particularly concerning its significance compared to the influence of predation (see Pawlik et al., 2018). Harris (2022) drew attention to the fact that while these debates have focused on tropical ecosystems (e.g., Lesser, 2006; Lesser & Slattery, 2013; Pawlik et al., 2015), a combination of research from New Zealand suggests that food limitation plays a significant role in structuring temperate sponge assemblages (Perea-Blázquez et al., 2012a, 2012b, 2013). Further research in New Zealand by Harris (2022) concluded that food limitation is likely to be a primary driver of abundance in temperate sponge reef communities. This underscores the importance of taking food limitation into consideration when seeking to understand patterns in sponge communities.

3.1.5 Aims

The aim of this chapter is to investigate key environmental stressors and their potential impacts on Motiti's mesophotic sponge communities. To comprehensively address this inquiry, analysis is structured around the following three research questions:

(1) Are there any effects of environmental variables on assemblage complexity, sponge cover, or sponge necrosis?

(2) Is variation in sediment cover explained by any environmental variables?

(3) Does sponge morphological dominance vary between depths or reefs? If so, is this difference explained by any of the observed environmental variables?

3.2 Methods

The footage collected and analysed in this chapter is the same as that collected in chapter two. To avoid repetition, please refer to Chapter Two for field collection methods.

This chapter is constructed in a 'nested' manner, examining the most characterising/consistent habitats on boulder tops and relatively flat reef platforms, rather than the edges of the reef to ensure that like is compared with like, i.e., so that tops of boulders and extreme habitats at reef edges are not compared as the same. Sediment deposition has a greater impact on flat spaces so this habitat shows the true extent of sedimentation stress, whereas sloping areas can have completely different communities and be less influenced by increased sediment level (Figure 36) (Battershill, 1987). There are other habitat types around these reefs such as large boulder fields, cliff faces, cobbles and sand flats around reef edges which are also important and warrant further study (Figure 37). But for the scope of this study, we are focusing on the relatively flat, rocky habitat areas of each reef.

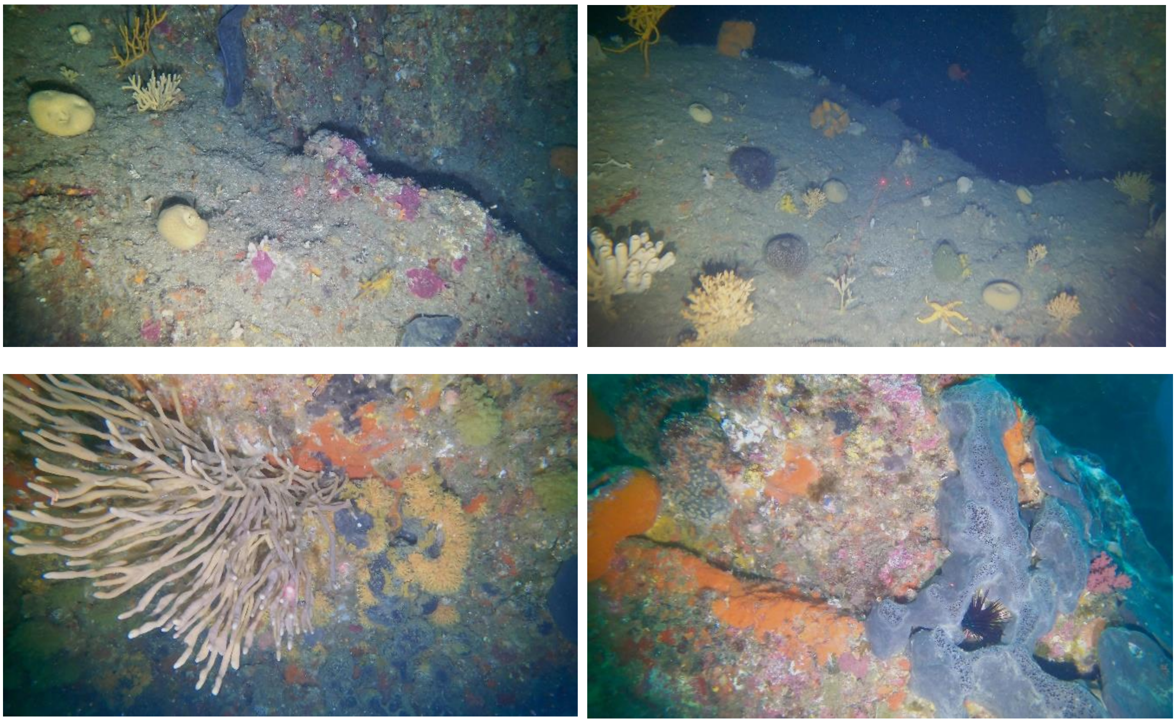


Figure 36. Example photos from Motuhaku Reef and showing how sedimentation levels and communities can differ between flat (top row) and sloping (bottom row) habitats.

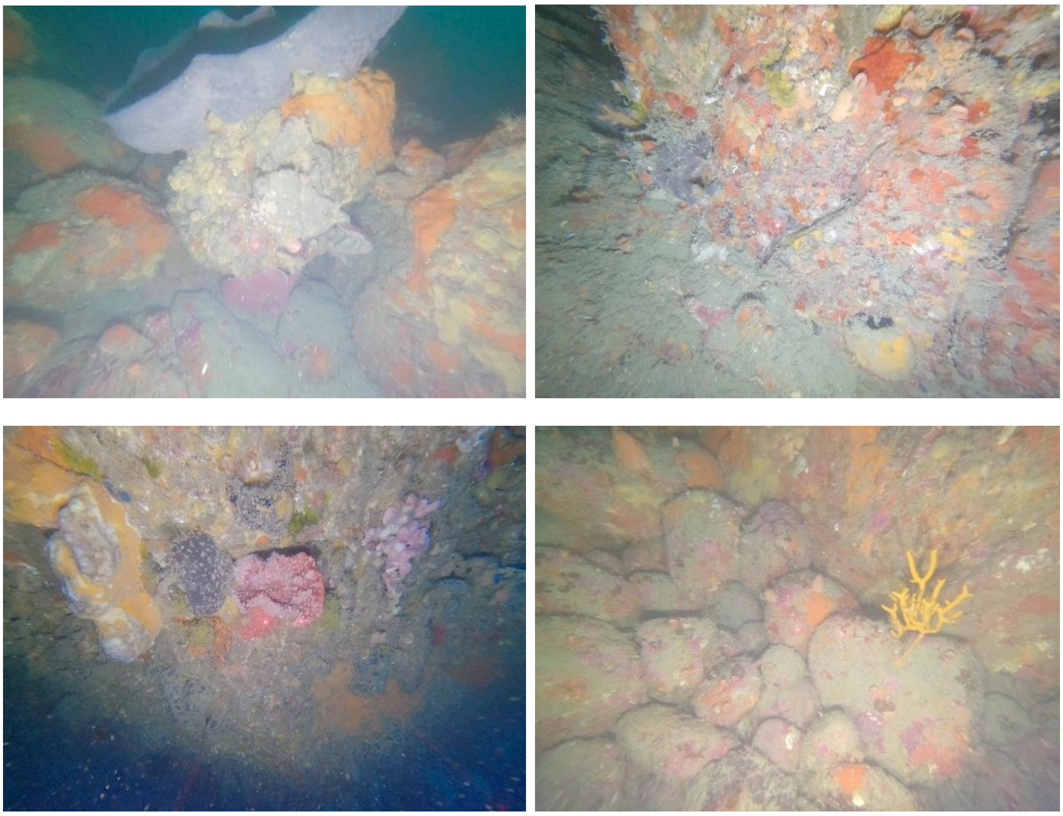


Figure 37. Other habitats present around the Motiti Island mesophotic reefs include large boulder fields (top left), cliff faces (top right, bottom left), and cobbles (bottom right).

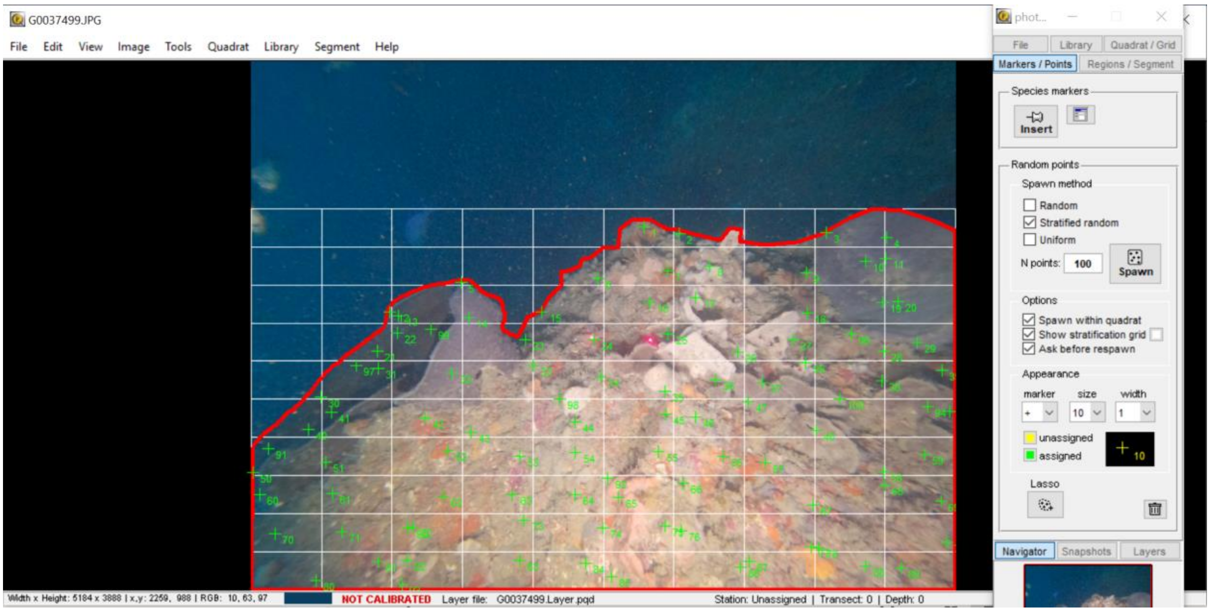
3.2.1 Image post-processing

From the high-quality photos identified in Chapter Two, a subset was created which only included images where the majority of reef pictured was the top of a boulder or a relatively flat reef surface. A maximum of ten images were analysed for each transect. Image sets for each transect were narrowed down where needed, by first prioritising images that were least blurry (mindful of fine sediment in the water column and on many surfaces), then most perpendicular to the substrate, and finally selecting ten from the resulting group using a random number generator. The number of suitable images per transect varied so some had fewer than ten images. Minor adjustments were made to the brightness, clarity, and saturation of images to aid analysis.

3.2.2 Percentage cover

Percentage cover was analysed using photoQuad (Trygonis & Sini, 2012). The broad categories identified were sponge, crustose coralline algae (CCA), bare substrate and other organisms. Bare substrate was used as a proxy for sedimentation level and includes areas of reef where there may be small organisms present, such as bryozoans, but they appear as bare substrate because they are smothered in a layer of fine deposited sediment. Bare substrate cover can be seen as a proxy for the level of sediment deposition because deposited sediment smothers benthic communities and as little as 10 mg cm^{-2} can exclude sponge larval recruitment (Abdul Wahab et al., 2019). In line with previous research on sponge reef ecology in NZ (Harris, 2022), the sponge category was further broken down into twelve morphological sub-categories. Sub-categories were based on recent literature by Schönberg (2021): encrusting, creeping, simple-massive, ball, composite-massive, fistular, tabular, cup, tube-like, simple-erect, two-dimensionally erect, and erect-branching in three dimensions. However, it is important to note that creeping sponges were likely underestimated as it was difficult to decipher between creeping and encrusting sponges at the scale and quality of these images (high water column turbidity). Also, any areas where other small organisms may have been present but were covered in sediment were categorised as bare substrate. This is because it was impossible to tell what may be hidden beneath smothering sediment, even if some ‘fuzziness’ could be seen that would indicate their presence.

Due to the difficulties with camera angle discussed in Chapter Two, analysis was restricted to only the immediate field of view where sponges were considered discernible in high enough detail for taxonomic identification. To achieve this, photo quadrats were manually drawn in photoQuad to only include reef area in the immediate field of view where organisms were most clearly discernible, ensuring that random points only fell within the target (Figure 38). Stratified random point sampling was employed to reduce clustering and under-sampling, while still minimising problems associated with parallax error as the whole area was not sampled (Harris et al., 2021). In photoQuad, stratified random sampling creates a grid over the quadrat area and distributes points randomly within each grid cell (Figure 38).



Spawn method
☐ Random
☑ Stratified random
☐ Uniform
N points: 100
Spawn

Options
☑ Spawn within quadrat
☑ Show stratification grid
☑ Ask before respawn

Appearance
marker: + size: 10 width: 1
unassigned
assigned
Lasso

Width x Height: 5184 x 3888 | x,y: 2259, 988 | RGB: 10, 63, 97 NOT CALIBRATED Layer file: G0037499.Layer.pqd Station: Unassigned | Transect: 0 | Depth: 0

Figure 38. Example of manually drawn transect (red line) including only the reef area in the immediate field of view where organisms are most clearly discernible. The grid is laid overtop in white with points (green crosses) randomly distributed within each grid cell.

The number of points used per photo quadrat to determine percentage cover in sponge communities varies drastically throughout the literature (Powell et al., 2010; Berman, 2012; Biggerstaff et al., 2017; Harris, 2022). This is because a crucial factor in survey design is choosing the Optimal Point Count (OPC), which is the minimum number of points required to ensure an accurate representation of the true coverage is given by the estimated percentage cover measurement taken (Pante & Dustan, 2012). The OPC for this study was calculated by testing a random image from each reef with incrementally greater numbers of points (10, 20, 40, 60, 80, 100, and 120) until the percentage cover curve reached a relative plateau for most groups, similar to a species accumulation curve: 100 points were deemed sufficient to represent the optimal coverage across most categories (Appendix F).

3.2.3 Assemblage complexity

Assemblage complexity was based on sponge morphological structure, which has been suggested to make an important contribution to habitat complexity in TMEs (Harris et al., 2021). Sponge morphological complexity was scored using the qualitative index created by Harris (2022) but adapted to recent morphological terminology used in Schönberg (2021) (Table 6). The overall assemblage complexity of each quadrat was calculated by multiplying the percentage cover of each morphology by their respective complexity scores, then taking the sum of the resulting scores.

Table 6. Sponge morphological complexity index, originally created by Harris (2022) but updated to recent morphological terminology by Schönberg (2021).

MORPHOLOGY	**COMPLEXITY RANK**	**COMPLEXITY SCORE**
Crust	Low	1
Creeping	Low	2
Ball	Low	2
Fistular	Low	2
Tabular	Medium	3
Cup	Medium	3
Simple-massive	Medium	3
Composite-massive	Medium	3
Fan, palmate or vertical mesh	Medium	3
Simple-erect	High	4
Tubes, amphoras	High	4
Erect-branching in 3 dimensions	High	5

3.2.4 Sponge stress

Recent research in New Zealand has highlighted the stress sponges are facing from rising temperatures, in particular marine heat waves (Bell et al., 2023). The Motiti Island archipelago is no exception in this regard. Through the ROV footage, stressed sponges were evident by their white patches (Figure 39). This was recorded as presence/absence ‘necrosis’ data based on whether white necrotic sponge tissue was visible in any given photo quadrat.

Figure 39. Example of visible necrotic tissue on an *Ecionemia alata* sponge seen on a mesophotic reef in the Motiti Island archipelago.

3.2.5 Rugosity

A qualitative visual index was created to describe variation in rugosity between photo quadrats within relatively the flat habitats analysed across Te Poroiti, Nukutai and Motuhaku reefs (Figure 40). Example photos for each level of rugosity can be seen in Appendix G.

LOW RUGOSITY ⟷ HIGH RUGOSITY

1	2	3	4	5
Flat, minimal surface variation	Some variation in surface but still all flat	Moderate surface variation, some sloping within quadrat	Moderate surface variation, some steep slopes within quadrat	Deeply dissected, highly variable surface

Figure 40. Qualitative visual index used to describe variation in rugosity between photo quadrats within relatively flat habitats across Te Poroiti, Nukutai and Motuhaku reefs.

3.2.6 Statistical analysis

Data analysis was carried out in R Studio (R Core Team, 2022) using a total of eight measured variables (Table 7). All Linear Mixed Effect (LME) models and Generalised Linear

Mixed Models (GLMM) used the R package “lme4” (Bates et al., 2015), while post-hoc Tukey’s tests for these models used the R package “emmeans” (Lenth, 2023). Again, aspect was not detected to have any correlation with dependant variables, likely due to the prevailing ocean current swinging in opposite directions between summer and winter (Montaño et al., 2023), and was therefore removed from statistical analyses.

Table 7. Measured variables analysed in this chapter, grouped by environmental and biological variables.

Environmental variables	**Biological variables**
Depth (m)	Assemblage complexity (qualitative value)
Bare substrate cover (%)	Sponge cover (%)
Reef (Te Poroiti, Nukutai and Motuhaku)	Necrosis (presence/absence [0,1])
Rugosity (index 1-5)	Sponge morphological coverage (%) x 12 morphological categories

(1) Do environmental variables affect sponge cover, assemblage complexity, or sponge necrosis?

To test for variation in sponge cover amongst reefs, depths and levels of rugosity, data were analysed using an LME model with a Gaussian error distribution. ‘Transect’, nested within ‘reef’, was taken as a random effect to best model the spatial dependency that may naturally occur with geographical proximity of photo quadrats within a transect, and transects within a reef. This spatial dependence is the reason why an LME model was employed rather than an analysis of covariance model (ANCOVA). Sponge cover was logit transformed for these proportional data to approximately satisfy the assumptions of linear models, while retaining interpretability and sensible predicted values (Warton & Hui, 2011). Diagnostic plots found that the data met the assumptions of normality, homoscedasticity and linearity (Appendix H: Figure 1) and assumptions of the LME model were met (Appendix H: Figure 2). A Tukey’s Test using Satterthwaite’s method was then used to examine which ‘reefs’ and ‘rugosities’ were significantly different (or otherwise) with regard to sponge cover.

To test for variation in sponge assemblage complexity between reefs, depths and levels of rugosity, data were analysed following the same procedure as above, the only difference being that complexity data was not required to be transformed. Diagnostic plots found that the data met the assumptions of normality, homoscedasticity and linearity as well as the assumptions of the LME model (Appendix I: Figures 1 & 2, respectively). Backward selection using *p*-values removed insignificant interactions and predictor variables to achieve the minimum adequate model.

Analysis of sponge necrosis was handled differently because it was recorded as binary presence/absence data. To test for variation in the probability of visible sponge necrosis in any given photo quadrat between reefs, depth, coverage of bare substrate and levels of rugosity, a GLMM with a binomial error distribution was employed. 'Transect', nested within 'reef', was included as a random effect to account for spatial dependency between photo quadrats within each transect. Interactions were removed to allow a non-singular model fit (Barr et al., 2013). Diagnostic plots using the R package "DHARMa" (Hartig, 2022) showed no over- or underdispersion in the model, and assumptions were satisfied (Appendix J: Figure 1).

(2) Is variation in bare substrate cover explained by any environmental variables?

To test for variation in bare substrate cover between reefs, depths and levels of rugosity, bare substrate percentage cover data were logit transformed and analysed following the same procedure as for sponge cover. Diagnostic plots found that the data met the assumptions of normality, homoscedasticity and linearity as well as the assumptions of the LME model (Appendix K: Figures 1 & 2, respectively).

(3) How does the morphological composition of sponge assemblages vary across reefs and depths?

To test for variation in the morphological composition of sponge assemblages between reefs and depths, as well as whether any of the observed environmental variables were good predictors of this variance, data were analysed using the 'manyglm' function in the R package "mvabund" (Wang et al., 2012). The manyglm function approaches multivariate abundance data by fitting a single GLM to each response variable (in this case each morphology), then resamples to test for significant community or morphology level responses to the predictor variables. In doing so, power is improved across a range of morphological categories with differing variances, as well as including an assumption of a mean-variance relationship (Appendix L: Figure 1). This is not accounted for in common alternative multivariate analyses such as PERMANOVA (Wang et al., 2012). Backward selection to identify the minimum adequate model was carried out using *p*-values.

A boral (Bayesian Ordination and Regression Analysis) latent variable ordination was used to visualise sponge assemblage morphological composition using the R package “boral”, version 2.0 (Hui, 2016, 2021). Due to the strong mean-variance relationship present (Appendix L: Figure 1), a Bayesian approach is preferred over distance-based analyses (e.g., NMDS, PCA), and also because it has greater power to detect differences in multivariate responses (i.e., species or morphological categories) with low variance (Warton et al., 2012; Hui, 2016; Osgood et al., 2019). Two latent variables as well as the three significant explanatory variables from the manyglm model were used, with a fixed row effect to control for site abundance and instead focus on composition. Both the manyglm model and boral ordination used negative binomial error distributions, which diagnostic plots found to be plausible and thus satisfied the assumptions of the models (Appendix L: Figures 2 & 3, respectively).

3.3 Results

In this section, the results of our study are presented sequentially following the three-part structure of this chapter’s research questions, with the main aim of addressing key stressors and their impacts on the mesophotic sponge communities of the Motiti archipelago.

3.3.1 Biophysical drivers

(1) How do environmental variables affect sponge cover, assemblage complexity, or sponge necrosis?

1a. Sponge cover

There was a significant difference in average sponge cover amongst reefs and levels of rugosity within reef systems (LME, $F = 5.29$, $p < 0.01$, df = 107.58, and $F = 7.4$, $p < 0.01$, df = 10.46, respectively) (Table 8). Therefore, we can accept with 99% confidence that reef and rugosity both influence sponge cover. Pairwise comparisons of the means revealed significant differences between Te Poroiti and Motuhaku (*t* ratio = -3.8, $p < 0.01$) as well as between rugosity levels 3 and 5 (*t* ratio = -4.19, $p < 0.01$) (Table 9). From looking at the plot below, we can see that overall sponge cover was higher on Te Poroiti compared to Motuhaku and higher at rugosity level 5 compared to 3 (Figure 41). But when rugosity is analysed separately at the level of ‘reef’, a trend seems to emerge whereby sponge cover generally increases as rugosity increases, but only at Motuhaku and Nukutai Reefs (Figure 41). Lower levels of rugosity appear to be having the greatest influence on the average observed sponge cover across reefs (Figure 41). Note that rugosity level 1 was not observed across all depths, which although a natural aspect of the reef, may impact average trends.

Table 8. Analysis of variance table with Satterthwaite's method for the LME model with Gaussian error distribution, where the predictor variables are reef and rugosity (index 1-5), and the response variable is sponge cover (%, logit transformed). Significant *p*-values are shown in bold.

	Sum of Squares	*Mean Squares*	*df*	*F-value*	*p-value*
Rugosity	8.5	2.12	107.58	5.29	**<0.01**
Reef	5.94	2.97	10.46	7.4	**<0.01**

Table 9. Tukey's pairwise tests using Satterthwaite's method for the three sampled reefs and levels of rugosity (index 1-5), where reef and rugosity are predictors and sponge cover (%, logit transformed) is the response. Significant *p*-values are shown in bold.

	Pairwise comparison	*Estimate*	*Std. Error*	*df*	*t ratio*	*p-value*
Reef	Motuhaku - Nukutai	-0.23	0.19	9.9	-1.21	0.48
	Motuhaku - Te Poroiti	-0.7	0.19	11	-3.8	**<0.01**
	Nukutai - Te Poroiti	-0.47	0.19	10.4	-2.45	0.08
Rugosity	Rug 1 – Rug 2	-0.34	0.34	110.8	-0.99	0.86
	Rug 1 – Rug 3	-0.2	0.32	110.8	-0.63	0.97
	Rug 1 – Rug 4	-0.53	0.33	109.9	-1.61	0.5
	Rug 1 – Rug 5	-0.86	0.32	102.2	-2.68	0.06
	Rug 2 – Rug 3	0.14	0.21	110.2	0.64	0.97
	Rug 2 – Rug 4	-0.19	0.22	110.3	-0.87	0.91
	Rug 2 – Rug 5	-0.52	0.21	96.2	-2.47	0.11
	Rug 3 – Rug 4	-0.34	0.17	106	-1.93	0.31
	Rug 3 – Rug 5	-0.66	0.16	109.8	-4.19	**<0.01**
	Rug 4 – Rug 5	-0.33	0.17	110.8	-1.98	0.28

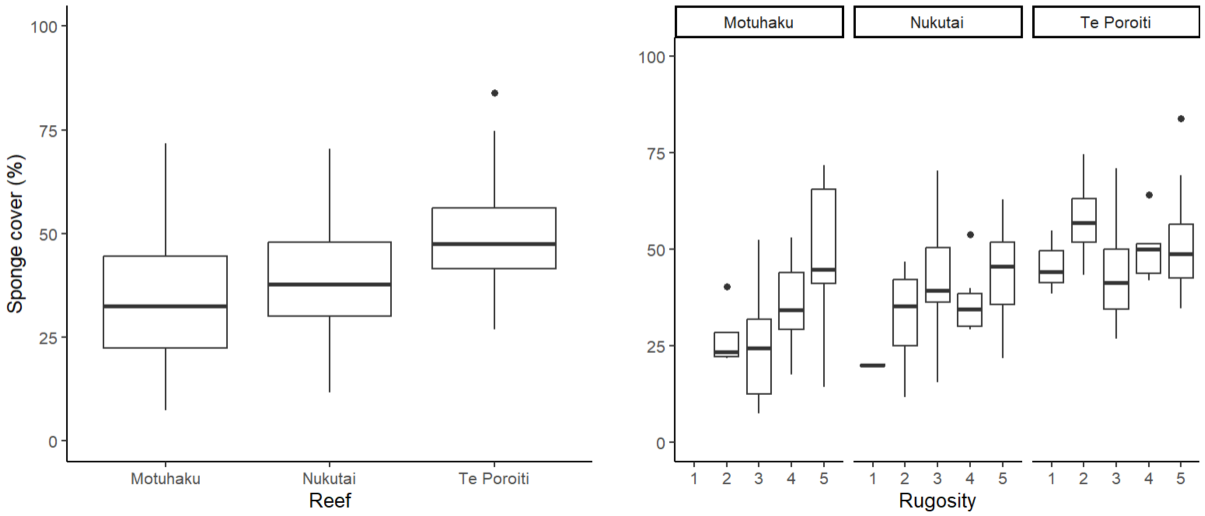


Figure 41. Left: Overall sponge cover (%) across Motuhaku, Nukutai and Te Poroiti reefs. Right: Sponge cover at different levels of rugosity (index 1-5) across the three surveyed reefs (Motuhaku, Nukutai and Te Poroiti). The lower and upper box boundaries show the 25th and 75th percentiles, respectively, black dots identify outlier data points, the line inside the box shows the median, and the upper and lower whiskers show the minimum and maximum.

1b. Assemblage complexity

The LME model showed that there is a significant difference in average sponge assemblage morphological complexity amongst the three reefs sampled ($F = 7.49$, $p < 0.01$, df = 11.93) (Table 10). Therefore, we can accept that assemblage complexity is influenced by reef with 99% confidence. Pairwise comparisons of the means revealed significant differences between Te Poroiti compared to Motuhaku and to Nukutai (t ratio = -3.57, $p < 0.05$, and t ratio = -3.12, $p < 0.05$, respectively) (Table 11). This tells us that the sponge assemblage complexity on Te Poroiti Reef was, on average, greater than that at Motuhaku and Nukutai Reefs at the time of sampling (Figure 42). When data were analysed separately across levels of rugosity, a similar though somewhat weaker trend emerged as was seen in sponge cover, whereby complexity generally increases as rugosity increases, except at Te Poroiti (Figure 43). Again, note that rugosity level 1 was not observed across all depths and reefs which may impact average trends (Figure 43).

Table 10. Analysis of variance table with Satterthwaite's method for the LME model with Gaussian error distribution, where the predictor variable is reef and the response variable is sponge assemblage complexity (qualitative value). Significant *p*-value is shown in bold.

	Sum of Squares	*Mean Squares*	*df*	*F-value*	*p-value*
Reef	25307	12653	11.93	7.49	**<0.01**

Table 11. Tukey's pairwise tests using Satterthwaite's method for the three sampled reefs and levels of rugosity (index 1-5), where reef and rugosity are predictors and sponge assemblage complexity (qualitative value) is the response. Significant *p*-values are shown in bold.

	Pairwise comparison	*Estimate*	*Std. Error*	*df*	*t ratio*	*p-value*
Reef	Motuhaku - Nukutai	-2.47	9.53	11.5	-0.26	0.96
	Motuhaku - Te Poroiti	-33.22	9.31	11.9	-3.57	**0.01**
	Nukutai - Te Poroiti	-30.75	9.89	12.4	-3.12	**0.02**

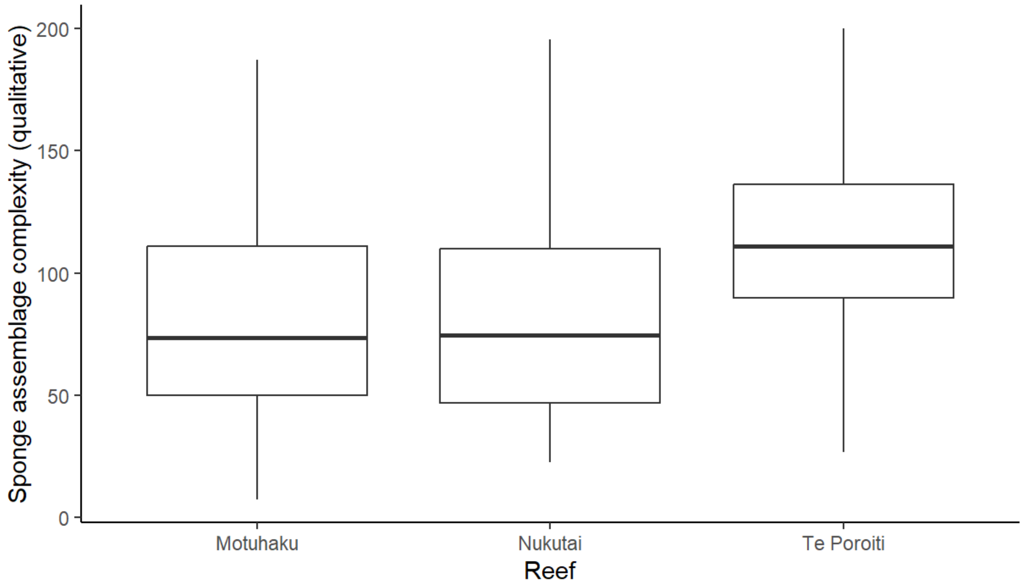


Figure 42. The effect of the three reefs sampled (Motuhaku, Nukutai and Te Poroiti) on sponge assemblage complexity (qualitative value). The lower and upper box boundaries show the 25th and 75th percentiles, respectively, the line inside the box shows the median, and the upper and lower whiskers show the minimum and maximum.

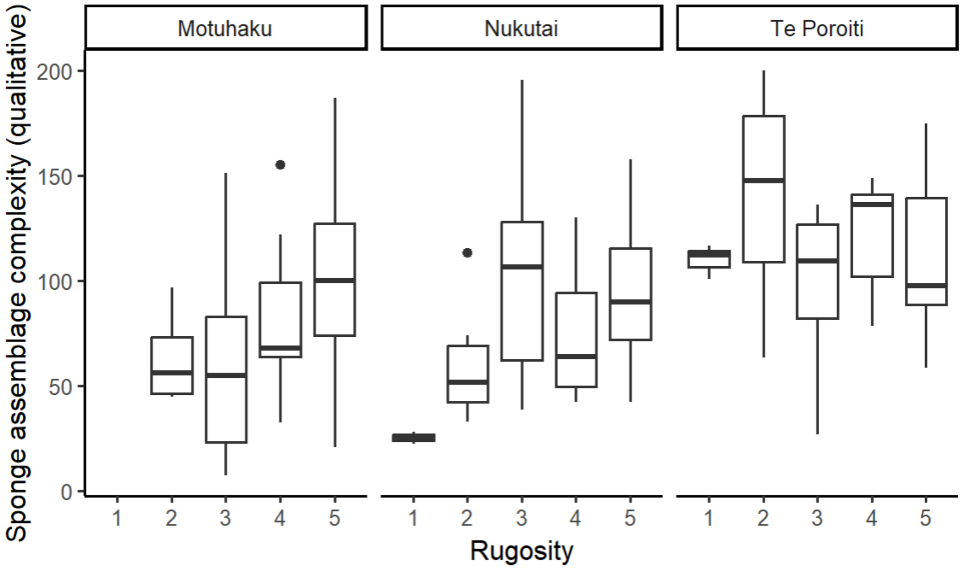


Figure 43. Sponge assemblage complexity (qualitative value) at different levels of rugosity (index 1-5) across the three surveyed reefs (Motuhaku, Nukutai and Te Poroiti). The lower and upper box boundaries show the 25th and 75th percentiles, respectively, black dots identify outlier data points, the line inside the box shows the median, and the upper and lower whiskers show the minimum and maximum.

1c. Sponge necrosis

On average, there were no significant differences in the probability of seeing sponge necrosis amongst reefs, depths, coverage of bare substrate or levels of rugosity (*p* >0.05 for all, df = 2, 1 and 4, respectively) (Appendix J: Table 1). Probabilities ranged widely at each reef, with the median relatively low across all reefs at approximately 10-20%, and the higher end of the range (within 95% confidence interval) reaching up to around 80% likelihood of seeing necrosis in a given photo quadrat (Figure 44). This means that at the time of sampling there was generally a low chance of seeing clearly visible signs of necrosis in a given photo quadrat at any of the three surveyed reefs (Figure 44). ‘Reef’ is the only predictor variable visualised due to the benefit of having a baseline record of sponge necrosis seen at these reefs for future research.

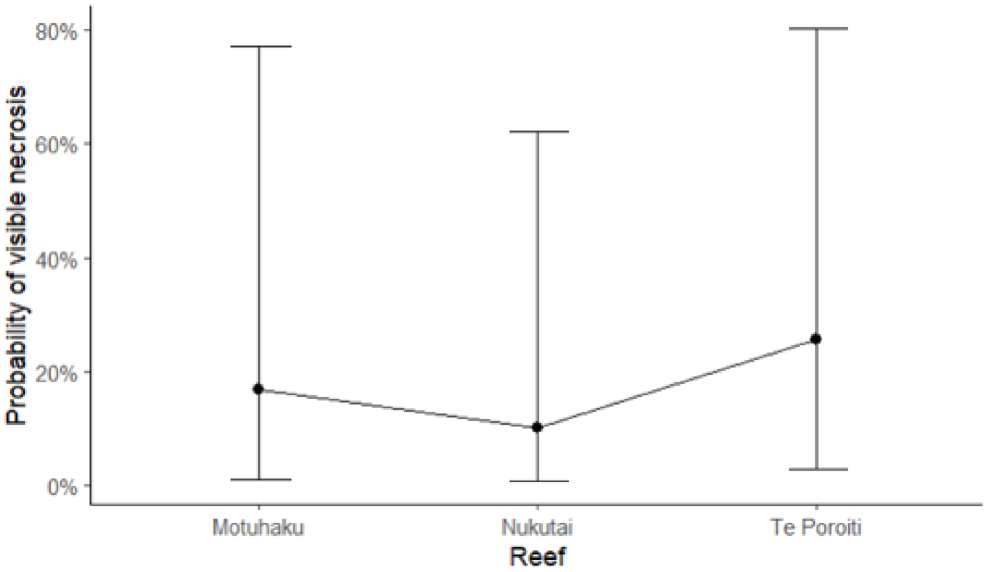


Figure 44. Non-significant difference (p >0.05) in the probability of visible necrosis (%) in a given photo quadrat across Motuhaku, Nukutai and Te Poroiti reefs. Dots show medians, lower and upper line bars show 95% confidence intervals, and the connecting lines aid in visualising the non-significant difference in probabilities between reefs.

3.3.2 Unoccupied space

(2) Is variation in bare substrate cover explained by any environmental variable?

A significant difference in average bare substrate cover was found amongst reefs, depths and levels of rugosity (LME, $F = 4.96$, $p < 0.05$, df = 12.15, and $F = 62.48$, $p < 0.01$, df = 42.83, and $F = 2.73$, $p < 0.05$, df = 105.84, respectively) (Table 12). Therefore, we can accept with 95% confidence that factors 'reef' and 'rugosity' both influence bare substrate cover, as well as 'depth' with 99% confidence. Pairwise comparisons of the means for 'reef' and 'rugosity' revealed significant differences between Motuhaku and Nukutai (t ratio = -2.6, $p < 0.05$) but potentially no significant differences between levels of 'rugosity' (Table 13). This is likely because Tukey's tests are slightly more conservative, which has left the comparison between rugosity levels 3 and 5 sitting on the edge of the 95% (i.e., <0.05) 'cutoff' limit for p-values (t ratio = 2.77, $p = 0.05$) (Table 13). The strong positive relationship between 'depth' and bare substrate cover is apparent, but bare substrate cover appeared to increase with depth slightly faster at Nukutai (Figure 45). We can also see that overall bare substrate cover was higher on Motuhaku Reef compared to Nukutai (Figure 45). Visualising the data also revealed a trend whereby bare substrate cover generally decreased as rugosity increased, except at Nukutai (Figure 45). It is interesting that no significant differences were found between the lowest and highest levels of rugosity when this trend is evident. However, it is only obvious at Te Poroiti and Motuhaku, but not at Nukutai, which is likely the reason why the means (i.e., averaged over all reefs for each level of rugosity) were not found to be different in the pairwise comparisons. Note here again though that ‘rugosity’ level 1 was not observed across all depths, which although a natural aspect of the reef, may have impacted average trends.

Table 12. Analysis of variance table with Satterthwaite's method for the LME model with Gaussian error distribution, where the predictor variables are reef, depth and rugosity (index 1-5), and the response variable is bare substrate cover (%, logit transformed). Significant *p*-values are shown in bold.

	Sum of Squares	*Mean Squares*	*df*	*F-value*	*p-value*
Reef	2.56	1.28	12.15	4.06	**<0.05**
Depth	19.67	19.67	42.83	62.48	**<0.01**
Rugosity	3.44	0.86	105.84	2.73	**<0.05**

Table 13. Tukey's pairwise tests using Satterthwaite's method for the three sampled reefs and rugosity (index 1-5), where reef, rugosity and depth (m) are the predictors and bare substrate cover (%, logit transformed) is the response. Significant *p*-values are shown in bold.

	Pairwise comparison	*Estimate*	*Std. Error*	*df*	*t ratio*	*p-value*
Reef	Motuhaku - Nukutai	-0.56	0.22	17.32	-2.6	**<0.05**
	Motuhaku - Te Poroiti	-0.17	0.2	15.12	-0.89	0.65
	Nukutai - Te Poroiti	0.39	0.17	9.62	2.32	0.1
Rugosity	Rug 1 – Rug 2	0.2	0.3	110	0.65	0.97
	Rug 1 – Rug 3	0.22	0.28	109.6	0.78	0.94
	Rug 1 – Rug 4	0.34	0.3	109.1	1.14	0.78
	Rug 1 – Rug 5	0.62	0.29	99.5	2.15	0.21
	Rug 2 – Rug 3	0.03	0.19	108.7	0.14	1
	Rug 2 – Rug 4	0.14	0.2	109.8	0.71	0.95
	Rug 2 – Rug 5	0.42	0.19	93.5	2.21	0.18
	Rug 3 – Rug 4	0.12	0.15	107.6	0.75	0.94
	Rug 3 – Rug 5	0.4	0.14	102	2.77	0.05
	Rug 4 – Rug 5	0.28	0.15	110	1.92	0.31

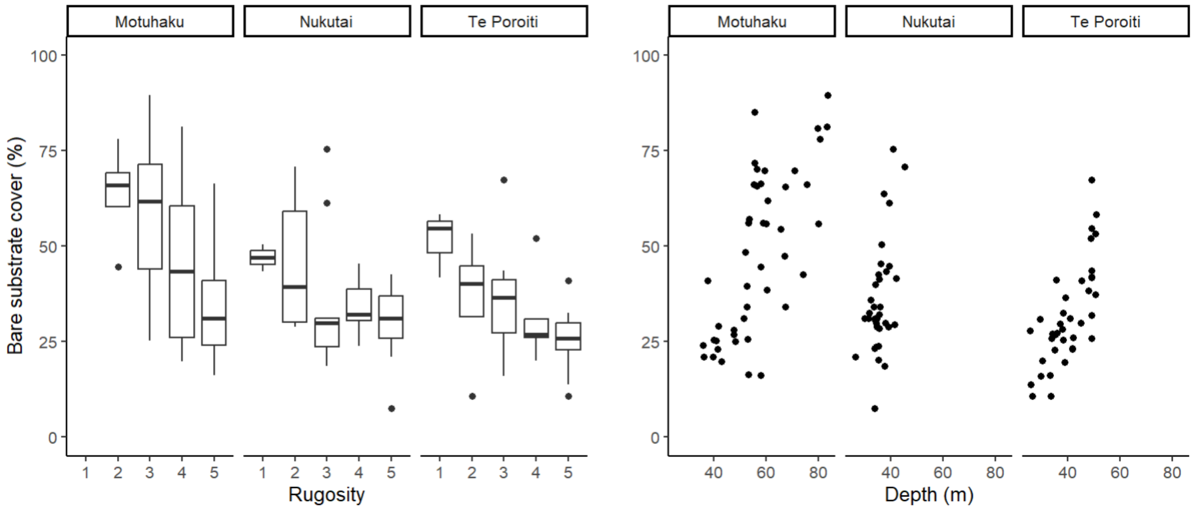


Figure 45. Left: The significant effect (*p* <0.05) of different levels of rugosity (index 1-5) on bare substrate cover (%) in a given quadrat across the three surveyed reefs (Motuhaku, Nukutai and Te Poroiti). The lower and upper box boundaries show the 25th and 75th percentiles, respectively, black dots show the outliers (data points), the line inside the box shows the median, and the upper and lower whiskers show the minimum and maximum. Right: The significant relationship (*p* <0.01) between depth (m) and bare substrate cover in a given quadrat across the three surveyed reefs. Dots show the data points.

3.3.3 Sponge functional morphology

(3) How does the morphological composition of sponge assemblages vary across reefs and depths?

Sponge communities when characterised by their morphological diversity varied significantly across different reefs, depths, and levels of bare substrate (GLM, LRT = 82, *p* <0.01, LRT = 30, *p* <0.01, and LRT = 53, *p* = 0.001, respectively) on the mesophotic reefs of the Motiti Island archipelago (Table 14). To examine this further and to examine which morphologies are responsible for driving observed differences in community structure, univariate tests were run for each separate morphology while taking into account the correlation between the response variables. After adjusting for multiple testing and removing the ‘fistular’ response due to it having less than three observations (Warton, 2022), the measured environmental predictor variables were found to have effects only on certain morphologies within the observed sponge communities. Also, depth on its own was no longer a significant predictor of morphological community composition but was important within its interaction with reef (Table 14).

Table 14. Summary of manyglm model with negative binomial error distribution where the predictor variable is 'reef' and the response variables are the 11 categories of sponge morphology (% cover). *P*-values were calculated using 999 iterations via PIT-trap resampling. Significant *p*-values are shown in bold.

Multivariate test:	**Res. df**		**Df. diff**		**Dev(LRT)**		***p*(Dev)**	
Intercept	117							
Reef	115		2		77.65		**0.001**	
Depth	114		1		27.65		**0.007**	
Bare substrate	113		1		52.72		**0.001**	
Reef : Depth	111		2		55.73		**0.002**	
Univariate tests:	**Ball**		**Composite-massive**		**Creeping**		**Encrusting**	
	Dev(LRT)	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**
Reef	1.72	0.85	1.63	0.85	3.22	0.76	4.02	0.66
Depth	0.09	0.86	0.51	0.86	5.05	0.24	3.43	0.41
Bare	1.73	0.77	2.23	0.73	0.62	0.92	9.14	**0.048**
Reef : Depth	3.78	0.65	1.1	0.92	4.19	0.64	4.3	0.64
	Cup		**Erect-branching**		**2D-erect**		**Simple-erect**	
	Dev(LRT)	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**
Reef	7.4	0.19	5.61	0.43	4.22	0.67	1.89	0.85
Depth	2.41	0.58	1.44	0.72	3.55	0.41	1.92	0.71
Bare	28.14	**0.001**	0.15	0.94	2.17	0.73	1.48	0.77
Reef : Depth	2.24	0.83	2.43	0.83	17.58	**0.008**	14.21	**0.02**
	Simple-massive		**Tabular**		**Tube-like**			
	Dev(LRT)	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**	**Dev(LRT)**	***p*(Dev)**		

Reef	2.08	0.85	9.85	0.07	36.03	**0.001**
Depth	1.57	0.72	0.39	0.86	7.29	0.09
Bare	0.002	0.97	6.76	0.12	0.3	0.94
Reef : Depth	0.94	0.92	3.78	0.65	1.17	0.92

The morphologies that seem to be significantly affected by certain measured environmental variables are the ones driving the differences seen in community composition. Cup and encrusting sponge average abundances both declined as bare substrate coverage increased (LRT = 9, $p < 0.05$ and LRT = 28, $p < 0.01$, respectively) (Table 14 & Figure 46). The relative abundance of tube-like sponges varied significantly across reefs, generally covering more substrate on Motuhaku Reef (LRT = 36, $p < 0.01$) (Table 14 & Figure 47). The interaction between reef and depth also significantly affected two-dimensionally erect and simple-erect sponges (LRT = 18, $p < 0.01$ and LRT = 14, $p < 0.05$, respectively), meaning that while these two erect sponge morphologies vary significantly across depths, the relationship depends on their location (i.e., reef) and vice versa (Table 14 & Figure 48).

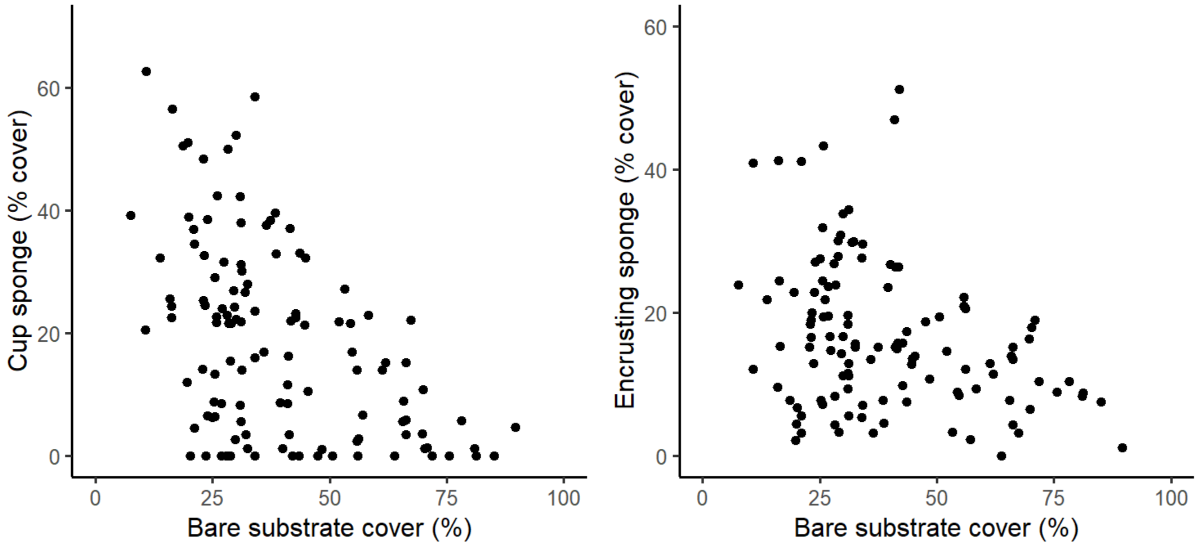


Figure 46. The significant relationship between bare substrate cover (%) and average abundance (%) of cup and encrusting sponges (left, $p < 0.01$ and right, $p < 0.05$, respectively). Dots show the data points.

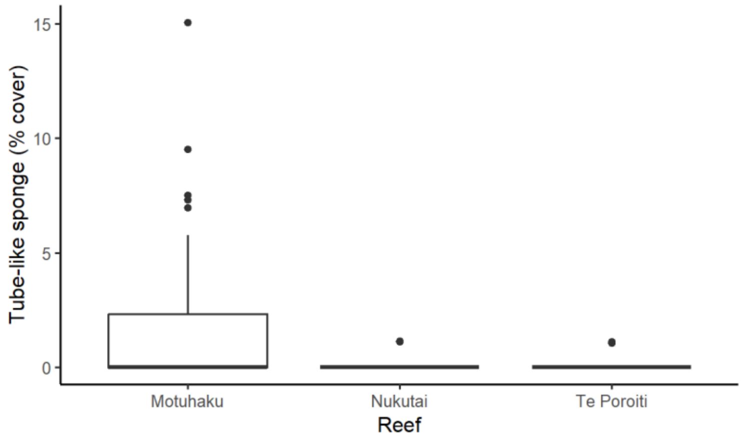


Figure 47. The significant difference in abundance of tube-like sponges (% cover) amongst the three reefs sampled (Motuhaku, Nukutai and Te Poroiti). The lower and upper box boundaries show the 25th and 75th percentiles, respectively, the line inside the box shows the median, and the upper and lower whiskers show the minimum and maximum.

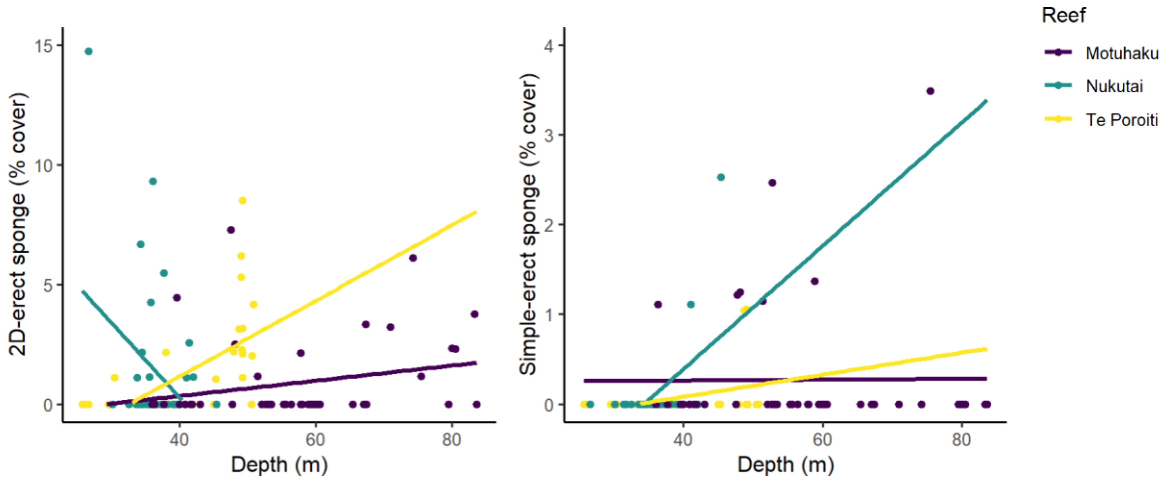
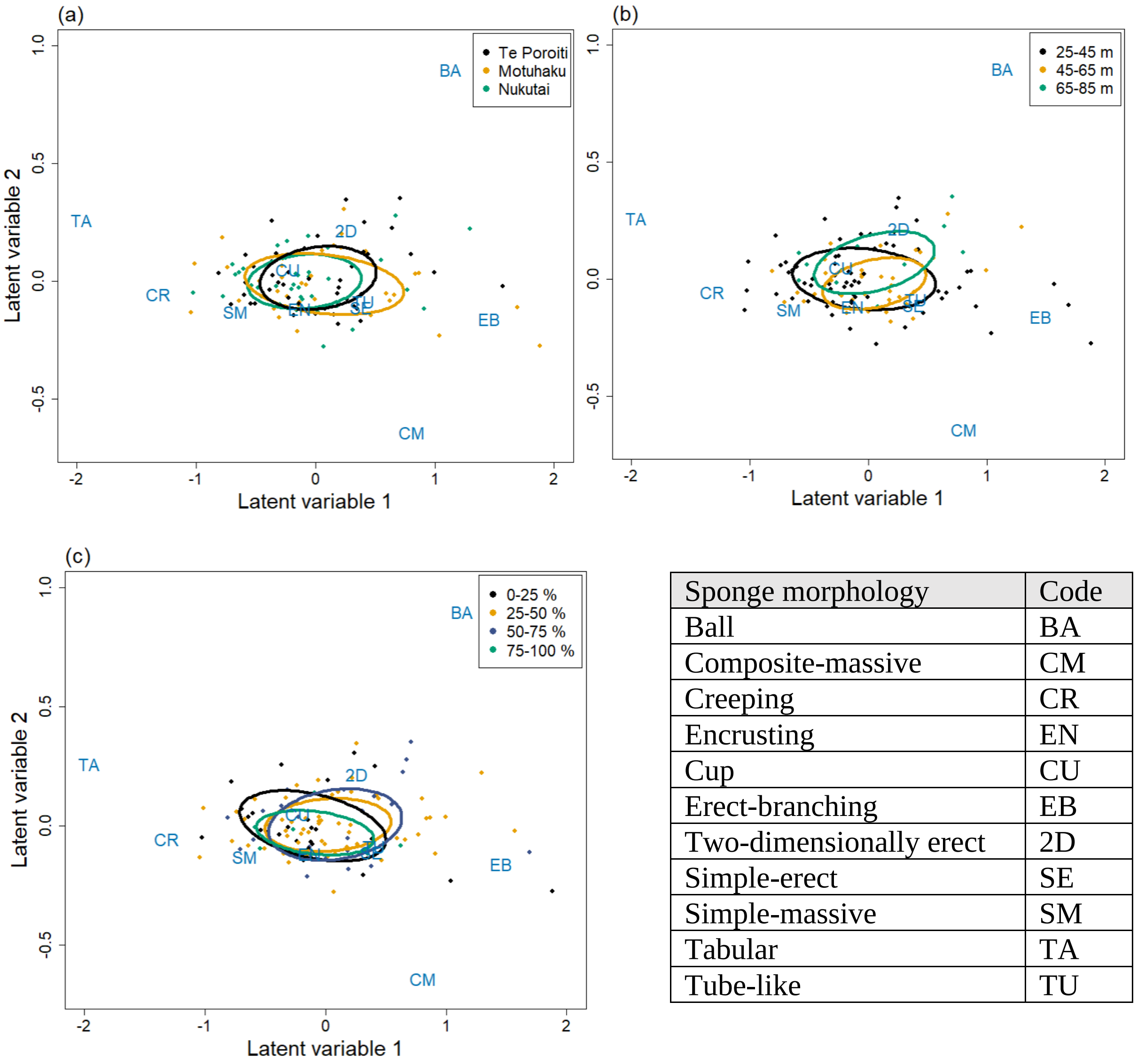


Figure 48. The significant interaction between depth (m) and average cover (%) of two-dimensionally erect sponges and simple-erect sponges (left, *p* <0.01 and right, *p* <0.05, respectively). Note that this figure is to aid in visualising the different slopes, not for showing the estimated values from the GLM model.

When the community data were visualised all together with boral ordination plots, morphological composition seemed relatively similar as can be seen by the overlap of ellipses (Figure 49). This is because the manyglm model picks up differences across a range of variances, while the ellipses in the boral plots only show 95% confidence intervals around the means, thus excluding outliers (Figure 49) (Wang et al., 2012; Warton et al., 2012). The manyglm model highlights that only a few certain morphologies seem to be driving the differences seen between communities at the time of sampling. The boral plots also reveal the tight grouping of simple-erect and tubular sponges, meaning these morphologies are positively correlated and are therefore likely to be found in the same habitats or under similar environmental conditions (Figure 49). However, is important to emphasise that not all erect sponges are similar in terms of their habitat requirements and ecology.



Sponge morphology	Code
Ball	BA
Composite-massive	CM
Creeping	CR
Encrusting	EN
Cup	CU
Erect-branching	EB
Two-dimensionally erect	2D
Simple-erect	SE
Simple-massive	SM
Tabular	TA
Tube-like	TU

Figure 49. Boral latent variable ordinations of the observed sponge communities, where the explanatory variable in (a) is reef, in (b) is depth (m) and in (c) is bare substrate cover (%). Points and ellipses are colour-coded by (a) reef, (b) depth group, and (c) level of bare substrate cover. Each point represents a photo quadrat while ellipses represent 95% confidence intervals around the mean composition for each (a) reef, (b) depth group, and (c) level of bare substrate cover. The position of two-letter morphology codes shows the relative values of each species' latent variable coefficients.

3.4 Discussion

3.4.1 Physical drivers of sponge communities in Motiti TME

3.4.1.1 Sponge abundance gradient

Sponges were found to be more prolific in abundance (i.e., overall sponge cover) on Te Poroiti Reef and significantly less so on Motuhaku Reef, suggesting the potential presence of a geographic gradient of increasing benthic biomass from East to West across the Motiti mesophotic reef system. Additionally, there was a positive influence of rugosity on sponge abundance, but this pattern was only evident at Nukutai and Motuhaku. In contrast, sponge abundance was relatively high across all levels of rugosity at Te Poroiti, which is likely the main reason why average abundance was greater there. Rugosity has long been known to influence benthic reef communities (Dunham et al., 2018; Mazzuco et al., 2020; Ventura et al., 2021), however the fact that its effect on sponge abundance seems to be strongest at Motuhaku, slightly weaker at Nukutai and non-existent at Te Poroiti tells us that another interaction is at play. This suggestion of a geographical gradient in sponge abundance, along with the influence of rugosity, may suggest heightened environmental stressors on the eastern side of Motiti Island (e.g., Motuhaku Reef). The increasing correlation between abundance and rugosity in the east hints at rugosity potentially providing refuge. This raises questions about whether environmental stress is more intense in the east or if sponge communities on the eastern reefs are simply more sensitive than those on the western reefs (e.g., Te Poroiti Reef). Although this is speculative, it warrants further investigation to understand the complex interactions occurring across local (<10 km) scales.

Further evidence of the presence of a range of ecological interactions is shown by the similarity (but not direct match) of the trends in sponge abundance and assemblage complexity. This is understandable as many inherently complex environmental and biological variables influence TME benthic communities, such as current exposure, competition for space, turbidity, sediment deposition, and trophic interactions, but only a few were measured in this study (Cárdenas et al., 2012; Schönberg, 2021; Bell et al., 2022). Harris (2022) suggested that food availability is a primary driver of patterns in abundance of New Zealand mesophotic sponge assemblages, which is likely to be an important contributing factor in this potential gradient of decreasing sponge abundance from East to West across the Motiti mesophotic reef system. However, it is expected that provision of refugia (i.e., the shelter provided by rugosity from sedimentation) is a much more important driver of sponge abundance on the Motiti mesophotic reefs than food availability, given the thorough mixing of currents in the coastal zone (Montaño et al., 2023). Although the scope of this Master's project limited the ability to investigate any differences in food availability amongst reefs, or other more complex variables, the gradients suggested by these findings warrants further research as it will have key implications for long term monitoring and management of the MNEMA.

3.4.1.2 Sponge complexity

Sponge assemblage morphological complexity reflects a combination of biophysical interactions which, in the case of Te Poroiti Reef, have created a variety of niches allowing this assemblage to grow with greater morphological complexity (Schönberg, 2021). Scientific literature has established the influence of sedimentation and food availability on sponge structural complexity, as greater complexity provides resilience against heavy sedimentation regimes and enhances particle capture efficiency, i.e., feeding (Hogg et al., 2010; Beazley et al., 2013; Bell et al., 2015; Bart et al., 2021). In slower currents, sponges tend to grow taller and in more elaborate configurations, as a balancing act is played out where extended sponges are more fragile but have the advantage of reaching further into the water column, allowing them to surpass the depleted boundary layer close to the substrate and maximise feeding and waste removal (Schönberg, 2021). While sedimentation is not likely the primary driver of increased morphological complexity at Te Poroiti, as indicated by similar levels of bare substrate cover at Motuhaku Reef, other factors come into play. Food availability, while potentially influential, may not play a major role in these well-mixed reef systems (Montaño et al., 2023). Food availability in part relies on nutrient influx carried by oceanic currents from freshwater sources, with diminishing influence farther from the shores of Tauranga and Motiti Island (Mc Cormack, 2021; Crawshaw, 2022). Slower currents, however, quite possibly represent a significant biophysical interaction contributing to the greater complexity observed at Te Poroiti. An eddy circulates on the Eastern side of Motiti Island during summer months (Figure 50) (Montaño et al., 2023). This reduced water velocity could allow the sponge community on Te Poroiti Reef to grow taller, thus enhancing structural complexity. Seasonal variations may also impact assemblage complexity, particularly considering that Te Poroiti is fully exposed to the westerly current during winter but slightly sheltered from the easterly current in the lee of Motiti Island during summer (Figure 50). The winter season brings increased turbidity, a deeper and well-mixed mixed layer, and distribution of particles further offshore driven by upwelling following Ekman transport dynamics in the BoP (Montaño et al., 2023). Considering the many biophysical interactions at play, it is likely that a balance exists among water quality, food availability, and current exposure in shaping the variation in sponge assemblage morphological complexity on the Motiti mesophotic reefs. More complex biophysical interactions are clearly working in conjunction with those already discussed from the investigation carried out in this study and require further research to disentangle.

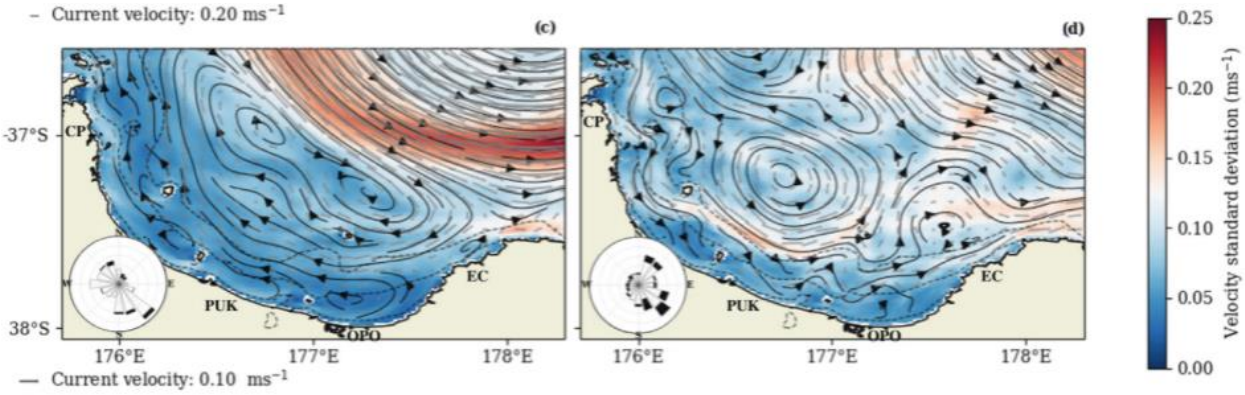


Figure 50. From Montaño et al. (2023): (c-d) Zoom in on the BoP showing the standard deviation velocity (m s^{-1}, colour map) over the first 10 m of the water column, corresponding to January (left) and July (right) (2003–2004). The windrose over the landmask corresponds to a point in the central region of the bay for each given period. The colour indicates the magnitude of the wind (■ > 10 m s−1 and □ < 10 m s−1). Mean streamlines (→), mean currents (→), and the 20, 65 and 200 m isobaths (- - -) are shown in both panels.

3.4.1.3 Sediment gradient

Sedimentation and fallout of 'marine snow' (sinking particles of decaying organic material) is a natural marine process and as such marine sponges will usually be exposed to some level of suspended and settling sediment (Alldredge & Silver, 1988; Airoldi, 2003; Turner, 2015). However, when sedimentation levels increase above natural levels as they have in the BoP (Crawshaw, 2022; Park et al., 2022), and increasingly around coastal regions globally (Herbert-Read et al., 2022; Cornwall et al., 2023), it can become a significant stressor for sponges and can have negative effects on sponge pumping activities, respiration, feeding, reproduction, growth and symbiotic relationships (as cited in Beets, 2017, p. 14). The strong trends this study uncovered between depth, rugosity and bare substrate cover align with oceanic physical processes, as sediment gets lifted into suspension by the wind-driven mixing closer to the surface but can fall out of suspension and smother greater extents of benthic substrate on deeper reef areas, especially where it accumulates on flat areas (i.e., low rugosity) (Airoldi, 2003). The variation in bare substrate cover amongst reefs is understandable as Motuhaku Reef extends deeper than the other two, therefore it will naturally have a greater average coverage of sediment as a result, given strong influence of depth on sediment cover shown. However, the rate of sediment cover increase was comparatively greater with depth and less uniform with rugosity at Nukutai Reef, pointing toward a general abiotic trend that is present at Motuhaku and Te Poroiti but for some reason is inhibited at Nukutai. Nukutai Reef is situated on the northern side of Motiti Island, whereas Te Poroiti and Motuhaku are both rocky pinnacles rising from depth. Its proximity to Motiti Reef offers some protection from water currents and therefore sedimentation, whereas the other two reefs are exposed to sediments being carried and deposited over the reef by currents from any direction. Even though Motiti Island itself is also a source of sediment, Crawshaw (2022) provides evidence that turbidity is lower at the northern end of the island which supports the suggestion of some sheltering dynamics occurring. Therefore, a natural trend in sediment deposition appears to be present on Motiti's TME, but it is not consistent across all reefs likely due to the influence of eddies and areas of slightly more protection, such as that given to Nukutai by Motiti Island. Our findings indicate that sedimentation stress is likely to be felt more acutely by deeper mesophotic reef benthic communities, which does not bode well for those extending deeper than were surveyed in this study. Again, more complex interactions are at play than were able to be measured within the scope of this project. Investigating these interactions further will enlighten predictions and enhance management of the MNEMA.

3.4.1.4 Limitations of 'snapshot' study

Considering the above, it is crucial to remember that sediment measure estimates from this study could be temporary given that the one-off ROV survey provides only a 'snapshot' in time, making it difficult to pin down causality. Heavy loads of sedimentation are often temporarily triggered by storm events, causing fluxes of land-runoff to flow through freshwater ways and out into the ocean (Hayward et al., 2006; Park et al., 2022). For example, from the 14th – 16th February 2023, Cyclone Gabrielle hit New Zealand causing floods to carry massive amounts of sediment from land to ocean, resulting in sediment plumes dissipating into the coastal waters of the BoP (Figure 51). Events such as these can confound ‘snapshot’ results. Having said that, heavy sedimentation was seen at Nukutai Reef recently in preliminary surveys by Donald (2021), substantiating the argument that heavy sediment deposition may be a consistent stressor for the Motiti Island reef communities. Further monitoring is needed to establish the ‘normal’ sediment load here, as well as how much and how often it fluctuates. Even so, observations so far suggest the Motiti mesophotic reef system is exposed to moderate sedimentation loads at the least, with fluxes of heavy sedimentation when extreme weather events occur.

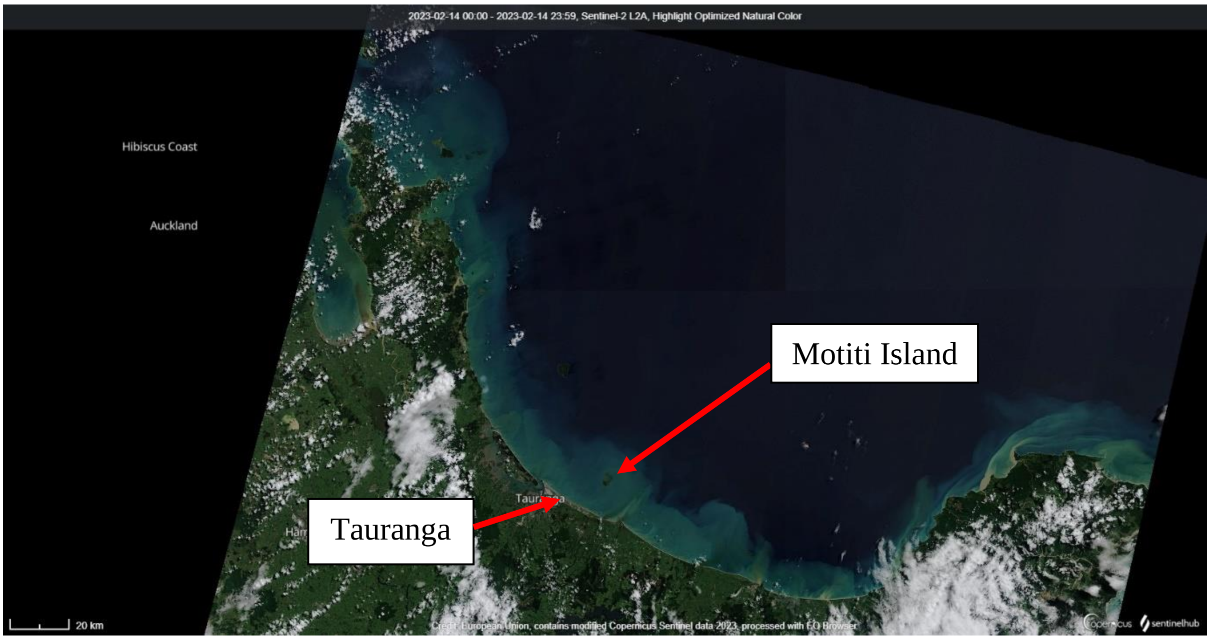


Figure 51. Satellite imagery from 14th February 2023 displaying far-reaching sediment plumes dissipating into the BoP, New Zealand during Cyclone Gabrielle.

3.4.2 Functional morphology

The variety or dominance of morphologies in sponge communities gives insight into the environmental conditions that a community is exposed to, especially regarding the sedimentation regime (Schönberg, 2021). Incorporating morphological analysis informs understanding of prevailing biophysical conditions permitting integration of multiple environmental drivers across a temporal scale. Morphological composition was relatively similar amongst reefs, depths and levels of bare substrate cover, with only a few certain morphologies driving any differences between them. The strong negative association of bare substrate cover on both encrusting and cup sponges is intuitive as more bare space naturally means less space for sponges to cover. And, conversely, less sponges potentially means more space that can be bare substrate. The key here is to understand what is causing the bare substrate cover; whether it be freshly vacated bare space due to fauna die-off and as yet unoccupied, or whether recruitment is not occurring in these bare substrate spaces for some reason. A fine sediment overlayer (a few mm) can inhibit settlement of sponge propagules (Battershill, 1987), so it is possible that if sediment deposition is smothering vacated substrate faster than sponge can recruit and grow, this would make it very difficult for sponge communities to recover after a die-off or disturbance event. In terms of the link between these specific morphologies and sedimentation, Schönberg (2021) explained that encrusting sponges on horizontal surfaces are not generally tolerant of heavy sedimentation. However, encrusting sponges don’t strictly signify low sedimentation environments, as thicker crusts (as was commonly seen in this study) with slightly convex form or raised papillae are slightly less vulnerable to sedimentation than thin crusts (Schönberg, 2021). Cup sponges are also known to generally not cope with high levels of sediment, but due to the organisation of exhalant pores on their upper and inhalant on their lower surface, they are able to wash away some sediment that falls into their cup and can therefore tolerate sedimentation to some degree (Bergquist, 1978; Pronzato, 1998; Schönberg, 2021; Swierts et al., 2018). Despite the general insights morphologies provide about environmental conditions, it is always crucial to consider that sponges can have species-specific physiological mechanisms to combat smothering, such as mucus production and hispidity (Bannister et al., 2012; Schönberg, 2015; Biggerstaff et al., 2017). However, if sediment deposition is occurring faster than sponge propagule settlement in vacated bare spaces, whether that be due to die-off or some other disturbance, then recruitment of new individuals into these communities could become limited to niches and slopes where minimal sediment deposition occurs.

3.4.2.1 Tube sponges

Tube sponges were found in greater relative abundance on Motuhaku Reef, which was the main driver of differences in community composition amongst reefs. One of these species, *Iophon laevistylus*, is usually found in clear water and does not survive for long if sedimentation events are frequent or persistent (Battershill et al., 2010). The presence of *I. laevistylus* on Motuhaku Reef thus indicates that conditions here were pristine at some point, which supports long term averages that show Motuhaku, the reef furthest from shore, as having the highest water clarity from 2002-2021 (Crawshaw, 2022). Now however, signs of severely degraded *I. laevistylus* further the hypothesis that water quality in Motiti’s TME is deteriorating rapidly and in recent times (Figure 52). We could be seeing a die-off where sensitive species have already mostly disappeared from the other two surveyed reefs (accounting for some of the observed bare space at least) but persisted longer here. Being large and easy to identify, *I. laevistylus* may only be one of many sponge species being similarly impacted by increasing environmental stressors, while smaller inconspicuous species could easily have been missed by our ROV footage. On the other hand, the greater abundance of *I. laevistylus* at Motuhaku Reef may mean they are able to better tolerate conditions at Motuhaku even though bare substrate cover measures indicate Motuhaku Reef is exposed to heavy sedimentation. Schönberg (2021) acknowledges that tube-like sponges are still a bit of an enigma in terms of their ecological role and how they inform on environmental conditions such as sedimentation regime. Again, investigation of other complex interactions and influences at play may disentangle some of the patterns seen in this study.

Figure 52. Deteriorating *Iophon laevistylus* showing clear tissue regression. Photo captured at 63 m depth on Motuhaku Reef, transect S04.

3.4.2.2 Erect sponges

Simple-erect and two-dimensionally erect sponges were also significant drivers of differences in community composition. In their case, they both generally increased with depth, although some significant variation was seen depending on the reef being looked at. Extending vertically up into the water column, this morphology leaves very little surface area for sediment to build up on and can tolerate high turbidity and greater sediment deposition (Bell et al., 2002, 2015; Schönberg, 2021). Environmental implications of simple-erect sponges are not well documented (Schönberg, 2021), but Bell et al. (2002) noted that branch reduction in erect sponges appeared to be induced by high sedimentation stress. When two-dimensionally erect sponges orientate perpendicular to the prevailing current, the microturbulence created enables optimised feeding efficiency and reduced sedimentation effects and in turn can be associated with strong bi- or uni-directional flow (McDonald et al., 2003). Inversely, when two-dimensionally erect sponges do not show organisation within the habitat, it usually means that multidirectional turbulence exists in their habitat (McDonald et al., 2003). Orientation within the Motiti mesophotic reef communities did not appear organised, suggesting multidirectional flow likely caused by the irregular reef topography. It is not clear why trends varied amongst reefs depending on depths in this case but, again, species-specific tolerance mechanisms likely have a part to play as not all erect sponges are made equal. Although *Callyspongia ramosa* and *Raspailia topsenti* are branching-erect sponges, not simple- or two-dimensionally erect, they make a good example of the importance of considering species-specificity. *C. ramosa* is a fast-growing sponge that can colonise a range of new surfaces, even anthropogenic ones such as shipwrecks (Battershill & Bergquist, 1990). Comparatively, *R. topsenti*, like many other Axinellids, is slower-growing and specialises in a distinctly defined habitat of a rock base with little to no coarse sand covering, not coping well in any fine sediment environments and requiring moderate current exposure (Battershill & Bergquist, 1990). However, given the broad basis that erect form sponges are the most resistant to sedimentation stress (Schönberg, 2021), the general increase of these morphologies with depth, depending on reef, supports the trend of increasingly heavy sediment deposition with depth.

3.4.2.3 Fistular sponges

A noteworthy aspect of the morphological community composition lies in the presence of fistular sponges. Although the fistular morphology was removed from the statistical model, as recommended by Warton (2022), its presence still provides valuable information. Fistular morphologies serve as a bioindicator of high sedimentation on these reefs (as cited in Schönberg, 2021, p. 10). Certain groups of fistular sponges, such as many

Heteroscleromorpha (Elliott & Leys, 2007; Musser et al., 2021), are recognised for their ability to expel sediments from their systems and surface through whole-body contraction, a process akin to ‘sneezing’ (Kornder et al., 2022). Active responses to sedimentation like ‘sneezing’, along with passive responses like their morphology (fistular oscula which project above sediment layers while their body remains partially buried underneath), enable them to inhabit environments where many other sponges would succumb to smothering (Schönberg, 2021). While acknowledging their presence is essential in painting the full picture, it was still important to exclude them from the model as their abundance was likely compromised due to most images being of inadequate proximity to the substrate or not of high enough quality to see them. Their underestimation means that this ‘snapshot’ survey may have missed key indicators of a shifting benthic community by being limited in image quality.

3.4.2.4 Morphological domination

Sponge communities on the surveyed Motiti Island mesophotic reefs were consistently dominated by cup and encrusting morphologies. While encrusting sponges can indicate strong, unpredictable currents, cup sponges generally cannot withstand strong currents, particularly the structurally tough *Ecionemia alata* species seen in this study (Schönberg, 2021). Based on this knowledge, the morphological composition of these communities illustrates low sedimentation rates with moderate current strong enough to re-suspend and wash some sediment off the benthos and thus sustain encrusting sponges (Schönberg, 2021). However, layers of fine deposited sediment seen in many of the cup sponges in this study showed the recent occurrence of a sedimentation event, which they appeared to be in the process of clearing, since these sponges did not appear to be visibly deteriorating (Figure 53). The heavy sedimentation seen in both this study and Donald (2021), combined with the presence of fistular sponges and the strong negative relationship between the dominant morphologies and bare substrate cover, suggests that the prevailing conditions on the Motiti mesophotic reefs leading up to August 2022 were moderate-high sedimentation with fluxes of heavier loads after storms. This contrast is interesting and emphasises the importance of observing more than one aspect of benthic reef communities before drawing conclusions.

Figure 53. Layers of fine deposited sediment present in massive cup sponges, both *Ecionemia alata*. Left: Photo captured on Motuhaku Reef at 62.2 m depth, transect S04. Right: Photo captured on Te Poroiti Reef at 38.8 m depth, transect B06.

3.4.2.5 Responses to sedimentation stress

Although observation of passive responses to the environment such as functional morphology can be used to provide generalised conclusions on the level of sedimentation stress a reef is exposed to (Schönberg, 2021), the highly species-specific nature of active responses highlighted by the literature (see Bell et al., 2015) emphasises the importance of identifying sponges at species level in order to be able to draw reliable conclusions of prevailing reef conditions. Given the importance of considering thickness and species-specific coping mechanisms (Schönberg, 2021), the contradicting indications discussed above point towards the common red encrusting Poecilosclerid species seen in this study possessing efficient physiological mechanisms to cope with high levels of sedimentation. On the other hand, we cannot rule out that these encrusting sponges are under not stress. Signs of stress could easily have gone unnoticed due to the ‘snapshot’ nature of this study and the image quality limiting detailed observations of encrusting species. Further research is urgently needed to determine this, for which I recommend sampling key species from these reefs and conducting the same surveys as Beets (2017) to better understand how community composition may change with predicted increases in anthropogenic stressors (Holbrook et al., 2020; Wernberg et al., 2021).

3.4.3 Heatwave events and sponge necrosis

3.4.3.1 Necrosis due to MHW

Seeing necrosis in the mesophotic zone of the Motiti reefs shows the significant extent of abnormally warm events occurring in New Zealand. New Zealand's coastal waters have experienced unprecedented marine heat waves in recent years, the most recent of which lasted for 381 consecutive days and saw departures of up to 2.5°C from the 25-year average in the BoP (Figure 54) (Bell et al., 2023; Moana Project, 2023; Salinger et al., 2023). The consistent presence of necrotic sponges across reefs, depths and levels of rugosity shows that some major event had recently occurred. Interestingly, the main species seen to have necrotic tissue were all large, tough sponges with many spicules (subclass Heteroscleromorpha, orders Haplosclerida and Tetractinellida). The species that commonly had visible necrotic tissue in the images analysed in this chapter were *Petrosia* (*Petrosia*) cf. *hebes*, *Ecionemia alata*, *Stelletta conulosa*, *Stelletta crater*, *Stelletta maori*, *Geodia regina*, as well as two unidentified morphotypes; 'orange meandering sponge', and 'black and orange cup'.

These findings are similar to a recent study in New Zealand by Bell et al., (2023) where the *E. alata* and *S. conulosa* were the most impacted species but tissue necrosis, regression and bleaching were also seen on some other species, including *Stelletta* spp. Their research is one of only three published studies on bleaching and necrosis in temperate marine sponges, one reporting necrosis of similar species as in this study (Ayling, 1981), and the other having focused purely on one cup morphospecies (Perkins et al., 2022). In both recent articles (Perkins et al., 2022 and Bell et al., 2023) causality was assumed to be heat stress due to correlation of necrosis and bleaching with marine heat waves (Perkins et al., 2022; Bell et al., 2023). Ayling (1981) reported the necrosis as outbreaks of bacterial/fungal disease, her description matching our observations exactly, but she noted that these outbreaks occurred during warm summer months when water temperature was warmer than 17ºC. Records of sea surface temperature show a severe marine heatwave occurred in the BoP in 2022, which was both long (>100 days) and strong (red shading in Figure 54) (Moana Project, 2023). The timing of the 2022 marine heatwave coincides with the footage collected during this study, supporting recent studies in pointing towards heat stress as the culprit for large-scale sponge necrosis in New Zealand (Perkins et al., 2022; Bell et al., 2023). The full extent of damage caused to the Motiti TME is likely yet unseen due to the marine heatwave beginning months before and lasting until months after this footage was taken (Figure 54).

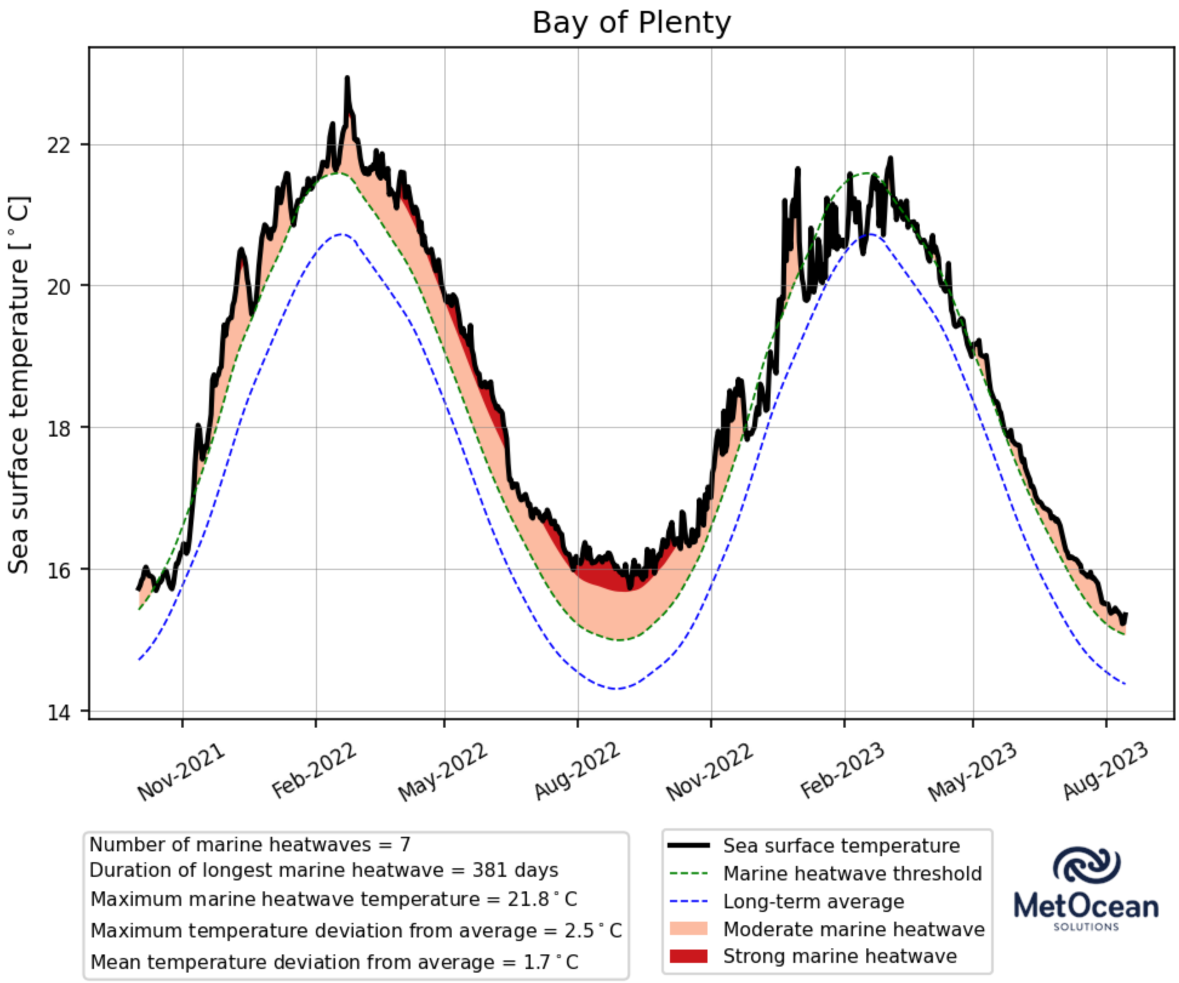


Figure 54. Historical sea surface temperatures in the BoP, provided by Moana Project (2023).

3.4.3.2 Tail end of a marine heatwave

This study has picked up on the ‘coping window’ of the 2022 marine heatwave (Spillman et al., 2021), as although necrosis is present, there are signs of some sponges healing (Figure 55). Healing sponges were identified to show an estimated 2-3 months of recovery, which can be seen in our photos as evidence of the pinacoderm coming back where hard lines are present between white tissue and pigmented tissue, rather than fuzzy, sloughing white tissue which shows the process of deterioration (Figure 55: A-B) (Ayling, 1981; Cerrano et al., 2001). Necrosis recovery in winter was likely aided by strong prevailing westerly winds, which drive cold water upwelling in the BoP (Black et al., 2006). Although some species showed signs of healing, the literature undeniably states that recovering sponges are a minority; once necrosis is visible on a sponge, it almost always results in death (López-

Legentil et al., 2008; Bennett et al., 2017; Thomsen et al., 2019; Perkins et al., 2022; Bell et al., 2023). In addition, extreme cases of sponge necrosis seen in Bell et al., (2023) were referred to as looking like they were “melting” off the reef, which is exactly as they appear in some cases in the Motiti Island TME where they are still in the process of deteriorating (Figure 55: C-D), and further confirms the extreme impact of this marine heat wave on Motiti’s mesophotic reefs. This leads to the hypothesis that there could be many more sponges under stress that were not seen in this study due to the ‘snapshot’ nature of this survey missing any previous or further damage. Sponges may have disappeared rapidly during the ‘reaction window’ of the marine heat wave (Spillman et al., 2021) and therefore the full impacts on benthic communities were missed by the time ROV surveys were undertaken. Rare images from ROV footage collected during this study support this hypothesis, where tissue regression can be seen on extremely degraded sponges which are not included in the aforementioned list of common, tough species (Figures 52 & 55: E). Image quality limited observations to relatively big organisms, often missing inconspicuous and smaller individuals. Therefore, the necrosis reported in this study is a conservative estimate which is concerning given its prevalence and also given the depths to which these effects are now evident. If the ‘rapid sponge death’ hypothesis is true, then the full implications of marine heat waves for TMEs in New Zealand, now and in the future, are unimaginably concerning.

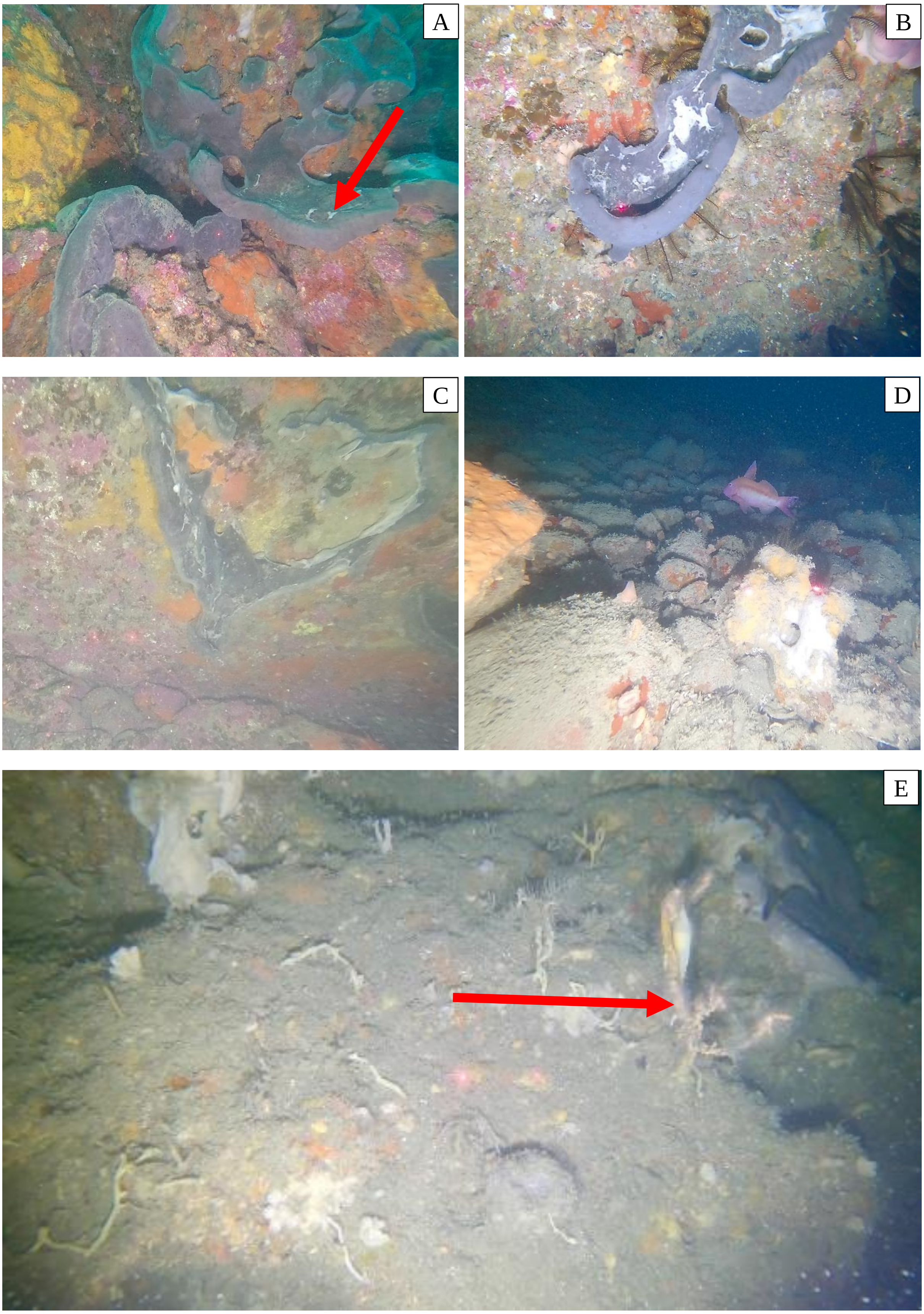


Figure 55. A-E, Necrotic sponges: A, Recovering *Ecionemia alata* sponge, showing hard lines between white tissue and pigmented pinacoderm. Photo captured at 26.6 m depth on Te

Poroiti Reef, transect B01 South; B, Deteriorating *E. alata*, edges of white tissue are fuzzy and can be seen sloughing off. Photo captured at 38.8 m depth on Motuhaku Reef, transect S02; C, “Melting” *E. alata* photographed at 39 m depth on Te Poroiti Reef, transect B04; D, unidentified sponge photographed at 54 m depth on Te Poroiti Reef, transect B01 North; E, Deteriorating erect-branching sponge showing tissue regression at 83.3 m depth on Motuhaku Reef, transect S02.

3.4.3.3 Necrosis may explain bare white CCA patches

Another hypothesis intuitively follows the former, whereby bleached white patches of CCA and dead barnacles represent bare scars in spaces that have been vacated by dead sponges (Figure 56). Observations by Ayling (1981) support this, as she described patches of bare substrate left behind after sponges became necrotic and fully disintegrated due to warm water-related fungal infection/disease, the description of which matches this study. Sponges often recruit into the microhabitats formed by CCA and barnacles (Ayling, 1980; Yu et al., 2020), and these patches were seen in places that would constitute optimum reef topography for sponges to grow on (Battershill & Bergquist, 1990). If this is the case, then to some degree the area of sediment smothered bare substrate over the rock reefs here may also reflect severe sponge necrosis in places where scars are older and so sediment has had time to settle.

One would at first assume that more damage is yet to occur in these benthic communities since the marine heat wave continued for months after this ROV footage was captured. However, it may be important to consider that although temperatures were still beyond the marine heat wave threshold (as indicated by the green dotted line in Figure 54), the lower temperatures of winter when this footage was captured would likely have provided some respite to sponge communities, allowing some individuals to start recovering from heat stress-caused necrosis before the recognised ‘recovery window’ (Spillman et al., 2021). Given that some necrotic sponges appear to be recovering from necrosis (Figure 55), combined with evidence of bare, bleached white CCA patches, it could be hypothesised that the worst has past and therefore not much evidence of badly affected sensitive sponge species (e.g., Figures 52 & 55) exists in this ‘snapshot’ study. This is conjecture but images do show preliminary evidence that warrants urgent further investigation due to the potential legacy damage to the ecosystem these bare scars could represent.

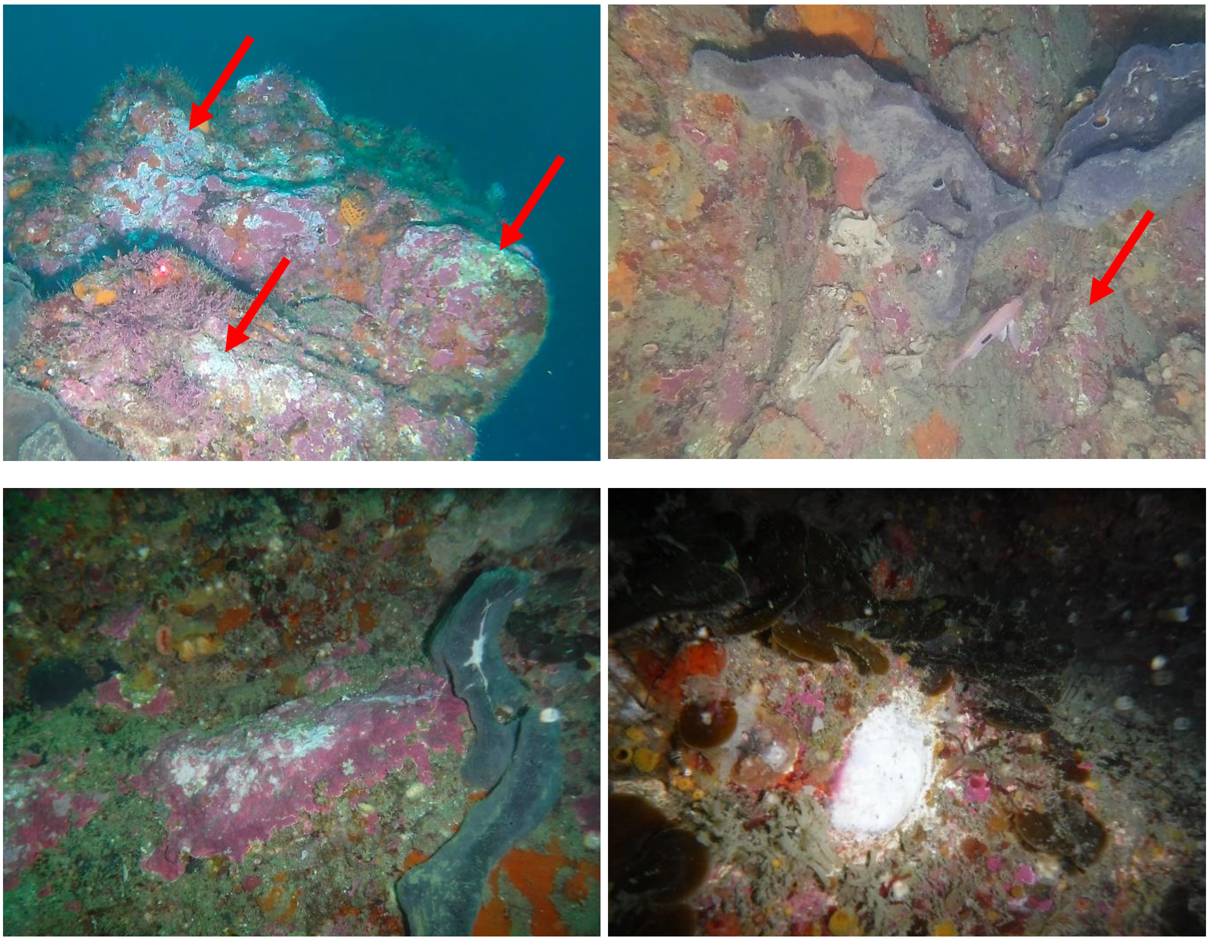


Figure 56. Bare, bleached white patches of CCA, hypothesised to represent bare scars vacated by dead sponges: Top left, photo captured at 33.9 m depth on Motuhaku Reef, transect S04; Top right, photo captured at 45.3 m depth on Te Poroiti Reef, transect B06; Bottom row, photos captured at approximately 20 m depth on Karewa Reef, during subsequent dives in August 2023.

3.4.3.4 Mesophotic zone not a refugia for temperate sponges

It is concerning that necrosis was consistently visible across all three reefs at all depths. Finding sponge necrosis reaching into the mesophotic zone is not unexpected, as Bell et al. (2023) observed bleached sponges down to 50-60 m and suggested they reach much deeper. However, many researchers have hypothesised that the mesophotic zone could serve as a refugia from rising heat stress with climate change (e.g., Idan et al., 2018; Raijman-Nagar et al., 2023) but this study supports those that point toward temperate marine sponges being climate change ‘losers’ (Perkins et al., 2022; Bell et al., 2023). Also, affected sponges observed by Bell et al. (2023) were found in relatively shallow, enclosed waters (Hauraki

Gulf and Fiordland) whereas the Motiti Island archipelago is open and exposed to all circulatory currents in the BoP. Clearly, the mesophotic zone is not exempt from the heavily felt impacts of rising temperatures, or at least the upper half as seen in this study. With the predicted increase in frequency and intensity of marine heatwaves, in addition to water temperature rising by an average of 0.4ºC per decade in the MNEMA (Crawshaw, 2022), it is possible that we will see a shift from cold-water to warmer-water benthic communities on the Motiti Island mesophotic reefs (Wernberg et al., 2016; Holbrook et al., 2020; Wernberg et al., 2021). Ultimately, the consequences are unknown, hence the need for further research and establishment of long-term monitoring.

3.4.4 Compounding stressors

Heat and sediment stress have a compounding effect on marine sponges (Scanes et al., 2018), even for tough, hardy species such as *Tethya burtoni* (Beets, 2017). The compounding effects of sedimentation putting pressure from the bottom-up and heat putting pressure from the top-down (spatially) may be ‘squeezing’ communities and potentially, in time, causing exclusion of impacted species and morphologies in these benthic assemblages (Wernberg et al., 2016). Currently sedimentation stress on the shallower sponge community is alleviated by the mixed layer washing sediment away, but clearly heat stress is also putting significant additional pressure on key species within the community. It is possible that we’re seeing a compositional shift in the Motiti mesophotic sponge communities, but only time, and further research, will tell.

3.5 Conclusions

The findings suggest this study has captured a snapshot of Motiti’s mesophotic reef system during an unstable time marked by shifts in benthic community composition under the intense pressure of escalating compounding stressors. Indications of previously pristine water quality and a lighter sedimentation regime contrasted with a combination of evidence pointing toward a prevailing moderate sedimentation regime with fluxes of heavy sedimentation following extreme weather events. This study was conducted in the middle of the 2022 BoP marine heatwave and captured large-scale sponge necrosis in the Motiti benthic TME. The full extent of damage was likely missed by this study, as the heatwave began months before and lasted until months after this footage was taken. The ‘snapshot’ scope of this Master’s project along with limited image quality makes it difficult to identify longer term implications, but the data certainly illustrate some complex and fast-changing dynamics within the Motiti reef archipelago. Potential gradients seen in overall sponge abundance and assemblage complexity may be linked to this possible stress-caused community shift or alternatively may be inherent processes of the Motiti reef system. However, the presence of slow-growing species typically characteristic of pristine environments (e.g., *Iophon laevistylus*), and the fact that we have observed them under severe stress, suggests these events are relatively recent (in the context of sponge-relevant time scales, i.e., decades), and implies that recovery could be exceedingly slow. Further research at these GPS recorded survey sites is urgently needed to capture the full picture and determine how other evident complex interactions are influencing this reef system, as well as how and to what extent the benthic community is changing over time. Placement of permanent quadrats at these sites is recommended for long term monitoring in addition to *ex situ* experimentation of compounding heat and sediment stressors on key sponge species characteristic of these reefs. This study provides conservative estimates from only a few easily observable environmental stressors, which emphasises the concern that these findings point toward TME sponges being climate change ‘losers’.

Chapter 4

General Discussion

4.1 Justification for the research

This study was motivated by the pressing challenges confronting marine ecosystems, primarily stemming from the effects of global warming (IPCC, 2023). In New Zealand, the consequences of these issues are becoming increasingly evident, marked by rising sea surface temperatures and the heightened occurrence and intensity of deeper water marine heatwaves (Bell et al., 2023; Moana Project, 2023). Additionally, escalating frequency and severity of weather events are exacerbating coastal sedimentation, which is already naturally high in New Zealand (Basher, 2013; Crawshaw, 2022; Park et al., 2022; Schiel & Battershill, 2023). Furthermore, the recent establishment of the Motiti Protection Areas (MPAs) added a critical impetus to this research. The mesophotic zone of these reefs, residing beyond depths accessible by SCUBA diving, came into focus following preliminary exploration by Donald (2021). This initial investigation highlighted the presence of vibrant sponge gardens within this previously unexplored habitat. Collectively, these factors underscored the necessity for establishing a foundational understanding of this ecosystem to support ongoing monitoring efforts. Thus, the overarching goal of this thesis was to create a baseline encompassing the diversity and current status of Motiti's mesophotic benthic communities. It also aimed to advance our comprehension of the environmental stressors and processes influencing this ecosystem, recognizing the crucial functional roles of sponges within the broader marine environment as outlined in Chapter One.

4.2 Sponge domination

The pivotal roles that sponges play in Temperate Mesophotic Ecosystems (TMEs) and the benefits they provide, as discussed in Chapter One, emphasise the critical significance of safeguarding and monitoring the mesophotic reefs surrounding Motiti Island. Footage collected by Remotely Operated Vehicle (ROV) revealed that the Motiti reefs are dominated by expansive sponge communities in the mesophotic zone, based on the observations reported here of Te Poroiti, Nukutai, and Motuhaku reefs. Given the dominance of these sponge communities combined with the high level of assemblage complexity seen consistently across all three reefs, this study supports previous research and further confirms that sponge communities play an important role in providing habitat complexity in TMEs (Harris et al., 2021).

As previously discussed, the habitat complexity that sponge gardens provide lays the foundation for a thriving and resilient ecosystem (Thrush et al., 2011; Idan et al., 2018; Harris et al., 2021). Sponge communities enhance local biodiversity and richness (McClintock et al., 2005; Bo et al., 2012), which is important for keeping the numerous popular dive sites here alive, as well as being a site of great cultural importance for local iwi (*Motiti Rohe Moana Trust v Bay of Plenty Regional Council*, [2020]). Additionally, they provide spawning and nursery grounds for many marine animals, including commercially important fish species (Battershill, 1987; Rossi, 2013; Paoli et al., 2017). The protection provided by the MPAs has the potential to create spillover effects, as similar protection areas elsewhere have done (Di Lorenzo et al., 2020). This allows for more sustainable and productive recreational fishing directly around Motiti Island and could have massive economic implications, potentially in the million-dollar range (Qu et al., 2021). Previous research has shown that small marine reserves in New Zealand benefit commercial fisheries by boosting fish stocks through recruitment effects (i.e., net export of larvae and juveniles) (Qu et al., 2021). Without sponges forming complex habitats, these reefs would likely be much more barren as it is too cold for reef building corals and too deep for domination by large kelp species (Beazley et al., 2013; Bell et al., 2022). Other animals and algae were present in this study’s surveys, such as crustose coralline algae (CCA), gorgonian corals, cup corals and bryozoans, but none of these were large or abundant enough at mesophotic depths to create habitat complexity comparable to the established sponge gardens.

4.3 Collective findings

When evaluating the collective findings of Chapters One and Two, patterns emerge that demonstrate species-specific responses among sponges and their varying sensitivities to compounding stressors. For example, a remnant tumbleweed sponge population was almost exclusively observed only at the deepest surveyed depths in stark contrast to their thriving presence in shallower habitats merely a year and a half prior to recording this ROV footage. The apparent retraction in their vertical distribution along with their overall decline in abundance and condition indicates that the tumbleweed sponge is more adversely affected by the top-down pressure of heat stress than the bottom-up pressure of sedimentation stress. In contrast, a more pronounced influence of sedimentation stress on encrusting sponge morphologies compared to heat stress is suggested by their decline as bare substrate coverage increased. The decline in abundance of cup sponges also correlated with increasing bare substrate coverage, and in addition they were the primary morphology that displayed obvious signs of necrosis in line with the 2022 Bay of Plenty (BoP) marine heat wave. This signifies the sensitivity of cup sponges to both sediment and heat stress. In contrast, tubular sponges such as *Iophon laevistylus* appear to be more affected by sedimentation, as indicated by their relatively greater abundance on Motuhaku Reef (highest water clarity in recent times (Crawshaw, 2022)), and by their known sensitivity to water quality (Battershill et al., 2010). Hence, while heat and sedimentation stress exert a compounding effect on sponges, their respective contributions appear to vary dynamically between species and morphologies (Scanes et al., 2018). What the effect of this top-down and bottom-up spatial ‘squeeze’ on benthic mesophotic communities may be regarding potential shifts in community composition, will depend on the relative strength and interplay between these compounding stressors. However, it is clear that this study has captured a snapshot during a period of significant stress, possibly mid-way through an event, whose impact on the Motiti mesophotic ecosystem urgently needs further investigation.

Another observation brought to light by the collective findings of this research is that sponge abundance was highest where diversity (average taxonomic distinctness (TD)) was lowest, and vice versa. Chapter Two illustrated higher sponge abundance and complexity on the western reefs (Te Poroiti), while Chapter Three revealed greater average TD on the eastern reefs (Motuhaku). As discussed earlier, there are indications that at some point Motuhaku Reef used to be a pristine environment with high water clarity, inhabited by sediment-sensitive species of which some still survive but were severely degraded at the time of surveying (see paragraph 3.4.2.1). In contrast, Te Poroiti exhibited characteristics of a more stress-tolerant assemblage, marked by the absence of sediment-sensitive species and greater structural complexity, possibly shaped under persisting suboptimal conditions. This might explain why Te Poroiti's sponge assemblage seems to have demonstrated greater resilience to the extreme weather event compared to the sponge community at Motuhaku Reef. At Motuhaku, some sediment-sensitive species (e.g., *Iophon laevistylus*) were degraded and bare substrate covered more reef area, hypothesized to represent bare spaces or ‘scars’ vacated by dead sponges (as described in paragraph 3.4.3.3).

Once again, these findings suggest that this study has captured a snapshot of the Motiti mesophotic reefs during a dynamic and unstable period, indicating a possible shift towards species assemblages more tolerant of environmental stressors, potentially following a spatial gradient from West to East. There appears to have been a significant change in sponge community composition between the drop camera survey in 2021 (Donald, 2021) and the ROV survey in 2022 (this study). If this shift is confirmed by future surveys, the pace of change is highly concerning considering that sponge communities are supposedly long-lived (Ayling, 1983; Teixidó et al., 2009; Bell et al., 2014). While speculative, these insights pave the way for further hypotheses which can be explored with subsequent research. They also highlight the importance of considering a variety of metrics when investigating community ecology.

4.4 Scope of natural environmental variability

With the mounting pressure of global warming and the subsequent imperative to mitigate the damage to our environment, it is crucial to ask the fundamental question: are these events that we are seeing the impacts of (in this case marine heatwaves and heavy sedimentation) still within the natural scope ‘expected’ over decadal periods? Within the context of New Zealand, sponge responses to sediment stress are important to understand due to the country’s natural susceptibility to high sedimentation arising from steep slopes, easily erodible rock, high rainfall and frequent storms (Basher 2013). Similarly, fluctuations in ocean temperature have naturally occurred throughout history (IPCC, 2023). While each of these stressors in isolation might fall within the natural scope, they are all occurring at the same time, all with increasing severity and for consistently longer periods, which magnifies their impact on marine ecosystems. Factors such as marine heat waves, and sedimentary plumes have a compounding effect on marine ecosystems (Beets, 2017; Scanes et al., 2018), including sponge communities as illustrated by this study. Moreover, the increasing frequency and intensity of marine heatwaves and extreme weather events leaves little room for doubt that these events now transcend the limits of natural variability (Wernberg et al., 2021; IPCC, 2023; Noll & Andrews, 2023).

4.5 Limitations of the study

It is crucial to remember that one-off surveys need to be treated with caution due to the ramifications of false conclusions, especially with the mounting pressure of climate change. These reefs were, at the time of surveying, still rich in biodiversity and taxonomic indices indicated that no serious degradation had been caused by anthropogenic stressors. Nevertheless, the combination of other results presented show evidence of complex changing dynamics and large-scale impacts of marine heatwaves in these mesophotic sponge assemblages. Especially at depths below the thermocline, these communities should theoretically be long-lived and relatively stable (Ayling, 1983; Teixidó et al., 2009; Bell et al., 2014).

Other constraints in the research methods that may have impacted the reliability of these findings were addressed within the scope of this study, as described in Chapters One and Two. The variety of metrics and analyses employed in this research lend confidence to the conclusions drawn. However, replicate studies that investigate these complex, changing dynamics at a finer level of detail need to be conducted over a temporal scale to verify these initial findings (George et al., 2018).

4.6 Summary of findings

The findings of this research suggest that water quality around Motiti's reefs is deteriorating. They now appear to experience a prevailing moderate sedimentation regime with fluxes of heavy sedimentation following extreme weather events, in contrast to indications of previously pristine conditions. This study reveals large-scale sponge necrosis across Motiti's mesophotic reefs, in line with the 2022 BoP marine heatwave. Furthermore, the dominant influence of the East Auckland Current observed in these sponge assemblages reinforces concerns about the escalating frequency and intensity of marine heatwaves transported from the tropics. This is of concern as clearly the biodiversity and the mix of subtropical and cold temperate affiliations of species present indicates a relative biodiversity 'hot spot' in a New Zealand context, which is under threat.

This research provides the basis for the following hypotheses: (1), a shift appears to be taking place in benthic community composition under the intense pressure of compounding stressors, to species less sensitive to the escalating frequency and intensity of heat and sedimentation stress; (2), the full extent of damage inflicted by marine heatwaves is yet unseen, due to limited image quality and the ‘snapshot’ nature of this survey; and (3), patches of bleached CCA and barnacles may represent bare scars vacated by ‘rapid sponge death’.

The timing of this study has been serendipitous, as the significant and concerning changes that this study appears to have captured are likely still in motion. The wider implications of a shift in sponge community composition must be considered for management of the Motiti Natural Environment Management Area. For instance, it could indicate a shifting contribution to coastal productivity as different taxonomic groups vary in their contributions to carbon flux (Maldonado et al., 2012; Snelgrove et al., 2018; McCormack, 2021). This study has importance not only for the biogeography of the region and of NZ, but also globally as a signal of mesophotic reefs under substantial environmental stress.

4.7 Future research

Future research questions and recommendations based on these findings include, in order of urgency:

1. To what extent are the Motiti mesophotic benthic communities changing over time?

   This could be approached by placing permanent transects/quadrats at these sites for regular, long-term monitoring. Analysis of historic taxonomic data from Donald (2021) should also be carried out, including video transects that were taken and stored but not analysed, to backdate the temporal record by incorporating comparable TD indices.

2. How often and by how much does sediment deposition fluctuate on the mesophotic zones of these reefs?

   This could be approached by deploying sediment traps across a range of reefs and depths.

3. How will the composition of mesophotic sponge communities in the Bay of Plenty be influenced by the increasing frequency and intensity of anthropogenic stressors predicted due to climate change, in particular marine heatwaves and coastal sedimentation?

This could be approached by carrying out *ex situ* experimentation of compounding heat and sediment stressors on key sponge species characteristic of these reefs (e.g., Beets, 2017).

4. How are other complex interactions not measured in this study influencing the Motiti reef system?

   This could be approached by carrying out regular monitoring of permanent transects/quadrats at a finer scale. More complex variables at these reefs could include food availability, current speed, turbidity, sponge reproduction and trophic interactions.

4.8 Conclusions

This unique investigation has provided a holistic yet thorough assessment of the biophysical processes and compounding stressors influencing Motiti's mesophotic benthic communities. Through comprehensive analysis of both ROV footage and sponge specimen samples, utilizing a variety of metrics at species, morphology and community level, this research has shed light on a significant biodiversity hotspot, important not only for sponges but for all trophic levels of our coastal ecosystem.

In addition, this research has substantially advanced knowledge of New Zealand's mesophotic sponge occurrence and distribution, offering valuable insight into the role of oceanic currents within the BoP. Notably, this study has captured a snapshot of Motiti's mesophotic reefs at an unstable time where there appears to be a rapid shift in the assemblage towards species more robust to increased sedimentation and elevated temperatures, but potentially less diverse. The conservative nature of this study emphasises concern that TME sponges could be climate change 'losers', particularly in light of the observed extent of necrosis. While the establishment of the no-take Motiti Protection Areas was an important first step in safeguarding this valuable ecosystem, the next step is to commence regular, long-term monitoring to inform management strategies. Given its proximity to Tauranga and the partial protection already in place, the Motiti Island archipelago presents a unique opportunity to serve as a hub for research and education.

References

Abdul Wahab, M. A., Maldonado, M., Luter, H. M., Jones, R., & Ricardo, G. (2019). Effects of sediment resuspension on the larval stage of the model sponge *Carteriospongia foliascens*. *Science of The Total Environment*, *695*, 133837. https://doi.org/10.1016/j.scitotenv.2019.133837

Achlatis, M., Pernice, M., Green, K., De Goeij, J., Guagliardo, P., Kilburn, M., Hoegh-Guldberg, O., & Dove, S. (2019). Single-cell visualization indicates direct role of sponge host in uptake of dissolved organic matter. *Proceedings of the Royal Society B*, *286*(1916). https://doi.org/10.1098/rspb.2019.2153

Airoldi, L. (2003). The effects of sedimentation on rocky coast assemblages. *Oceanography and Marine Biology: An Annual Review*, *41*, 161–236. https://doi.org/10.1201/9780203180570-23

Alldredge, A. L., & Silver, M. W. (1988). Characteristics, dynamics and significance of marine snow. *Progress in Oceanography*, *20*(1), 41–82. https://doi.org/10.1016/0079-6611(88)90053-5

Alvarez, B., Bergquist, P., & Battershill, C. (2002). Taxonomic revision of the genus *Latrunculia* Du Bocage (Porifera: Demospongiae: Latrunculiidae) in New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *36*, 151–184. https://doi.org/10.1080/00288330.2002.9517078

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. *PRIMER-E*: *Plymouth, UK.*

Andradi-Brown, D., Head, C., Exton, D., Hunt, C., Hendrix, A., Gress, E., & Rogers, A. (2017). Identifying zooplankton community changes between shallow and upper-mesophotic reefs on the Mesoamerican Barrier Reef, Caribbean. *PeerJ*, *2017*(1), 1–13. https://doi.org/10.7717/peerj.2853

Ayling, A. L. (1980). Patterns of sexuality, asexual reproduction and recruitment in some subtidal marine Demospongiae. *The Biological Bulletin*, *158*(3), 271–282. https://doi.org/10.2307/1540854

Ayling, A. L. (1983). Growth and regeneration rates in thinly encrusting Demospongiae from temperate waters. *The Biological Bulletin*, *165*(2), 343–352. https://doi.org/10.2307/1541200

Ayling, A. M. (1981). The role of biological disturbance in temperate subtidal encrusting communities. *Ecology*, *62*(3), 830–847. https://doi.org/10.2307/1937749

Baillon, S., Hamel, J.-F., Wareham, V., & Mercier, A. (2012). Deep cold-water corals as nurseries for fish larvae. *Frontiers in Ecology and the Environment*, *10*(7), 351–356. https://doi.org/10.1890/120022

Baker, E., Puglise, K., & Harris, P. (Eds.). (2016). *Mesophotic Coral Ecosystems - A Lifeboat for Coral Reefs?* The United Nations Environment Programme and GRID-Arendal, Nairobi and Arendal, 98p.

Ballesteros, E. (2006). Mediterranean coralligenous assemblages: a synthesis of present knowledge. *Oceanography and Marine Biology: An Annual Review*, *44*, 123–195.

Bannister, R., Battershill, C., & de Nys, R. (2012). Suspended sediment grain size and mineralogy across the continental shelf of the Great Barrier Reef: Impacts on the physiology of a coral reef sponge. *Continental Shelf Research*, *32*, 86–95. https://doi.org/10.1016/J.CSR.2011.10.018

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bart, M., Hudspith, M., Rapp, H., Verdonschot, P., & de Goeij, J. (2021). A deep-sea sponge loop? Sponges transfer dissolved and particulate organic carbon and nitrogen to associated fauna. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.604879

Basher, L. (2013). Erosion processes and their control in New Zealand. In *Ecosystem Services in New Zealand - Conditions and Trends* (pp. 363–374). Manaaki Whenua Press.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Battershill, C. (1987). *Factors affecting the structure and dynamics of subtidal communities characterised by sponges* [Doctoral dissertation, University of Auckland]. ResearchSpace. http://hdl.handle.net/2292/1740

Battershill, C., & Bergquist, P. (1990). The influence of storms on asexual reproduction, recruitment, and survivorship of sponges. In K. Rutzler (Ed.), *New perspectives in sponge biology* (pp. 397–403). Smithsonian Institution.

Battershill, C., Bergquist, P., & Cook, S. (2010). Phylum Porifera. In *New Zealand Coastal Marine Invertebrates* (Vol. 1, pp. 57–137). Canterbury University Press.

Battershill, C., Ross, P. R., & Schiel, D. R. (2016). The MV *Rena* shipwreck: time-critical scientific response and environmental legacies. *New Zealand Journal of Marine and Freshwater Research*, *50*(1), 173–182. https://doi.org/10.1080/00288330.2015.1134593

Bay of Plenty Regional Council. (2019). *Bay of Plenty Regional Coastal Environment Plan*. https://www.boprc.govt.nz/your-council/plans-and-policies/plans/regional-plans/regional-coastal-environment-plan

Beazley, L. I., Kenchington, E. L., Murillo, F. J., & Sacau, M. del M. (2013). Deep-sea sponge grounds enhance diversity and abundance of epibenthic megafauna in the Northwest Atlantic. *ICES Journal of Marine Science*, *70*(7), 1471–1490. https://doi.org/10.1093/icesjms/fst124

Beets, F. L. (2017). *Marine demosponge responses to a changing ocean; effects of sedimentation and temperature increases on Tethya burtoni metabolism* [Master's thesis, University of Waikato]. Research Commons. https://hdl.handle.net/10289/11535

Behrens, E., Rickard, G., Rosier, S., Williams, J., Morgenstern, O., & Stone, D. (2022). Projections of future marine heatwaves for the oceans around New Zealand using New Zealand's Earth System Model. *Frontiers in Climate*, *4,* 798287. https://doi.org/10.3389/fclim.2022.798287

Bell, J. (2004). Evidence for morphology-induced sediment settlement prevention on the tubular sponge *Haliclona urceolus*. *Marine Biology, 146*, 29–38. https://doi.org/10.1007/S00227-004-1429-0

Bell, J., Barnes, D. K. A., & Shaw, C. (2002). Branching dynamics of two species of arborescent demosponge: the effect of flow regime and bathymetry. *Journal of the Marine Biological Association of the United Kingdom, 82*(2), 279–294. https://doi.org/https://doi.org/10.1017/S0025315402005465

Bell, J., Bennett, H. M., Rovellini, A., & Webster, N. S. (2018). Sponges to be winners under near-future climate scenarios. *BioScience*, *68*(12), 955–968. https://doi.org/10.1093/biosci/biy142

Bell, J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., & Shaffer, M. (2015). Sediment impacts on marine sponges. *Marine Pollution Bulletin*, *94*(1–2), 5–13. https://doi.org/10.1016/j.marpolbul.2015.03.030

Bell, J., Micaroni, V., Harris, B., Strano, F., Broadribb, M., & Rogers, A. (2022). Global status, impacts, and management of rocky temperate mesophotic ecosystems. *Conservation Biology*, *00*, e13945. https://doi.org/10.1111/cobi.13945

Bell, J., Smith, D., Hannan, D., Haris, A., Jompa, J., & Thomas, L. (2014). Resilience to disturbance despite limited dispersal and self-recruitment in tropical barrel sponges: Implications for conservation and management. *PLoS ONE, 9*(3), e91635. https://doi.org/10.1371/journal.pone.0091635

Bell, J., Smith, R., Micaroni, V., Strano, F., Balemi, C., Caiger, P., Miller, K., Spyksma, A., & Shears, N. (2023). Marine heat waves drive bleaching and necrosis of temperate sponges. *Current Biology*, *33*(1), 158–163. https://doi.org/10.1016/j.cub.2022.11.013

Bennett, H. M., Altenrath, C., Woods, L., Davy, S. K., Webster, N. S., & Bell, J. (2017). Interactive effects of temperature and pCO_2 on sponges: from the cradle to the grave. *Global Change Biology*, *23*(5), 2031–2046. https://doi.org/10.1111/gcb.13474

Bergquist, P. (1961a). Biological results of the Chatham Islands 1954 Expedition. Part 5, Porifera: Demospongiae. *New Zealand Oceanographic Institute Memoir*, *13*, 169–206.

Bergquist, P. (1961b). Biological results of the Chatham Islands 1954 Expedition. Part 5, Porifera: Keratosa. *New Zealand Oceanographic Institute Memoir*, *13*, 207–219.

Bergquist, P. R. (1968). The marine fauna of New Zealand: Porifera, Demospongiae, Part 1 (Tetractinomorpha and Lithistida). *New Zealand Oceanographic Institute Memoir*, *37*, 1–105.

Bergquist, P. R. (1970). The marine fauna of New Zealand: Porifera, Demospongiae, Part 2 (Axinellida and Halichondrida). *New Zealand Oceanographic Institute Memoir*, *51*, 9–85.

Bergquist, P. (1996). The marine fauna of New Zealand: Porifera, Part 5 (Dendroceratida and Halisarcida). *New Zealand Oceanographic Institute Memoir*, *107*, 1–53.

Bergquist, P. R., & Fromont, P. J. (1988). The marine fauna of New Zealand: Porifera, Demospongiae, Part 4 (Poecilosclerida). *New Zealand Oceanographic Institute Memoir*, *96*, 1–197.

Bergquist, P. R., & Warne, K. P. (1980). The marine fauna of New Zealand: Porifera, Demospongiae, Part 3 (Haplosclerida and Nepheliospongida). *New Zealand Oceanographic Institute Memoir*, *87*, 1–77.

Berman, J. (2012). *Patterns of temporal and spatial variability of sponge assemblages* [Doctoral dissertation, Victoria University of Wellington]. Open Access Te Herenga Waka-Victoria University of Wellington. https://doi.org/10.26686/wgtn.16993576.v1

Berman, J., & Bell, J. (2011). Spatial variability of sponge assemblages on the Wellington South Coast, New Zealand. *The Open Marine Biology Journal*, *4*(1), 12–25. https://doi.org/10.2174/1874450801004010012

Biggerstaff, A., Smith, D., Jompa, J., & Bell, J. (2017). Metabolic responses of a phototrophic sponge to sedimentation supports transitions to sponge-dominated reefs. *Scientific Reports*, *7*, 2725. https://doi.org/10.1038/s41598-017-03018-y

Black, K., Haggitt, T., Mead, S., Longdill, P., Prasetya, G., & Bosserelle, C. (2006). *Bay of Plenty Primary Production Modelling: Influence of climatic variation and change*. ASR Marine Consulting and Research.

Blain, C. O., Hansen, S. C., & Shears, N. T. (2021). Coastal darkening substantially limits the contribution of kelp to coastal carbon cycles. *Global Change Biology*, *27*(21), 5547–5563. https://doi.org/10.1111/gcb.15837

Bo, M., Bertolino, M., Bavestrello, G., Canese, S., Giusti, M., Angiolillo, M., Pansini, M., & Taviani, M. (2012). Role of deep sponge grounds in the Mediterranean Sea: A case study in southern Italy. *Hydrobiologia*, *687*(1), 163–177. https://doi.org/10.1007/S10750-011-0964-1

Boavida, J., Assis, J., Reed, J., Serrão, E., & Gonçalves, J. (2016). Comparison of small remotely operated vehicles and diver-operated video of circalittoral benthos. *Hydrobiologia*, *766*, 247–260. https://doi.org/10.1007/S10750-015-2459-Y

Boffa Miskell Limited. (2020). *Motiti Natural Environment Management Area: Marine Ecological Literature Review*. Report prepared by Boffa Miskell Limited for Bay of Plenty Regional Council.

Boyd, P. W., & Law, C. S. (2011). An ocean climate change atlas for New Zealand waters. *NIWA Information Series*, *79*, 1-24.

Brøndsted, H. V. (1924). Papers from Dr. Th. Mortensen's Pacific Expedition 1914-16. XV. Sponges from the Auckland and Campbell Islands. *Videnskabelige Meddelelser Fra Dansk Naturhistorisk Forening i Kjøbenhavn*, *75*, 117–167.

Buscher, E., Mathews, D., Bryce, C., Bryce, K., Joseph, D., & Ban, N. (2020). Applying a low cost, mini remotely operated vehicle (ROV) to assess an ecological baseline of an indigenous seascape in Canada. *Frontiers in Marine Science*, *7*, 669. https://doi.org/10.3389/fmars.2020.00669

Cárdenas, C., Davy, S., & Bell, J. (2012). Correlations between algal abundance, environmental variables and sponge distribution patterns on southern hemisphere temperate rocky reefs. *Aquatic Biology*, *16*(3), 229–239. https://doi.org/10.3354/ab00449

Cerrano, C., Bastari, A., Calcinai, B., Di Camillo, C., Pica, D., Puce, S., Valisano, L., & Torsani, F. (2019). Temperate mesophotic ecosystems: gaps and perspectives of an emerging conservation challenge for the Mediterranean Sea. *The European Zoological Journal*, *86*(1), 370–388. https://doi.org/10.1080/24750263.2019.1677790

Cerrano, C., Magnino, G., Sarà, A., Bavestrello, G., & Gaino, E. (2001). Necrosis in a population of *Petrosia ficiformis* (Porifera, Demospongiae) in relation with environmental stress. *Italian Journal of Zoology*, *68*(2), 131–136. https://doi.org/10.1080/11250000109356397

Chiswell, S., & Sutton, P. (2020). Relationships between long-term ocean warming, marine heat waves and primary production in the New Zealand region. *New Zealand Journal of Marine and Freshwater Research*, *54*(4), 614–635. https://doi.org/10.1080/00288330.2020.1713181

Clarke, K. R., & Gorley, R. N. (2015). PRIMER v7: User Manual/Tutorial. *PRIMER-E: Plymouth.*

Clarke, K. R., & Warwick, R. M. (1998). A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology*, *35*(4), 523–531. https://doi.org/https://doi.org/10.1046/j.1365-2664.1998.3540523.x

Clarke, K. R., & Warwick, R. M. (1999). The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. *Marine Ecology Progress Series*, *184*, 21–29. https://doi.org/10.3354/meps184021

Clarke, K. R., & Warwick, R. M. (2001). A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine Ecology Progress Series*, *216*, 265–278. https://doi.org/10.3354/meps216265

Cook, S. de C., & Bergquist, P. R. (1996). New species of Dictyoceratid sponges (Porifera: Demospongiae: Dictyoceratida) from New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *30*(1), 19–34. https://doi.org/10.1080/00288330.1996.9516694

Cook, S. de C., & Bergquist, P. R. (2001). New species of Spongia (Porifera: Demospongiae: Dictyoceratida) from New Zealand, and a proposed subgeneric structure. *New Zealand Journal of Marine and Freshwater Research*, *35*(1), 33–58. https://doi.org/10.1080/00288330.2001.9516977

Coppari, M., Gori, A., Viladrich, N., Saponari, L., Canepa, A., Grinyó, J., Olariaga, A., & Rossi, S. (2016). The role of Mediterranean sponges in benthic–pelagic coupling processes: *Aplysina aerophoba* and *Axinella polypoides* case studies. *Journal of Experimental Marine Biology and Ecology*, *477*, 57–68. https://doi.org/10.1016/j.jembe.2016.01.004

Cornwall, C. E., Nelson, W. A., Aguirre, J. D., Blain, C. O., Coyle, L., D’Archino, R., Desmond, M. J., Hepburn, C. D., Liggins, L., Shears, N. T., & Thomsen, M. S. (2023). Predicting the impacts of climate change on New Zealand’s seaweed-based ecosystems. *New Zealand Journal of Botany*, 1–28. https://doi.org/10.1080/0028825X.2023.2245786

Costantini, F., & Abbiati, M. (2016). Into the depth of population genetics: pattern of structuring in mesophotic red coral populations. *Coral Reefs*, *35*, 39–52. https://doi.org/10.1007/s00338-015-1344-5

Crawshaw, J. (2022). *Investigation of satellite derived water quality products in the Motiti Protection Areas using NIWA-SCENZ*. Bay of Plenty Regional Council.

Cummings, V. J., Beaumont, J., Mobilia, V., Bell, J., Tracey, D., Clark, M. R., & Barr, N. (2020). Responses of a common New Zealand coastal sponge to elevated suspended sediments: Indications of resilience. *Marine Environmental Research*, *155*, 104886. https://doi.org/10.1016/j.marenvres.2020.104886

Dawson, E. (1993). The marine fauna of New Zealand: Index to the Fauna: 2 Porifera. *New Zealand Oceanographic Institute Memoir*, *100*, 1–98.

Dayton, P., Robilliard, G., Paine, R., & Dayton, L. (1974). Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecological Monographs*, *44*(1), 105–128. https://doi.org/10.2307/1942321

de la Mare, W. K. (2005). Marine ecosystem-based management as a hierarchical control system. *Marine Policy*, *29*(1), 57–68. https://doi.org/10.1016/j.marpol.2004.02.002

Dendy, A. (1924). Porifera. Part I. Non-Antarctic sponges. Natural History Report. *British Antarctic (Terra Nova) Expedition, 1910 (Zoology)*, *6*(3), 269–392.

Di Lorenzo, M., Guidetti, P., Di Franco, A., Calò, A., & Claudet, J. (2020). Assessing spillover from marine protected areas and its drivers: A meta-analytical approach. *Fish and Fisheries*, *21*(5), 906–915. https://doi.org/10.1111/faf.12469

Donald, E. P. (2021). *Deep reef discoveries: Exploration of deep reef biodiversity in the Bay of Plenty*. https://atlas.boprc.govt.nz/api/v1/edms/document/A3760677/content

Dunham, A., Archer, S. K., Davies, S. C., Burke, L. A., Mossman, J., Pegg, J. R., & Archer, E. (2018). Assessing condition and ecological role of deep-water biogenic habitats: Glass sponge reefs in the Salish Sea. *Marine Environmental Research*, *141*, 88–99. https://doi.org/10.1016/j.marenvres.2018.08.002

Elliott, G., & Leys, S. (2007). Coordinated contractions effectively expel water from the aquiferous system of a freshwater sponge. *Journal of Experimental Biology*, *210*(21), 3736–3748. https://doi.org/10.1242/jeb.003392

Filbee-Dexter, K., & Wernberg, T. (2020). Substantial blue carbon in overlooked Australian kelp forests. *Scientific Reports*, *10*, 12341. https://doi.org/10.1038/s41598-020-69258-7

Folkers, M., & Rombouts, T. (2020). Sponges Revealed: A Synthesis of Their Overlooked Ecological Functions Within Aquatic Ecosystems. *YOUMARES 9 - The Oceans: Our Research, Our Future*, 181–193. https://doi.org/10.1007/978-3-030-20389-4_9

Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, *560*, 360–364. https://doi.org/10.1038/s41586-018-0383-9

Garrabou, J., Gómez-Gras, D., Medrano, A., Cerrano, C., Ponti, M., Schlegel, R., Bensoussan, N., Turicchia, E., Sini, M., Gerovasileiou, V., Teixido, N., Mirasole, A., Tamburello, L., Cebrian, E., Rilov, G., Ledoux, J., Souissi, J. B., Khamassi, F., Ghanem, R., … Harmelin, J. (2022). Marine heatwaves drive recurrent mass mortalities in the Mediterranean Sea. *Global Change Biology*, *28*(19), 5708–5725. https://doi.org/10.1111/gcb.16301

George, A., Brodie, J., Daniell, J., Capper, A., & Jonker, M. (2018). Can sponge morphologies act as environmental proxies to biophysical factors in the Great Barrier Reef, Australia? *Ecological Indicators*, *93*, 1152–1162. https://doi.org/10.1016/j.ecolind.2018.06.016

Gerovasileiou, V., Chintiroglou, C., Konstantinou, D., & Voultsiadou, E. (2016). Sponges as “living hotels” in Mediterranean marine caves. *Scientia Marina*, *80*(3), 279–289. http://doi.org/10.3989/scimar.04403.14B

Godefroy, N., Le Goff, E., Martinand-Mari, C., Belkhir, K., Vacelet, J., & Baghdiguian, S. (2019). Sponge digestive system diversity and evolution: filter feeding to carnivory. *Cell and Tissue Research*, *377*, 341–351. https://doi.org/10.1007/S00441-019-03032-8

Grant, N., Matveev, E., Kahn, A., & Leys, S. (2018). Suspended sediment causes feeding current arrests in situ in the glass sponge *Aphrocallistes vastus*. *Marine Environmental Research*, *137*, 111–120. https://doi.org/10.1016/j.marenvres.2018.02.020

Gray, J. E. (1843). Fauna of New Zealand. In E. Dieffenbach (Ed.), *Travels in New Zealand* (Vol. 2, pp. 177–295). William Clows and Sons, Samford Street.

Guy, G., & Metaxas, A. (2022). Recruitment of deep-water corals and sponges in the Northwest Atlantic Ocean: implications for habitat distribution and population connectivity. *Marine Biology*, *169*(8), 107. https://doi.org/10.1007/s00227-022-04089-w

Harrington, L. J., Dean, S. M., Awatere, S., Rosier, S., Queen, L., Gibson, P. B., Barnes, C., Zachariah, M., Philip, S., Kew, S., Koren, G., Pinto, I., Grieco, M., Vahlberg, M., Snigh, R., Heinrich, D., Thalheimer, L., Li, S., Stone, D., … Otto, F. E. L. (2023). *The role of climate change in extreme rainfall associated with Cyclone Gabrielle over Aotearoa*

New Zealand's East Coast. World Weather Attribution Initiative Scientific Report. Grantham Institute.

Harris, B. (2022). *The distribution and feeding ecology of temperate marine sponges through shallow and mesophotic habitats* [Doctoral dissertation, Victoria University of Wellington]. Open Access Te Herenga Waka-Victoria University of Wellington. https://doi.org/10.26686/wgtn.19669398

Harris, B., Davy, S. K., & Bell, J. (2021). Benthic community composition of temperate mesophotic ecosystems (TMEs) in New Zealand: sponge domination and contribution to habitat complexity. *Marine Ecology Progress Series*, *671*, 21–43. https://doi.org/10.3354/meps13758

Hartig, F. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R package. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

Hayward, B. W., Grenfell, H. R., Sabaa, A. T., Morley, M. S., & Horrocks, M. (2006). Effect and timing of increased freshwater runoff into sheltered harbor environments around Auckland City, New Zealand. *Estuaries and Coasts*, *29*(2), 165–182. https://doi.org/10.1007/BF02781987

Herbert-Read, J. E., Thornton, A., Amon, D. J., Birchenough, S. N. R., Côté, I. M., Dias, M. P., Godley, B. J., Keith, S. A., McKinley, E., Peck, L. S., Calado, R., Defeo, O., Degraer, S., Johnston, E. L., Kaartokallio, H., Macreadie, P. I., Metaxas, A., Muthumbi, A. W. N., Obura, D. O., … Sutherland, W. J. (2022). A global horizon scan of issues impacting marine and coastal biodiversity conservation. *Nature Ecology & Evolution*, *6*, 1262–1270. https://doi.org/10.1038/s41559-022-01812-0

Hill, A. F. (2017). *Brief of Evidence of Andrew Francis Hill in the matter of: Of the Resource Management Act 1991 and of an appeal under Clause 14 of the First Schedule of the Act and an application under section 311 of the Act between Motiti Rohe Moana Trust, appellant, and Bay of Plenty Regional Council, respondent.* Ministry of Justice, New Zealand. https://www.justice.govt.nz/assets/Andrew-Hill-Evidence-in-Chief.pdf

Hinde, G. J., & Holmes, W. M. (1892). On the sponge-remains in the lower tertiary strata near Oamaru, Otago, New Zealand. *Zoological Journal of the Linnean Society*, *24,* 177–262. https://doi.org/10.1111/j.1096-3642.1892.tb02480.x

Hogg, M. M., Tendal, O. S., Conway, K. W., Pomponi, S. A., van Soest, R. W. M., Gutt, J., Krautter, M., & Roberts, J. M. (2010). *Deep-sea sponge grounds: Reservoirs of biodiversity* (Report No. 32). https://www.researchgate.net/publication/254914411_Deep-sea_sponge_grounds_Reservoirs_of_biodiversity

Holbrook, N. J., Sen Gupta, A., Oliver, E. C. J., Hobday, A. J., Benthuysen, J. A., Scannell, H. A., Smale, D. A., & Wernberg, T. (2020). Keeping pace with marine heatwaves. *Nature Reviews Earth & Environment*, *1*, 482–493. https://doi.org/10.1038/s43017-020-0068-4

Hu, G., & Zhang, Q. (2016). Seasonal variations in macrobenthic taxonomic diversity and the application of taxonomic distinctness indices in Bohai Bay, northern China. *Ecological Indicators*, *71*, 181–190. https://doi.org/10.1016/j.ecolind.2016.07.001

Hui, F. K. C. (2016). boral - Bayesian Ordination and Regression Analysis of Multivariate Abundance Data in R. *Methods in Ecology and Evolution*, *7*(6), 744–750. https://doi.org/10.1111/2041-210X.12514

Hui, F. K. C. (2021). *boral: Bayesian Ordination and Regression AnaLysis*. R package. https://CRAN.R-project.org/package=boral

Idan, T., Sheffer, S., Feldstein, T., Yahel, R., Huchon, D., & Ilan, M. (2018). Shedding light on an East-Mediterranean mesophotic sponge ground community and the regional sponge fauna. *Mediterranean Marine Science, 19*(1), 84–106. https://doi.org/10.12681/mms.13853

IPCC. (2023). *Climate Change 2023: Synthesis Report* (Core Writing Team, H. Lee, & J. Romero, Eds.). IPCC. https://doi.org/https://doi.org/10.59327/IPCC/AR6-9789291691647

Jiang, X., Pan, B., Sun, Z., Cao, L., & Lu, Y. (2020). Application of taxonomic distinctness indices of fish assemblages for assessing effects of river-lake disconnection and eutrophication in floodplain lakes. *Ecological Indicators*, *110*, 105955. https://doi.org/10.1016/j.ecolind.2019.105955

Kahng, S., Copus, J., & Wagner, D. (2014). Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability*, *7*, 72–81. https://doi.org/10.1016/j.cosust.2013.11.019

Kane, C., Kosaki, R. K., & Wagner, D. (2014). High levels of mesophotic reef fish endemism in the Northwestern Hawaiian Islands. *Bulletin of Marine Science*, *90*(2), 693–703. https://doi.org/10.5343/bms.2013.1053

Keegan, L. J., White, R. S. A., & Macinnis-Ng, C. (2022). Current knowledge and potential impacts of climate change on New Zealand’s biological heritage. *New Zealand Journal of Ecology*, *46*(1), 1–24. https://doi.org/10.2307/48652113

Kelly, M. (2007). The Marine Fauna of New Zealand: Porifera: Lithistid Demospongiae (rock sponges). *NIWA Biodiversity Memoir*, *121*, 1–100.

Kelly, M. (2022). *Splendid Sponges, a guide to the sponges of New Zealand. Version 4 (2022)* (M. Kelly & S. Mills, Eds.). NIWA. https://niwa.co.nz/oceans/resources/marine-identification-guides-and-fact-sheets

Kelly, M., Lee, D., Kelly, S., & Buckeridge, J. S. (2003). A recent sponge, *Pleroma aotea* Kelly ("Order” Lithistida: Family Pleromidae), in the late Eocene Ototara Limestone of Otago, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *37*(1), 129–148. https://doi.org/10.1080/00288330.2003.9517152

Kelly, M., & Sim-Smith, C. (in press 2023). Chapter 4. Kingdom Animalia, phylum Porifera (sponges). In M. Kelly, S. Mills, M. Terezow, C. Sim-Smith, & W. A. Nelson (Eds.), *The marine biota of Aotearoa New Zealand. Updating our marine biodiversity inventory. NIWA Biodiversity Memoir* 136.

Kelly-Borges, M., & Bergquist, P. R. (1994). A redescription of *Aaptos aaptos* with descriptions of new species of *Aaptos* (Hadromerida: Suberitidae) from northern New Zealand. *Journal of Zoology*, *234*(2), 301–323.

Kelly-Borges, M., & Bergquist, P. R. (1997). Revision of Southwest Pacific Polymastiidae (Porifera: Demospongiae: Hadromerida) with descriptions of new species of *Polymastia* Bowerbank, *Tylexocladus* Topsent, and *Acanthopolymastia* gen. nov. from New Zealand and the Norfolk Ridge, New Caledonia. *New Zealand Journal of Marine and Freshwater Research*, *31*(3), 367–402. https://doi.org/10.1080/00288330.1997.9516772

Kenchington, E., Power, D., & Koen-Alonso, M. (2013). Associations of demersal fish with sponge grounds on the continental slopes of the northwest Atlantic. *Marine Ecology Progress Series*, *477*, 217–230. https://doi.org/10.3354/meps10127

Kenchington, E., Wang, Z., Lirette, C., Murillo, F. J., Guijarro, J., Yashayaev, I., & Maldonado, M. (2019). Connectivity modelling of areas closed to protect vulnerable marine ecosystems in the northwest Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, *143*, 85–103. https://doi.org/10.1016/j.dsr.2018.11.007

Kornder, N., Esser, Y., Stoupin, D., Leys, S., Mueller, B., Vermeij, M., Huisman, J., & de Goeij, J. (2022). Sponges sneeze mucus to shed particulate waste from their seawater inlet pores. *Current Biology*, *32*(17), 3855–3861. https://doi.org/10.1016/j.cub.2022.07.017

Kosaki, R., Pyle, R., Leonard, J., Hauk, B., Whitton, R., & Wagner, D. (2017). 100% endemism in mesophotic reef fish assemblages at Kure Atoll, Hawaiian Islands. *Marine Biodiversity*, *47*, 783–784. https://doi.org/10.1007/s12526-016-0510-5

Lang, J. (1974). Biological Zonation at the Base of a Reef: Observations from the submersible Nekton Gamma have led to surprising revelations about the deep fore-reef and island slope at Discovery Bay, Jamaica. *American Scientist*, *62*(3), 272–281.

von Lendenfeld, R. (1888). *Descriptive Catalogue of the Sponges in the Australian Museum, Sidney*. Taylor & Francis.

Lenth, R. V. (2023). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package. https://github.com/rvlenth/emmeans

Leonard, D. R. P., Robert Clarke, K., Somerfield, P. J., & Warwick, R. M. (2006). The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. *Journal of Environmental Management*, *78*(1), 52–62. https://doi.org/10.1016/j.jenvman.2005.04.008

Lesser, M. P. (2006). Benthic–pelagic coupling on coral reefs: Feeding and growth of Caribbean sponges. *Journal of Experimental Marine Biology and Ecology*, *328*(2), 277–288. https://doi.org/10.1016/j.jembe.2005.07.010

Lesser, M. P., & Slattery, M. (2013). Ecology of Caribbean Sponges: Are top-down or bottom-up processes more important? *PLoS ONE*, *8*(11), e79799. https://doi.org/10.1371/journal.pone.0079799

Lesser, M., & Slattery, M. (2021). Mesophotic coral reef community structure: the constraints of imagery collected by unmanned vehicles. *Marine Ecology Progress Series*, *663*, 229–236. https://doi.org/10.3354/meps13650

Lesser, M., Slattery, M., & Mobley, C. D. (2018). Biodiversity and functional ecology of mesophotic coral reefs. *Annual Review of Ecology, Evolution, and Systematics*, *49*(1), 49–71. https://doi.org/10.1146/annurev-ecolsys-110617-062423

López-Legentil, S., Song, B., McMurray, S. E., & Pawlik, J. R. (2008). Bleaching and stress in coral reef ecosystems: hsp70 expression by the giant barrel sponge *Xestospongia muta*. *Molecular Ecology*, *17*(7), 1840–1849. https://doi.org/10.1111/j.1365-294X.2008.03667.x

Maldonado, M., Aguilar, R., Bannister, R. J., Bell, J. J., Conway, K. W., Dayton, P. K., Díaz, C., Gutt, J., Kelly, M., Kenchington, E. L. R., Leys, S. P., Pomponi, S. A., Rapp, H. T., Rützler, K., Tendal, O. S., Vacelet, J., & Young, C. M. (2017). Sponge grounds as key marine habitats: A synthetic review of types, structure, functional roles, and conservation concerns. *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*, 145–183. https://doi.org/10.1007/978-3-319-21012-4_24

Maldonado, M., Ribes, M., & van Duyl, F. C. (2012). Nutrient Fluxes Through Sponges. In M. A. Becerro, M. J. Uriz, M. Maldonado, & X. Turon (Eds.), *Advances in Marine Biology* (Vol. 62, pp. 113–182). Academic Press. https://doi.org/10.1016/B978-0-12-394283-8.00003-5

Maldonado, M., & Uriz, M.-J. (1995). Biotic affinities in a transitional zone between the Atlantic and the Mediterranean: A biogeographical approach based on sponges. *Journal of Biogeography*, *22*(1), 89–110. https://doi.org/10.2307/2846075

Marliave, J., Conway, K., Gibbs, D., Lamb, A., & Gibbs, C. (2009). Biodiversity and rockfish recruitment in sponge gardens and bioherms of southern British Columbia, Canada. *Marine Biology*, *156*, 2247–2254. https://doi.org/10.1007/s00227-009-1252-8

Mazzuco, A. C. de A., Stelzer, P. S., & Bernardino, A. F. (2020). Substrate rugosity and temperature matters: patterns of benthic diversity at tropical intertidal reefs in the SW Atlantic. *PeerJ*, *8*, e8289. https://doi.org/10.7717/peerj.8289

Mc Cormack, S. (2015). *The taxonomy of Demospongiae (Porifera) from the Bay of Plenty, New Zealand - Connecting Linnaean and phylogenetic classification* [Master's thesis, University of Waikato]. Research Commons. https://hdl.handle.net/10289/9511

Mc Cormack, S. (2021). *The biogeography and trophic roles of coastal marine sponges (Porifera) from the west coast of the North Island, New Zealand: Influences of catchments* [Doctoral dissertation, University of Waikato]. Research Commons. https://hdl.handle.net/10289/14690

Mc Cormack, S. P., Kelly, M., & Battershill, C. N. (2020). Description of two new species of *Dysidea* (Porifera, Demospongiae, Dictyoceratida, Dysideidae) from Tauranga Harbour, Bay of Plenty, New Zealand. *Zootaxa*, *4780*(3), 523–542. https://doi.org/10.11646/zootaxa.4780.3.5

McClintock, J., Amsler, C., Baker, B., & Van Soest, R. (2005). Ecology of Antarctic marine sponges: An overview. *Integrative and Comparative Biology*, *45*, 359–368. https://doi.org/https://doi.org/10.1093/icb/45.2.359

McDonald, J. I., McGuinness, K. A., & Hooper, J. N. (2003). Influence of re-orientation on alignment to flow and tissue production in a *Spongia* sp. (Porifera:Demospongiae:Dictyoceratida). *Journal of Experimental Marine Biology and Ecology*, *296*(1), 13–22. https://doi.org/10.1016/S0022-0981(03)00302-2

McIntyre, F., Drewery, J., Eerkes-Medrano, D., & Neat, F. (2016). Distribution and diversity of deep-sea sponge grounds on the Rosemary Bank Seamount, NE Atlantic. *Marine Biology*, *163*, 1–11. https://doi.org/10.1007/S00227-016-2913-z

Micaroni, V. (2022). *Effects of anthropogenic stressors on temperate mesophotic ecosystems* [Doctoral dissertation, Victoria University of Wellington]. Open Access Te Herenga Waka-Victoria University of Wellington. https://doi.org/10.26686/wgtn.19372754

Ministry for the Environment & Stats NZ. (2022). *New Zealand's Environmental Reporting Series: Our marine environment 2022*. https://environment.govt.nz/

Moana Project. (2023). *Recent marine heatwaves in Aotearoa New Zealand*. https://www.moanaproject.org/recent-marine-heatwaves

Montaño, M. M., Suanda, S. H., & de Souza, J. M. A. C. (2023). Modelled coastal circulation and Lagrangian statistics from a large coastal embayment: The case of Bay of Plenty, Aotearoa New Zealand. *Estuarine, Coastal and Shelf Science*, *281*, 108212. https://doi.org/10.1016/j.ecss.2023.108212

Motiti Rohe Moana Trust v Bay of Plenty Regional Council [2020] NZ EnvC 050. https://atlas.boprc.govt.nz/api/v1/edms/document/A3526046/content

Musser, J., Schippers, K., Nickel, M., Mizzon, G., Kohn, A., Pape, C., Ronchi, P., Papadopoulos, N., Tarashansky, A., Hammel, J., Wolf, F., Liang, C., Hernández-Plaza, A., Cantalapiedra, C., Achim, K., Schieber, N., Pan, L., Ruperti, F., Francis, W., … Arendt, D. (2021). Profiling cellular diversity in sponges informs animal cell type and nervous system evolution. *Science*, *374*(6568), 717–723. https://doi.org/10.1126/science.abj2949

Mustaffa, N. I. H., Kallajoki, L., Biederbick, J., Binder, F. I., Schlenker, A., & Striebel, M. (2020). Coastal ocean darkening effects via terrigenous DOM addition on plankton: An indoor mesocosm experiment. *Frontiers in Marine Science*, *7*, 547829. https://doi.org/10.3389/fmars.2020.547829

Noll, B., & Andrews, C. (2023). Cyclone Gabrielle, more to come? *Coastal News*, *81*, 3–6.

Orejas, C., Gori, A., Lo Iacono, C., Puig, P., Gili, J., & Dale, M. (2009). Cold-water corals in the Cap de Creus canyon, northwestern Mediterranean: Spatial distribution, density and anthropogenic impact. *Marine Ecology Progress Series*, *397*, 37–51. https://doi.org/10.3354/meps08314

Osgood, G. J., McCord, M. E., & Baum, J. K. (2019). Using baited remote underwater videos (BRUVs) to characterize chondrichthyan communities in a global biodiversity hotspot. *PLoS ONE*, *14*(12). https://doi.org/10.1371/journal.pone.0225859

Pante, E., & Dustan, P. (2012). Getting to the point: Accuracy of point count in monitoring ecosystem change. *Journal of Marine Biology*, *2012*, 1–7. https://doi.org/10.1155/2012/802875

Paoli, C., Montefalcone, M., Morri, C., Vassallo, P., & Bianchi, C. (2017). Ecosystem functions and services of the marine animal forests. In S. Rossi, L. Bramanti, A. Gori, & C. Orejas (Eds.), *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots* (pp. 1271–1312). Springer, Cham. https://doi.org/10.1007/978-3-319-21012-4_38

Park, S., Crawshaw, J., & Fox, E. (2022). *Setting sediment load limits to protect ecological values of Tauranga Harbour sub-estuaries*. Bay of Plenty Regional Council.

Pawlik, J. R., Loh, T.-L., & McMurray, S. E. (2018). A review of bottom-up vs. top-down control of sponges on Caribbean fore-reefs: what’s old, what’s new, and future directions. *PeerJ*, *6*, e4343. https://doi.org/10.7717/peerj.4343

Pawlik, J. R., McMurray, S. E., Erwin, P., & Zea, S. (2015). A review of evidence for food limitation of sponges on Caribbean reefs. *Marine Ecology Progress Series*, *519*, 265–283. https://doi.org/10.3354/meps11093

Perea-Blázquez, A., Davy, S. K., & Bell, J. (2012a). Estimates of particulate organic carbon flowing from the pelagic environment to the benthos through sponge assemblages. *PLoS ONE*, *7*(1), e29569. https://doi.org/10.1371/journal.pone.0029569

Perea-Blázquez, A., Davy, S. K., & Bell, J. (2012b). Nutrient utilisation by shallow water temperate sponges in New Zealand. *Hydrobiologia*, *687*(1), 237–250. https://doi.org/10.1007/s10750-011-0798-x

Perea-Blázquez, A., Davy, S. K., Magana-Rodríguez, B., & Bell, J. (2013). Temporal variation in food utilisation by three species of temperate demosponge. *Marine Ecology Progress Series*, *485*, 91–103. https://doi.org/10.3354/meps10316

Perkins, N. R., Monk, J., Soler, G., Gallagher, P., & Barrett, N. S. (2022). Bleaching in sponges on temperate mesophotic reefs observed following marine heatwave events. *Climate Change Ecology*, *3*, 100046. https://doi.org/10.1016/j.ecochg.2021.100046

Pineda, M., Strehlow, B., Sternel, M., Duckworth, A., Haan, J., Jones, R., & Webster, N. (2017). Effects of sediment smothering on the sponge holobiont with implications for dredging management. *Scientific Reports*, *7*, 5156. https://doi.org/10.1038/s41598-017-05243-x

Pinkerton, M., Sutton, P., & Wood, S. (2019). *Satellite indicators of phytoplankton and ocean surface temperature for New Zealand*. Ministry for the Environment, New Zealand.

Pomponi, S., Diaz, C., Van Soest, R., Bell, L., Busutil, L., Gochfeld, D., Kelly, M., & Slattery, M. (2019). Sponges. In Y. Loya, K. Puglise, & T. Bridge (Eds.), *Mesophotic Coral Ecosystems* (Vol. 12, pp. 563–588). Springer, Cham. https://doi.org/10.1007/978-3-319-92735-0_32

Powell, A., Hepburn, L., Smith, D., & Bell, J. (2010). Patterns of sponge abundance across a gradient of habitat quality in the Wakatobi Marine National Park, Indonesia. *The Open Marine Biology Journal*, *4*, 31–38. https://doi.org/10.2174/1874450801004010031

Pritchard, K., Battershill, C., Ward, V., & Bergquist, P. (1984). *Marine sponges: forty-six sponges of northern New Zealand* (Vol. 14). Leigh Marine Laboratory.

Pronzato, R., Bavestrello, G., & Cerrano, C. (1998). Morpho-functional adaptations of three species of *Spongia* (Porifera, Demospongiae) from a Mediterranean vertical cliff. *Bulletin of Marine Science, 63*(2), 317–328.

Pyle, R., Kosaki, R., Pinheiro, H., Rocha, A., Whitton, R., & Copus, J. (2019). Fishes: Biodiversity. In Y. Loya, K. Puglise, & T. Bridge (Eds.), *Mesophotic Coral Ecosystems* (Vol. 12, pp. 749–777). Springer, Cham. https://doi.org/10.1007/978-3-319-92735-0_40

Qu, Z., Thrush, S., Parsons, D., & Lewis, N. (2021). Economic valuation of the snapper recruitment effect from a well-established temperate no-take marine reserve on adjacent fisheries. *Marine Policy, 134*, 104792. https://doi.org/10.1016/j.marpol.2021.104792

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Raijman-Nagar, L., Goren, L., Shefer, S., Moskovich, R., Li, Z., & Ilan, M. (2023). A comparison of mesophotic and shallow sponge holobionts resilience to predicted future temperature elevation. *Frontiers in Marine Science, 10*, 1161648. https://doi.org/10.3389/fmars.2023.1161648

Ross, P., Tremblay, L., Champeau, O., TMC Limited, & Kelly, F. (2018). *Physical Environment Reference Report. Resource Consent RC67891*. Astrolabe Community Trust.

Rossi, S. (2013). The destruction of the “animal forests” in the oceans: Towards an over-simplification of the benthic ecosystems. *Ocean & Coastal Management*, *84*, 77–85. https://doi.org/10.1016/j.ocecoaman.2013.07.004

Salinger, M. J., Diamond, H. J., Bell, J., Behrens, E., Fitzharris, B. B., Herod, N., McLuskie, M., Parker, A. K., Ratz, H., Renwick, J., Scofield, C., Shears, N. T., Smith, R. O., Sutton, P. J., & Trought, M. C. T. (2023). Coupled ocean-atmosphere summer heatwaves in the New Zealand region. *Weather and Climate, 42*(1), 18–41. https://doi.org/10.2307/27226713

Scanes, E., Kutti, T., Fang, J. K. H., Johnston, E. L., Ross, P. M., & Bannister, R. J. (2018). Mine waste and acute warming induce energetic stress in the deep-sea sponge *Geodia* *atlantica* and coral *Primnoa resedeaformis*; Results from a mesocosm study. *Frontiers in Marine Science*, *5*, 129. https://doi.org/10.3389/fmars.2018.00129

Schiel, D., & Battershill, C. (2023, March 1). Sediments are wrecking our coastal ecosystems. *Stuff*. https://www.stuff.co.nz/opinion/131362618/sediments-are-wrecking-our-coastal-ecosystems

Schiel, D. R., Ross, P. M., & Battershill, C. N. (2016). Environmental effects of the MV *Rena* shipwreck: cross-disciplinary investigations of oil and debris impacts on a coastal ecosystem. *New Zealand Journal of Marine and Freshwater Research*, *50*(1), 1–9. https://doi.org/10.1080/00288330.2015.1133665

Schönberg, C. (2015). Self-cleaning surfaces in sponges. *Marine Biodiversity*, *45*, 623–624. https://doi.org/10.1007/S12526-014-0302-8

Schönberg, C. (2021). No taxonomy needed: Sponge functional morphologies inform about environmental conditions. *Ecological Indicators, 129*, 107806. https://doi.org/10.1016/j.ecolind.2021.107806

Sim-Smith, C., Janussen, D., Ríos, P., Macpherson, D., & Kelly, M. (2022). The Marine Biota of New Zealand: A review of New Zealand and Antarctic latrunculid sponges with new taxa and new systematic arrangements within family Latrunculiidae (Demospongiae, Poecilosclerida). *NIWA Biodiversity Memoir, 134*, 1-144. https://docs.niwa.co.nz/library/public/NIWAbm134.pdf

Slattery, M., & Lesser, M. (2012). Mesophotic coral reefs: a global model of community structure and function. In D. Yellowlees & T. P. Hughes (Eds.), *Proceedings of the 12th International Coral Reef Symposium*. James Cook University.

Snelgrove, P. V. R., Soetaert, K., Solan, M., Thrush, S., Wei, C.-L., Danovaro, R., Fulweiler, R. W., Kitazato, H., Ingole, B., Norkko, A., Parkes, R. J., & Volkenborn, N. (2018). Global carbon cycling on a heterogeneous seafloor. *Trends in Ecology & Evolution, 33*(2), 96–105. https://doi.org/10.1016/j.tree.2017.11.004

Soares, M., Araújo, J., Ferreira, S., Santos, B., Boavida, J., Costantini, F., & Rossi, S. (2020). Why do mesophotic coral ecosystems have to be protected? *Science of The Total Environment*, *726*. https://doi.org/10.1016/j.scitotenv.2020.138456

Soares, M., Tavares, T. C. L., & Carneiro, P. B. de M. (2018). Mesophotic ecosystems: Distribution, impacts and conservation in the South Atlantic. *Diversity and Distributions*, *25*(2), 255–268. https://doi.org/10.1111/ddi.12846

Spalding, H., Amado-Filho, G., Bahia, R., Ballantine, D., Fredericq, S., Leichter, J., Nelson, W., Slattery, M., & Tsuda, R. (2019). Macroalgae. In Y. Loya, K. Puglise, & T. Bridge (Eds.), *Mesophotic Coral Ecosystems* (Vol. 12, pp. 507–536). Springer, Cham. https://doi.org/10.1007/978-3-319-92735-0_29

Spillman, C. M., Smith, G. A., Hobday, A. J., & Hartog, J. R. (2021). Onset and decline rates of marine heatwaves: Global trends, seasonal forecasts and marine management. *Frontiers in Climate*, *3*, 801217. https://doi.org/10.3389/fclim.2021.801217

Stevens, C., & Chiswell, S. (2006). *Ocean currents and tides - Currents*. Te Ara - the Encyclopedia of New Zealand. http://www.teara.govt.nz/en/map/5912/ocean-currents-around-new-zealand

Swierts, T., Huang, Y., & de Voogd, N. (2018). The giant barrel sponge facilitates the recovery of coral fragments after a tropical storm in Taiwan. *Coral Reefs*, *37*, 675. https://doi.org/10.1007/S00338-018-1691-0

Tau Ki Ākau. (2023). *Ridge to Reef MBIE Endeavour*. https://taukiakau.org/

Teixidó, N., Pineda, M. C., & Garrabou, J. (2009). Decadal demographic trends of a long-lived temperate encrusting sponge. *Marine Ecology Progress Series*, *375*, 113–124. https://doi.org/10.3354/meps07757

Thomsen, M., Mondardini, L., Alestra, T., Gerrity, S., Tait, L., South, P., Lilley, S., & Schiel, D. (2019). Local extinction of bull kelp (*Durvillaea* spp.) due to a marine heatwave. *Frontiers in Marine Science*, *6*(84). https://doi.org/10.3389/fmars.2019.00084

Thrush, S., Hewitt, J., Lundquist, C., Townsend, M., & Lohrer, A. (2011). *A strategy to assess trends in the ecological integrity of New Zealand's marine ecosystems*. https://www.doc.govt.nz/globalassets/documents/conservation/marine-and-coastal/marine-protected-areas/ecological-integrity-marine-ecosystems.pdf

Tompkins-Macdonald, G., & Leys, S. (2008). Glass sponges arrest pumping in response to sediment: Implications for the physiology of the hexactinellid conduction system. *Marine Biology, 154,* 973–984. https://doi.org/10.1007/S00227-008-0987-Y

Trygonis, V., & Sini, M. (2012). photoQuad: A dedicated seabed image processing software, and a comparative error analysis of four photoquadrat methods. *Journal of Experimental Marine Biology and Ecology, 424–425,* 99–108. https://doi.org/10.1016/j.jembe.2012.04.018

Turner, J. A., Andradi-Brown, D., Gori, A., Bongaerts, P., Burdett, H., Ferrier-Pagès, C., Voolstra, C., Weinstein, D., Bridge, T., Costantini, F., Gress, E., Laverick, J., Loya, Y., Goodbody-Gringley, G., Rossi, S., Taylor, M., Viladrich, N., Voss, J., Williams, J., … Eyal, G. (2019). Key questions for research and conservation of mesophotic coral ecosystems and temperate mesophotic ecosystems. *Coral Reefs of the World*, *12*, 989–1003. https://doi.org/10.1007/978-3-319-92735-0_52

Turner, J. A., Babcock, R. C., Hovey, R., & Kendrick, G. (2017). Deep thinking: a systematic review of mesophotic coral ecosystems. *ICES Journal of Marine Science*, *74*(9), 2309–2320. https://doi.org/10.1093/icesjms/fsx085

Turner, J. T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Progress in Oceanography, 130,* 205–248. https://doi.org/10.1016/j.pocean.2014.08.005

van Gennip, S. J., Popova, E. E., Yool, A., Pecl, G. T., Hobday, A. J., & Sorte, C. J. B. (2017). Going with the flow: the role of ocean circulation in global marine ecosystems under a changing climate. *Global Change Biology*, *23*(7), 2602–2617. https://doi.org/10.1111/gcb.13586

Ventura, D., Dubois, S. F., Bonifazi, A., Jona Lasinio, G., Seminara, M., Gravina, M. F., & Ardizzone, G. (2021). Integration of close-range underwater photogrammetry with inspection and mesh processing software: a novel approach for quantifying ecological dynamics of temperate biogenic reefs. *Remote Sensing in Ecology and Conservation*, *7*(2), 169–186. https://doi.org/10.1002/rse2.178

Wang, Y., Naumann, U., Wright, S. T., & Warton, D. I. (2012). Mvabund - an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, *3*(3), 471–474. https://doi.org/10.1111/j.2041-210X.2012.00190.x

Warton, D. I. (2022). *Eco-Stats: Data Analysis in Ecology* (1st ed.). Springer Cham. https://doi.org/https://doi.org/10.1007/978-3-030-88443-7

Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: The analysis of proportions in ecology. *Ecology*, *92*(1), 3–10. https://doi.org/10.1890/10-0340.1

Warton, D. I., Wright, S. T., & Wang, Y. (2012). Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, *3*(1), 89–101. https://doi.org/10.1111/j.2041-210X.2011.00127.x

Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C. J., Hovey, R. K., Harvey, E. S., Holmes, T. H., Kendrick, G. A., Radford, B., Santana-Garcon, J., Saunders, B. J., Smale, D. A., Thomsen, M. S., Tuckett, C. A., … Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, *353*(6295), 169–172. https://doi.org/10.1126/science.aad8745

Wernberg, T., Smale, D. A., Frölicher, T. L., & Smith, A. J. P. (2021). ScienceBrief Review: Climate change increases marine heatwaves harming marine ecosystems. In P. Liss, C. Le Quéré, & P. Forster (Eds.), *Critical Issues in Climate Change Science*. https://doi.org/10.5281/zenodo.5596820

WoRMS Editorial Board. (2023). *World Register of Marine Species*. https://doi.org/https://doi.org/10.14284/170

Wulff, J. (2008). Collaboration among sponge species increases sponge diversity and abundance in a seagrass meadow. *Marine Ecology*, *29*, 193–204. https://doi.org/10.1111/J.1439-0485.2008.00224.X

Yu, M.-C., Dreyer, N., Kolbasov, G. A., Høeg, J. T., & Chan, B. K. K. (2020). Sponge symbiosis is facilitated by adaptive evolution of larval sensory and attachment structures in barnacles. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1927), 20200300. https://doi.org/10.1098/rspb.2020.0300

Zurowietz, M., & Nattkemper, T. W. (2021). Current trends and future directions of large scale image and video annotation: observations from four years of BIIGLE 2.0. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.760036

Appendices

Appendix A. Camera settings and number of images analysed in Chapter 2

Table 1. Digital settings of the ROV inbuilt camera and GoPro camera used during surveys.

Camera	Specifications	Settings
Chasing M2 Pro ROV inbuilt camera	4K video / 12MP camera 1/2.3 Sony CMOS Sensor 152° field of view Lens F 1.8	4K video 30 frames per second 60Mb bitrate Auto white balance and ISO EIS image stabilisation Image overlay information: ● Date and time (NZST) ● Water temperature (^oC) ● Vehicle heading relative to True North ● Vehicle pitch (bow down negative, bow up positive) ● Depth (m)
GoPro Hero 9 Black	Up to 5K video 20MP photos GoPro camera mounted facing 15 degrees down from ROV level	2-second timelapse still images Linear lens correction (19-39 mm) to digitally reduce the fisheye effect Auto white balance and ISO Flat colour correction GoPro time offset from ROV camera:

		B01 North = 1m 30s ahead B01 South = 1m 30s ahead B04 = 50s ahead B05 = 2m 14s ahead B06 = 50s ahead N02 East = 50s ahead N02 West = 50s ahead N04 = 50s ahead N05 = 50s ahead S01_NW = 50s ahead S01_SE = 50s ahead S02 = No timestamp on images S03 = No timestamp on images S04 = Some images timestamped (when ROV cam was recording), and these are 50s ahead. Worked out the timestamp on the rest from these.

Table 2. Number of high-quality images analysed from each transect in Chapter 2.

Site	Transect	Number of images
Te Poroiti Reef	B01 North	30
	B01 South	6
	B04	30
	B05	30
	B06	30
Nukutai Reef	N02 East	21
	N02 West	17
	N04	29
	N05	30
Motuhaku Reef	S01 NW	30
	S01 SE	30
	S02	30
	S03	30
	S04	30

Appendix B. Sponge collection dive notes

<u>Ōtāiti/Astrolabe Reef</u>

Date of dive: 26 March 2023

Location: -37.5603° S, 176.3962° E

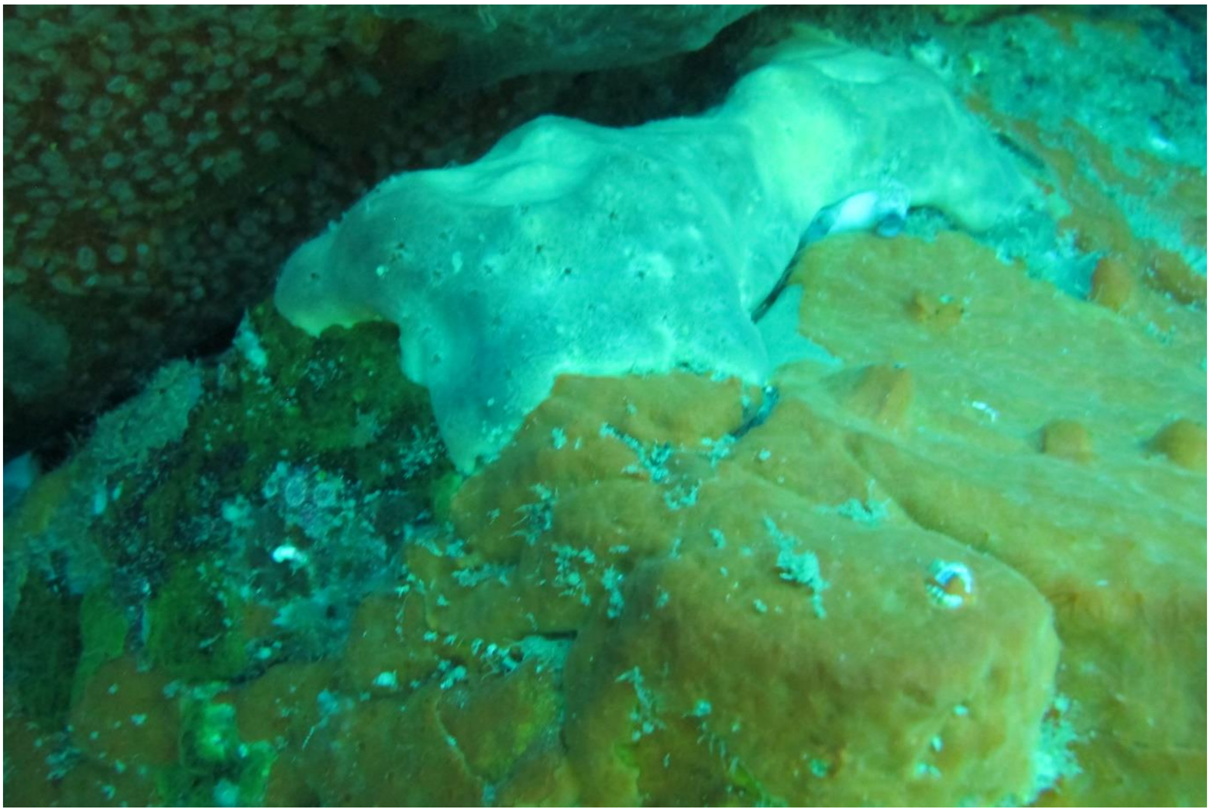
Depth: 15-28 m

Site Description

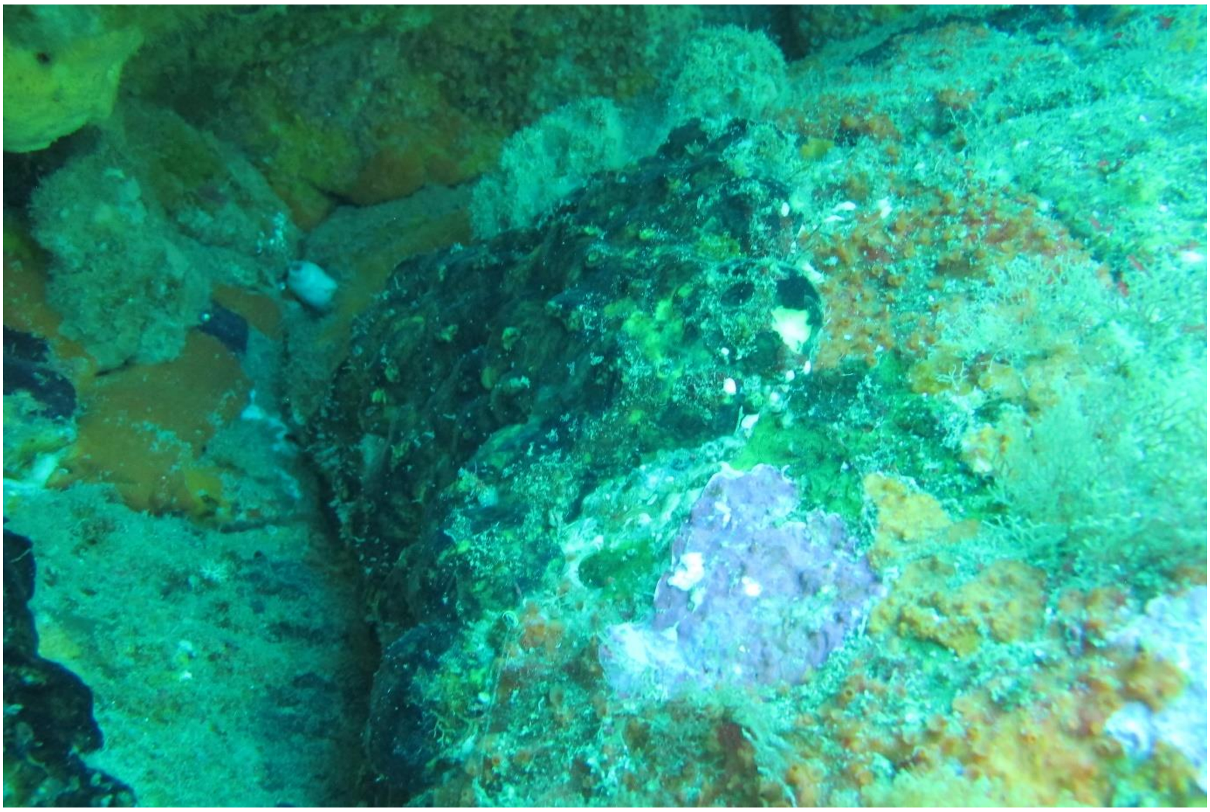
A large rocky reef system rising from 60-80 m. Steep cliff drop offs dropping to over 25 m to a shallower sloping reef extension that extends to close to 60 m and sand flats beyond. The top of the reef system is deeply dissected but with some shallow reef flat 'embayment's' well covered in kelp (*Carpophyllums* and *Ecklonia* forest in good health). Walls and drop-offs are characteristic of much of the sloping region of this reef affording areas for encrusting biota beneath healthy kelp canopies.

Code	Description	Initial ID	Image
23AR1-1	Fawn liver sponge	Texture Like *Plakortis*??	*Yes*
23AR1-2	Darker coloured specimen of 23AR 1-1	Texture Like *Plakortis*?	*Yes*
23AR1-3	Fawn Haplosclerid? Crumbly sponge	*Xestospongia novaezealandii*	
23AR1-4	<u>*Penares tylotaster*</u>?		*Yes*

Images



23 AR1-1, 1-2 (Fawn sponge in centre image)



23 AR1-4

Motiti Island

Date of dive: 19 March 2023

Location: -37.638377° S, 176.404649° E

Depth: 15-20 m

Site description

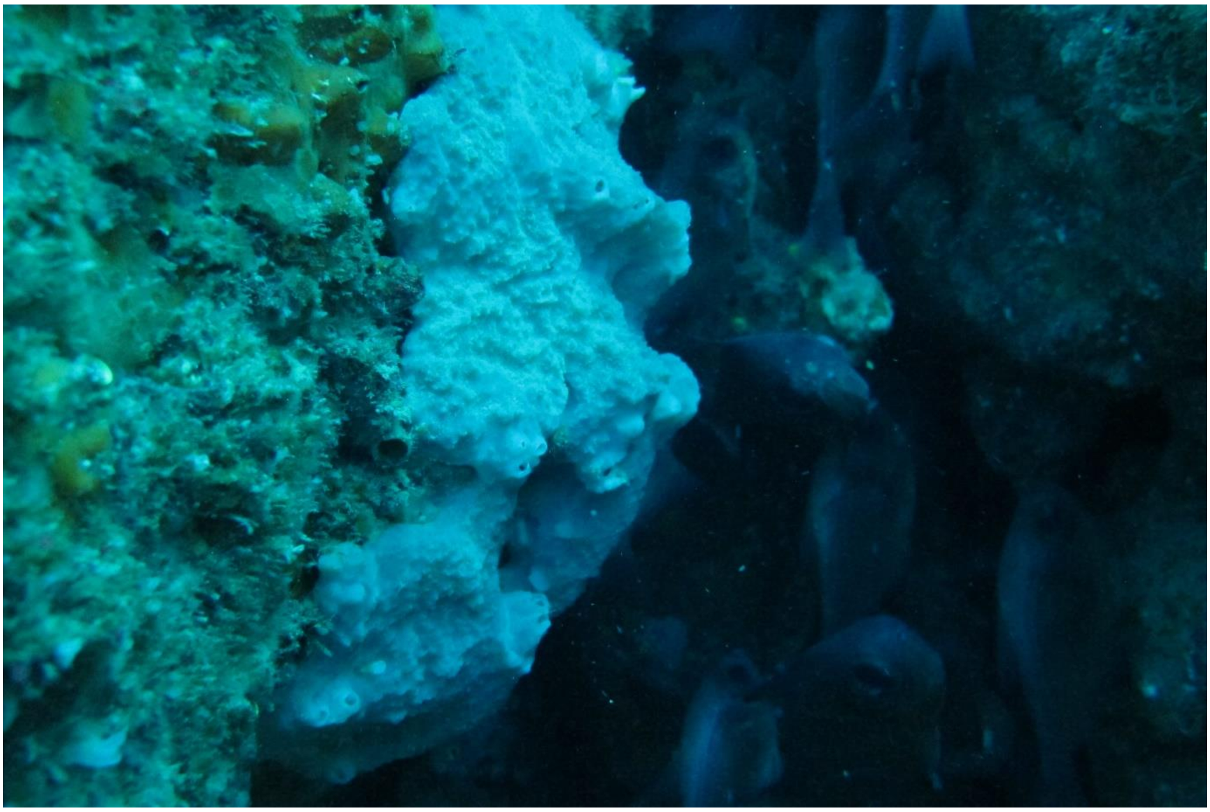
A shallow shelving reef of dissected rock with frequent guts descending to sand flats. The reef was once covered in a canopy of *Ecklonia radiata*, that has recently succumbed to massive sedimentation such that remaining fronds are covered in a thick layer of sticky mud. Most of the lower regions of the kelp forest are dead represented by rotting stipes. The subcanopy is significantly burdened with fine sediment 1-2 mm thick over all surfaces in in some areas up to 5 mm.

Finger sponges are evident in the subcanopy and become more frequent at deeper extensions of the reef. Other sponges are more abundant also in deeper reef extensions close to the sand flats. There is evidence of recent sponge disease with scarring prominent on some species (especially *Ecionemia*). Noticeably absent are other encrusting subcanopy species (bryozoans, hydroids, ascidians).

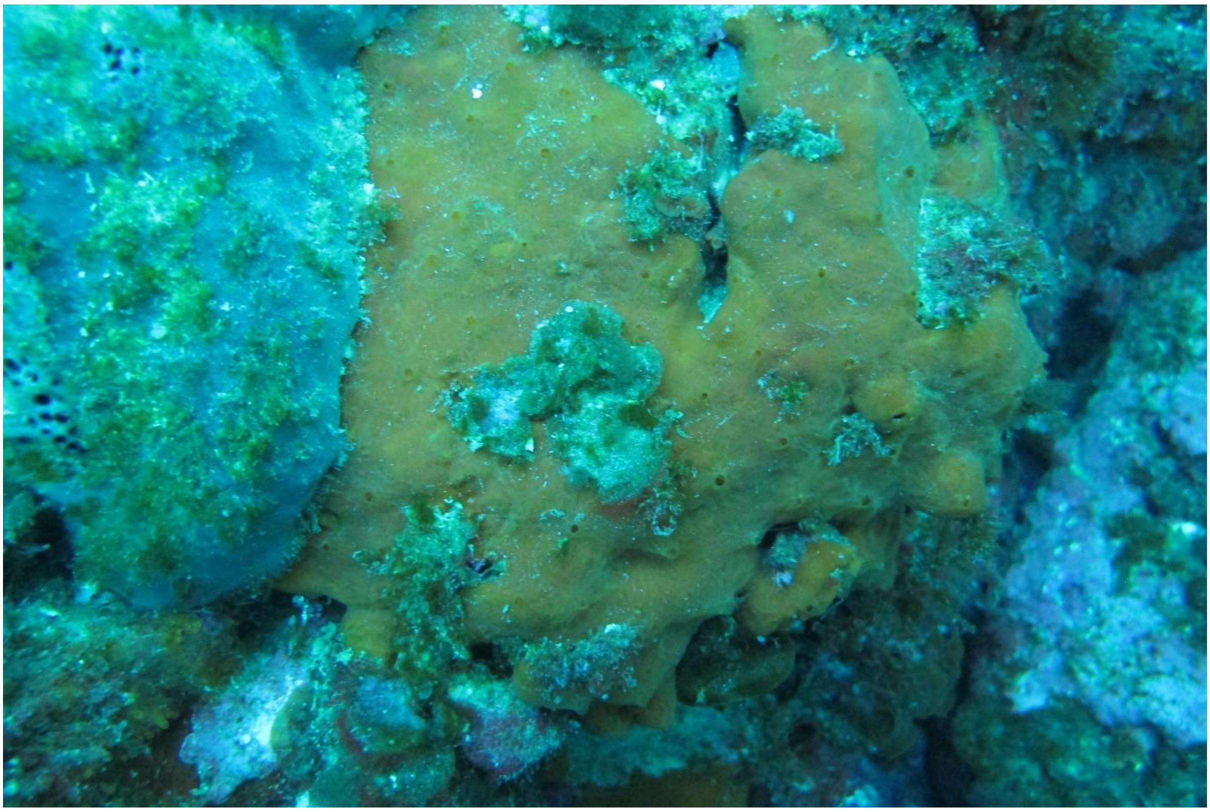
Code	**Description**	**Initial ID**	**Image**
23 Mot 1-1	Orange ‘pointy’ finger sponge	*Trachycladus* or *Pararhaphoxya*	
23 Mot 1-2	Orange (blunt) finger sponge	*Raspailia topsenti*	
23 Mot 1-3	Brown stumpy Axinellid?		
23 Mot 1-4	Orange-brown leathery amorphous	*Spirastrella*?	*Yes*
23 Mot 1-5	Cup Haplosclerid	*Petrosia hebes*	
23 Mot 1-6	Dirty white Choristid (=1-9)	*Asteropus?*	
23 Mot 1-7	Light grey Dictyoceratid	*Psammocinia papillata*	*Yes*
23 Mot 1-8	Bright red slimy encrusting	*Tedania battershilli*	*Yes*
23 Mot 1-9	Heavily encrusted Choristid (=1-6)	*Stelletta sandalinum*?	
23 Mot 1-10	Orange fingers (Clathrinid?)		
23 Mot 1-11	Dark khaki *Latrunculia* thin encrust	*Latrunculia procumbens*	
23 Mot 1-12	*Cinachyrella*?		

Images

23 MOT1-4



23 MOT1-7 (Dark sponge in back of rock crevice)



23 MOT1-8

Okarapu Reef

Date of dive: 26 March 2023

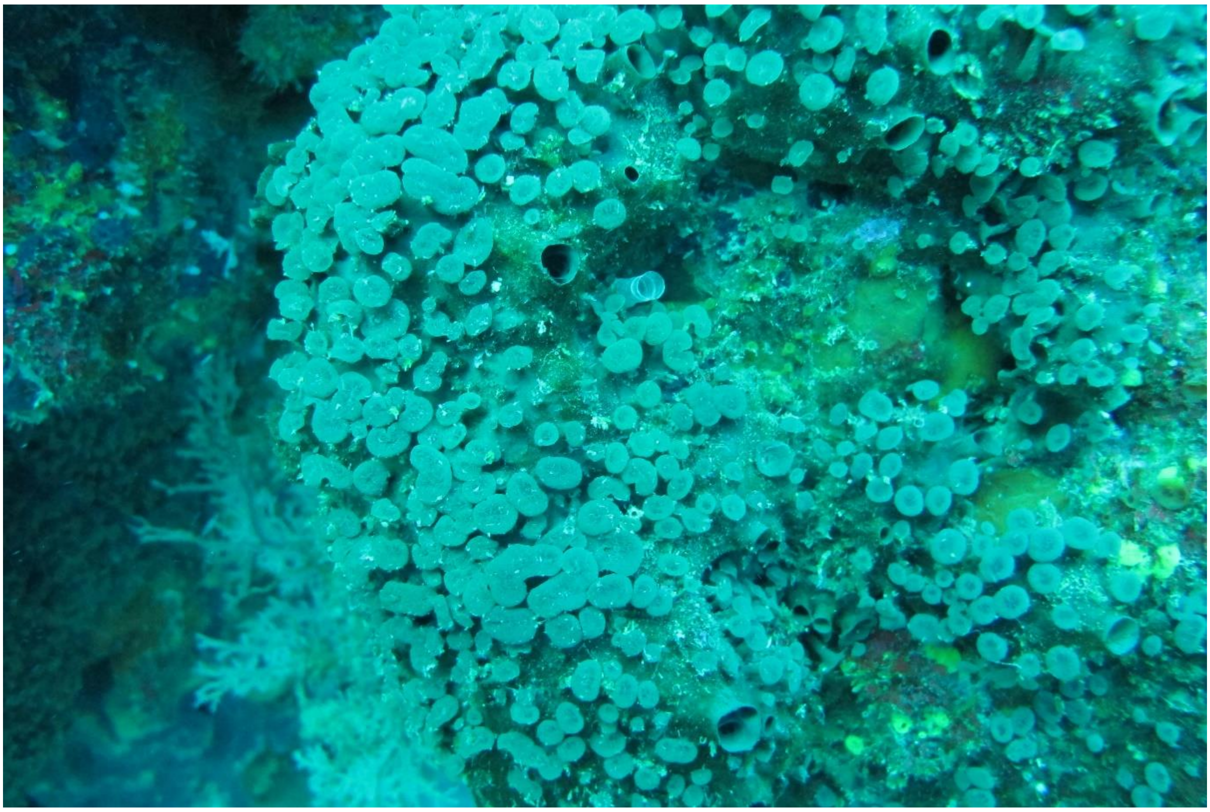
Location: -37.58364677° S, 176.36621760º E

Depth: 15-26 m

Site Description

A large rocky pinnacle with steep cliff drop-offs dropping to over 25 m to a shallower sloping reef extension that extends to close to 30 m and sand flats beyond. The top of the pinnacle is relatively flat with some dissected rock and is largely barren with kina and *Centrostephanus* in large numbers. Kelp is limited to the seaward fringes of this system. The rock walls are deeply dissected with several caves and swim throughs. The sponge cover in these systems is good and *Ecklonia radiata* stands are healthy on the more well-lit slopes and at depth.

Code	**Description**	**Initial ID**	**Image**
23OR1-1	Dictyoceratid	*Spongiidae?*	
23OR1-2	Dictyoceratid	*Psammocinia beresfordae*	
23OR1-3	Dictyoceratid	*Psammocinia beresfordae*	
23OR1-4	*Latrunculia*	*Latrunculia procumbens*	*Yes*
23OR1-5	*Aciculites?* Red, lamellate	*Petrosia hebes?*	*Yes*
23OR1-6	*Aciculites*? Pink fingers	*Petrosia hebes?*	
23OR1-7	Thin red encrusting on rock/spg	*Desmacella dendyi* (+ *Lithistid*)	



23 OR1-4 *Latrunculia sp.*

23 OR1-5

Appendix C. Supplemental tables for Chapter 2 results

Table 1. Number (richness) of species, genera, families, orders and classes identified from ROV footage of the Motiti mesophotic reefs. Note that OTUs are included in species richness, but not in higher level taxonomic groups due to unidentified family and/or genus.

Reef	Species	Genera	Family	Order	Class
Te Poroiti	46	28	25	16	2
Nukutai	40	28	25	17	2
Motuhaku	45	28	23	15	2
Total	53	34	27	17	2

Table 2. Values for average taxonomic distinctness (Δ+) and variation in taxonomic distinctness (Λ+).

Sample	**M**	**Δ+ Value**	**Δ+ Sig %**	**Λ+ Value**	**Λ+ Sig %**
B01 North	18	74.25	0.4	212.67	8.8
B01 South	9	73.89	6	218.21	21
B04	10	74.67	6.8	184.89	34.6
B05	24	80.94	41.2	145.49	62.3
B06	16	77	25	111	72.9
N02 East	10	76.44	33	147.36	61.1
N02 West	13	74.1	2	226.76	12.8
N04	20	82.11	13.4	126.09	98.5
N05	16	82.83	15.8	161.97	47.6
S01 NW	17	80.15	81.9	132.33	84.1
S01 SE	17	80.74	57.1	108.28	71.9
S02	22	81.3	33.4	135.11	83.1
S03	25	81.2	18.8	126.56	95.3
S04	25	80.6	50.3	147.64	58.1

Table 3. Permutational analysis of variance (PERMANOVA) output, where the predictor variable is reef and the response variables are Δ+ and Λ+.

	df	*SS*	*MS*	*Pseudo-F*	*p*(perm)	Unique perms
Δ+						
Reef	2	0.005	0.002	3.34	0.079	9586
Residual	11	0.008	0.001			
Total	13	0.013				
Λ+						
Reef	2	0.161	0.081	2.003	0.19	9554
Residual	11	0.444	0.04			
Total	13	0.605				

Appendix D. Sponge OTU example photos

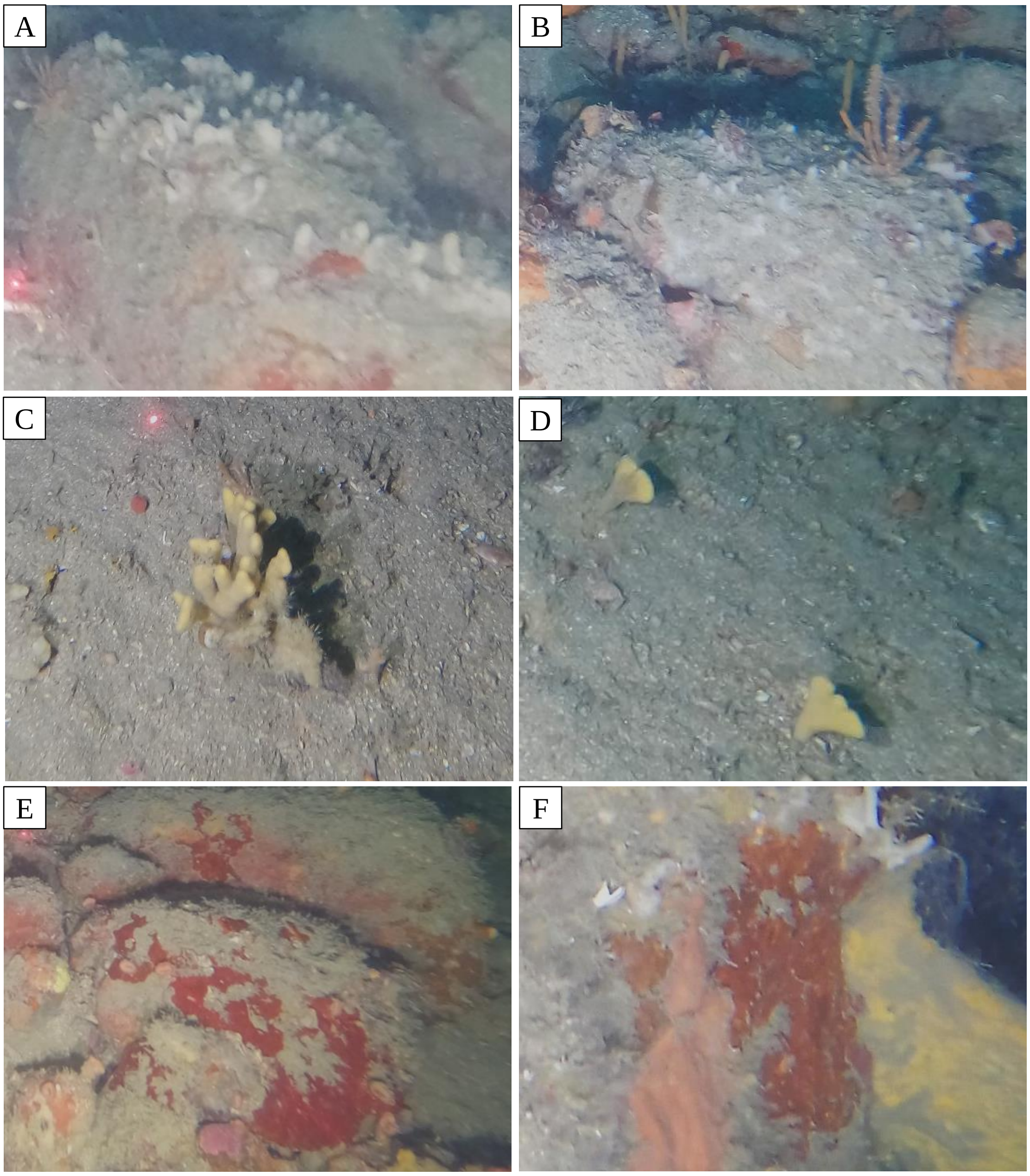


Figure 1. A-F, Example images of sponge OTUs from ROV footage: A-B, Calcarea n. sp. 1; C-D, Callyspongiidae n. sp. 1; E-F, Thin encrusting red Poecilosclerid.

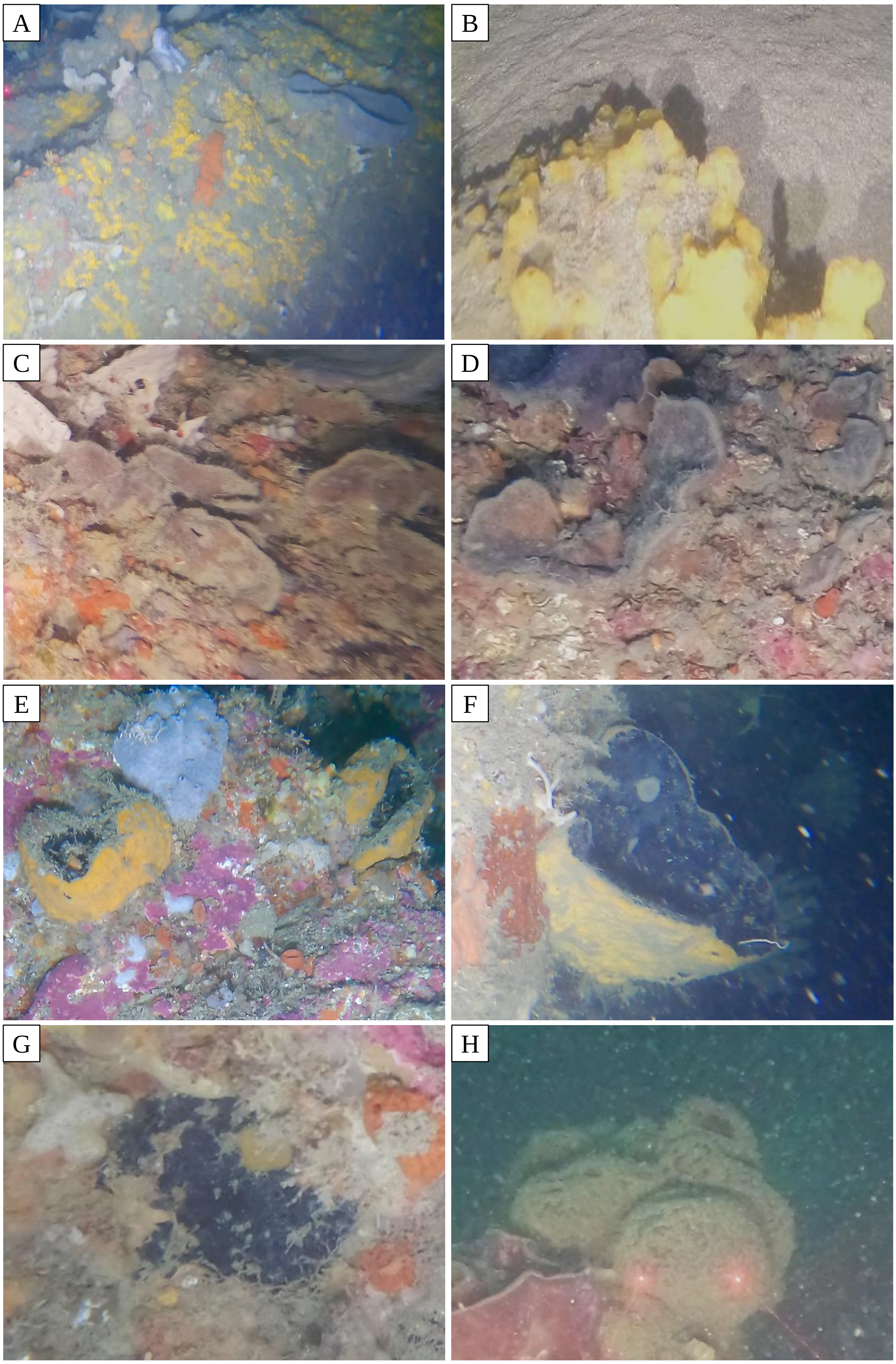


Figure 2. A-H, Example images of sponge OTUs from ROV footage: A-B, Yellow thick encrusting Poecilosclerid; C-D, Heteroscleromorpha n. sp. 1; E-F, Black & orange cup; G, Dark encrusting sponge; H, Fluffy cluster sponge.

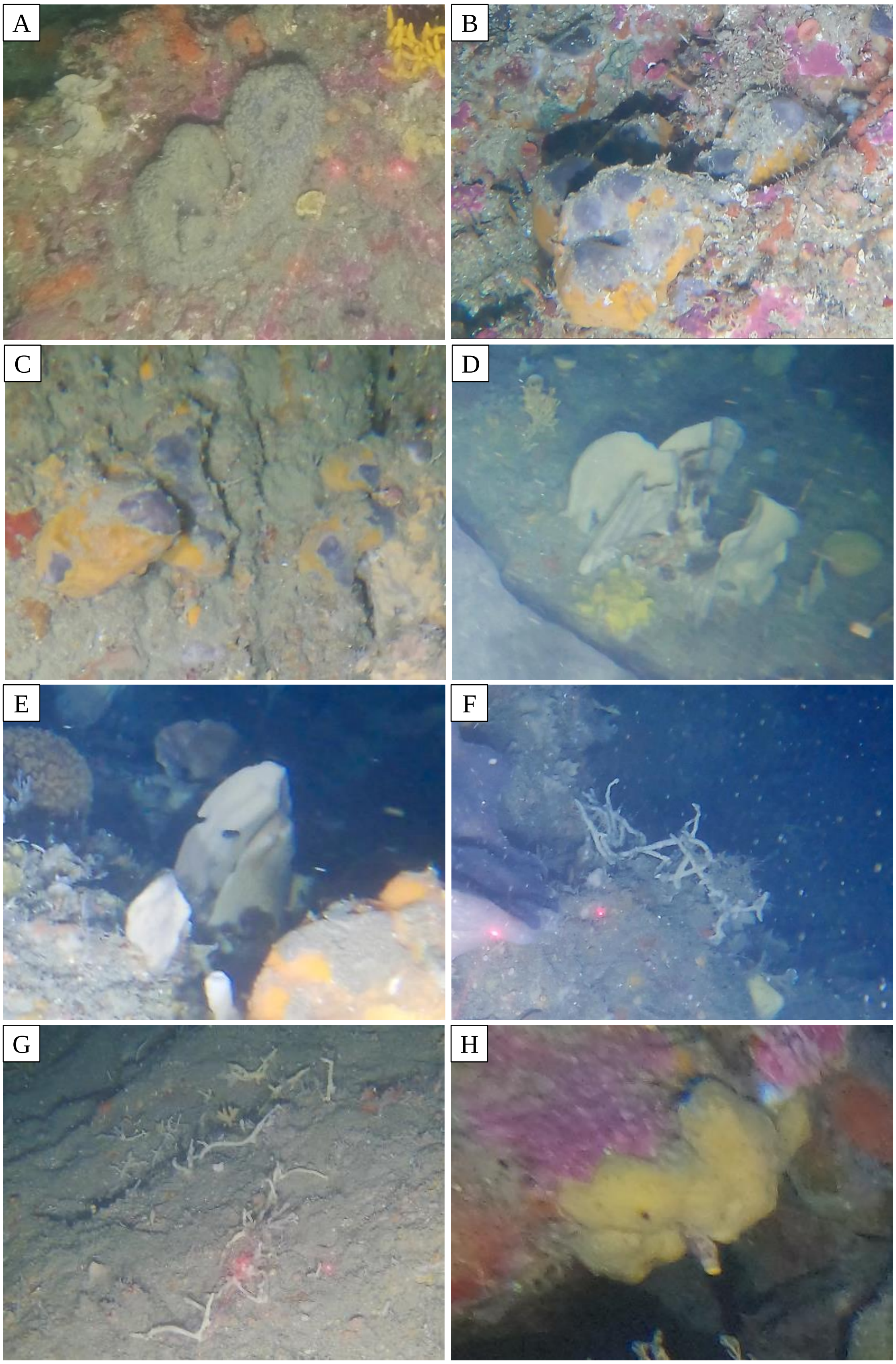


Figure 3. A-H, Example images of sponge OTUs from ROV footage: A, Fluffy cluster sponge; B-C, Orange meandering sponge; D-E, Oyster mushroom sponge; F-G, Possibly tumbleweed sponge; H, Yellow smooth massive sponge.

Figure 4. Example image of sponge OTU from ROV footage: Yellow smooth massive sponge.

Appendix E. Geographic affinities for total species list

Table 1. Total list of all species and OTUs from Te Poroiti, Nukutai and Motuhaku reefs. Includes those recorded from both ROV footage in August 2022 and samples collected by diving in March 2023. Geographic affinities are coded as follow: S-Southern; N-Northern; T-Temperate; C-Cosmopolitan; “-” -Unknown.

Affinity	**Class**	**Order**	**Family**	**Genus**	**Species**
S	Calcarea	**Clathrinida**	Leucettidae	*Rowella*	*Rowella* spp.
S		**Leucosolenida**	Leucosoleniidae	*Leucosolenia*	*Leucosolenia rosea*
-		**Unknown**			Calcarea n. sp. 1
C	Demospongiae	**Axinellida**	Axinellidae	*Pararhaphoxya*	$^+$*Pararhaphoxya* cf. *pulchra*
N					**Pararhaphoxya sinclairi*
-			Raspailiidae	*Raspailia*	^$^+$*Raspailia* sp. nov. 1 (spathulate, Motiti Island, Donald)
T					**Raspailia (Raspaxilla) topsenti*
N		**Biemnida**	Biemnidae	*Biemna*	*Biemna rufescens*
N		**Bubarida**	Desmanthidae	*Petromica*	*Petromica* sp.
C		**Clionaida**	Clionaidae	*Cliona*	*Cliona* sp.

N		Spirastrellidae	cf. *Spirastrella*	^+*Spirastrella* sp. 01 (0CDN6683-X, Three Kings)
C	**Dendroceratida**	Darwinellidae	*Darwinella*	*Darwinella* cf. *gardineri*
C				*Darwinella oxeata*
C			*Dendrilla*	*Dendrilla* cf. *rosea*
C	**Dictyoceratida**	Irciniidae	*Psammocinia*	#*Psammocinia* spp.
T				+*Psammocinia beresfordae*
N		Spongiidae	*Spongia*	+*Spongia* (*Heterofibria*) cf. *manipulatus*
N		Thorectidae	*Taonura*	*Taonura* cf. *marginalis*
S			*Thorecta*	*Thorecta* cf. *reticulatus*
C	**Haplosclerida**	Callyspongiidae	*Callyspongia*	*Callyspongia (Callyspongia) nuda*
C			Unknown	Callyspongiidae n. sp. 1
C		Chalinidae	*Haliclona*	*Haliclona* sp.
-		Petrosiidae	*Neopetrosia*	+*Neopetrosia* sp. 1 (spicules 152 – 183 µm, Astrolabe Reef, Donald)
N			*Petrosia*	**Petrosia (Petrosia) hebes*
C			*Xestospongia*	#*Xestospongia* spp.
S				+*Xestospongia* cf. *novaezealandiae*

S	**Poecilosclerida**	Acarnidae	*Iophon*	*Iophon laevistylus*
C		Chondropsidae	*Chondropsis*	cf. *Chondropsis* sp.
N		Crambeidae	*Crambe*	+*Crambe* sp. 01 (NIWA 51235, Spirits Bay, Kelly)
T		Desmacididae	*Desmacidon*	*Desmacidon mamillatum*
N		Latrunculiidae	*Latrunculia (Biannulata)*	+*Latrunculia (Biannulata) procumbens*
N		Tedaniidae	*Tedania (Tedania)*	+*Tedania (Tedania) battershilli*
-		Unknown		Thin encrusting red Poecilosclerid
-				^Yellow thick encrusting Poecilosclerid
T	**Polymastiida**	Polymastiidae	*Polymastia*	*Polymastia* cf. *massalis*
T				*Polymastia crocea*
T				*Polymastia hirsuta*
C	**Suberitida**	Halichondriidae	*Ciocalypta*	*Ciocalypta* cf. *penicillus*
T			*Halichondria*	*Halichondria (Halichondria) moorei*
T			*Hymeniacidon*	*Hymeniacidon* cf. *perlevis*
N		Suberitidae	*Aaptos*	+*Aaptos conferta*

T				[+]*Aaptos globosa*
C				[#]*Aaptos* spp.
T			*Homaxinella*	*Homaxinella* cf. *erecta*
N			*Suberites*	[+]*Suberites* sp. (cf. big cheese sponge)
C				[#]*Suberites* spp.
C	**Tethyida**	Tethyidae	*Tethya*	*Tethya* cf. *bergquistae*
N				*Tethya* spp.
T	**Tetractinellida** (Astrophorina)	Ancorinidae	*Ecionemia*	*Ecionemia alata*
S			*Jaspis*	[+]*Jaspis novaezealandiae*
T			*Stelletta*	*Stelletta conulosa*
S				*Stelletta crater*
S				*Stelletta maori*
T				*Stelletta sandalinum*
C		Geodiidae	*Geodia*	*Geodia regina*
N	(Spirophorina)	Scleritodermidae	*Aciculites*	*Aciculites pulchra*
N		Tetillidae	*Cinachyrella*	*Cinachyrella* spp.

N		**Trachycladida**	Trachycladidae	*Trachycladus*	*Trachycladus stylifer*
C	(Subclass Heteroscleromorpha)	**Desmacellida**	Desmacellidae	*Desmacella*	*Desmacella dendyi*
-		**Unknown**			*Heteroscleromorpha* n. sp. 1
-	**Unknown**				^Black+orange cup
-					Dark encrusting sponge
-					^Fluffy cluster sponge
-					^Orange meandering sponge
-					^Oyster mushroom sponge
-					^Possibly tumbleweed sponge
-					Yellow smooth massive sponge

*Indicates species identified in ROV footage and with samples.

^New or undescribed species.

[+] Indicates species only identified in samples, not identified in ROV footage and thus not included in statistical analysis.

[#] Indicates those identified as ‘spp.’ in ROV footage which were included in statistical analysis but not in the combined total species richness calculation as they are not certainly different to the species identified from samples.

Appendix F. Example of optimum point count (OPC) calculation

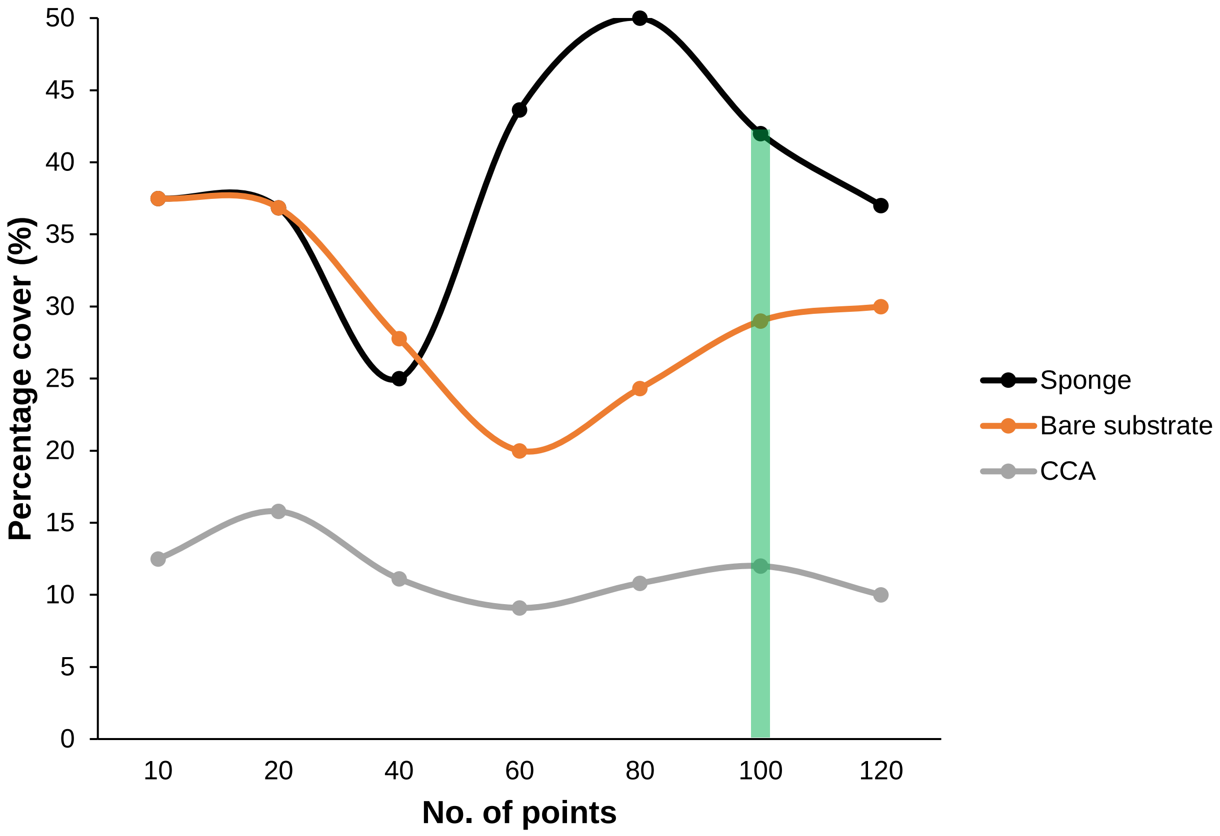


Figure 1. Optimum point count calculation by testing incrementally greater number of stratified random points on a photo quadrat, until the percentage cover curves reach a relative plateau for most groups (represented by the green vertical line). ‘Sponge’ represents all sponge morphologies grouped together, ‘bare substrate’ represents unoccupied rocky substrate covered in a layer of sediment, and ‘CCA’ represents crustose coralline algae.

Appendix G. Example photos of rugosity levels

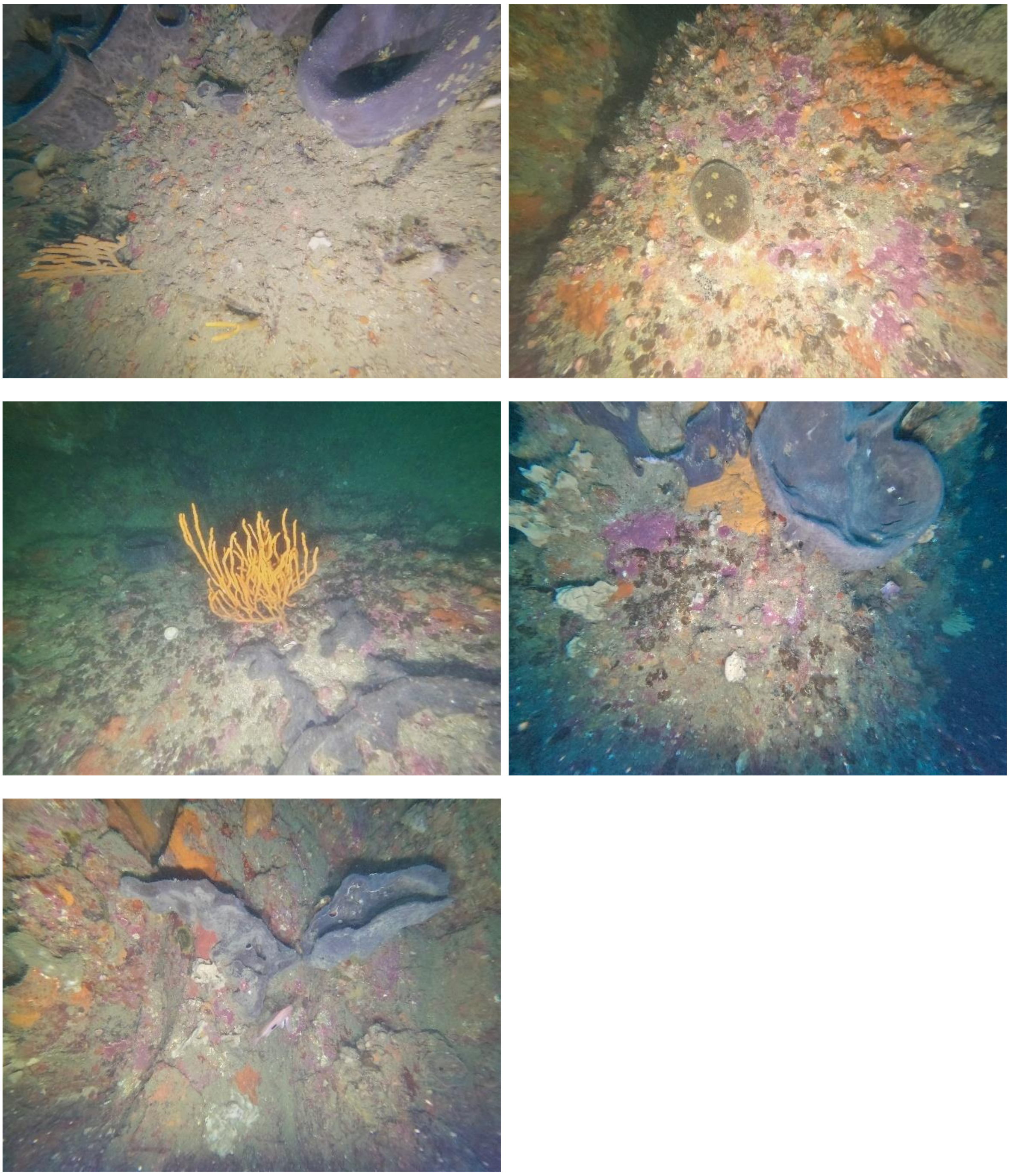


Figure 1. From left to right, top to bottom: examples of each level of rugosity from 1-5.

Appendix H. Diagnostics for Q 1a, Chapter 3

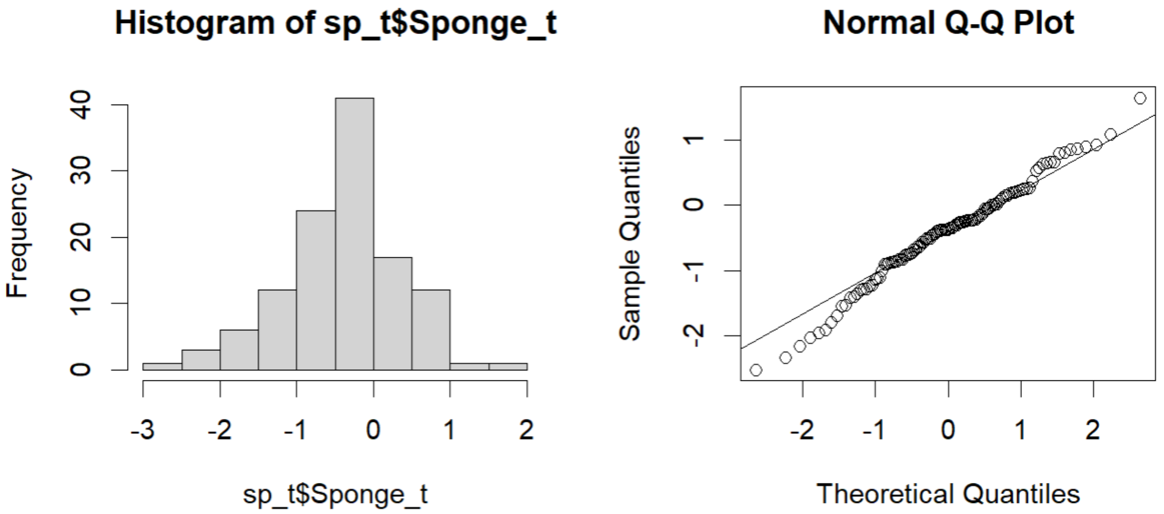


Figure 1. Diagnostic plots of raw response data for testing the assumptions normality, where sponge cover (%, logit transformed) is the response variable. Left: Shows an approximate bell-curve, satisfies the assumption of normality. Right: Shows a relatively straight line of data points suggesting normal distributions, satisfies the assumption of normality.

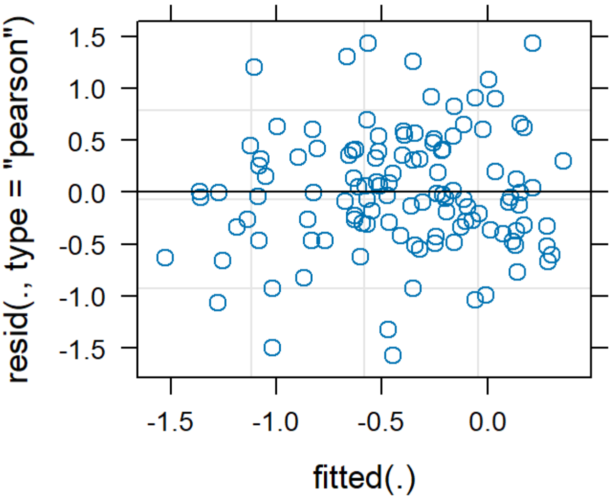


Figure 2. Diagnostic plot of residual vs fitted values for the LME model with Gaussian error distribution, where sponge cover (%, logit transformed) is the response variable, and reef, depth (m), rugosity (index 1-5) and their interaction are the predictor variables. Transect, nested within reef, is included as a random effect. Shows no obvious patterns, satisfies assumptions of model.

Appendix I. Diagnostics for Q1b, Chapter 3

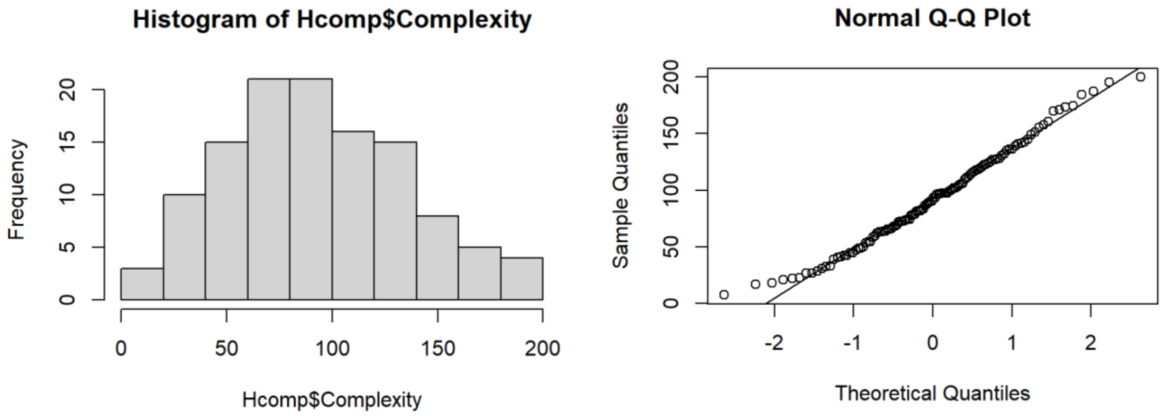


Figure 1. Diagnostic plots of raw response data, where sponge assemblage complexity (qualitative) is the response variable. Left: Shows an approximate bell-curve, satisfies the assumption of normality. Right: Shows a relatively straight line of data points suggesting normal distributions, satisfies the assumption of normality.

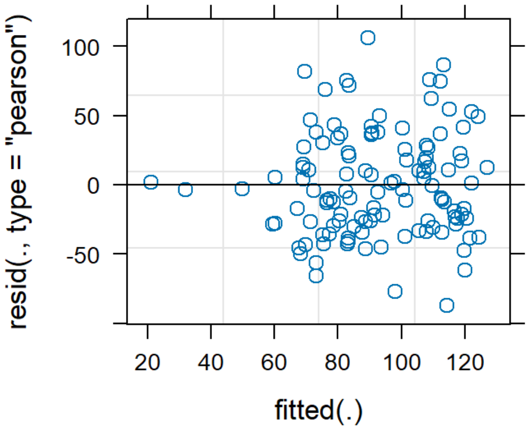


Figure 2. Diagnostic plot of residual vs fitted values for the LME model with Gaussian error distribution, where sponge assemblage complexity (qualitative) is the response variable and reef, depth (m), rugosity (index 1-5) and their interaction are the response variables. Transect, nested in reef, is included as a random effect. Note there is some funnelling of points to the left due to enormously variable data, which is not unexpected. Meets assumptions of the model but the model power may be weakened, which leads to more conservative estimation of trends.

Appendix J. Diagnostics & ANOVA for Q1c, Chapter 3

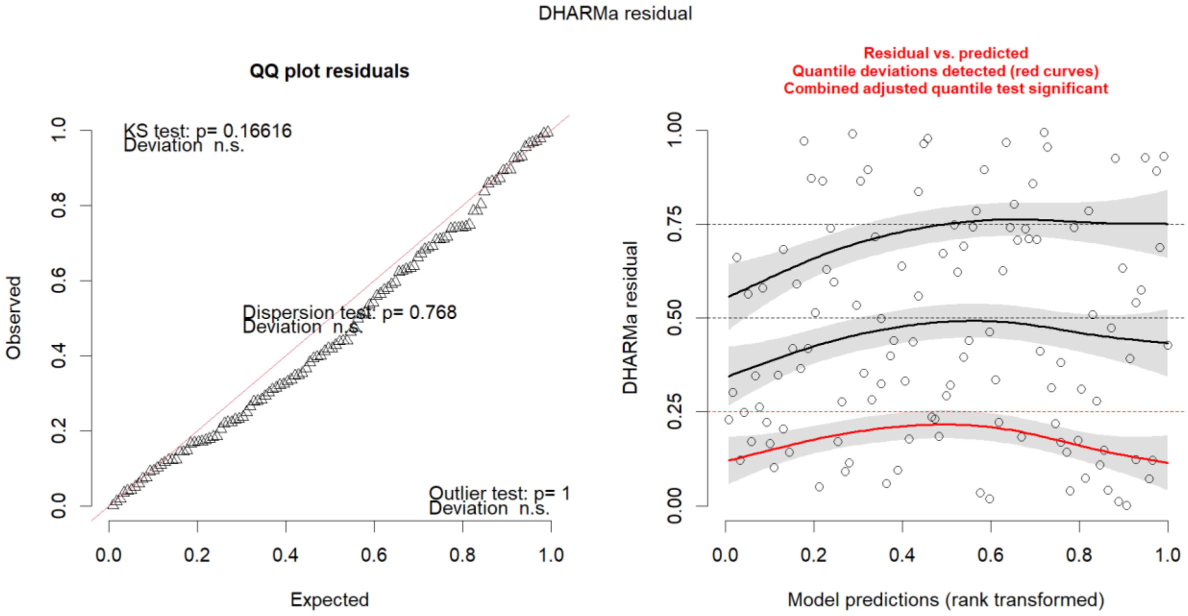


Figure 1. Residuals analysis diagnostic plots for the GLMM with binomial error distribution. The predictor variables are reef, depth (m), rugosity (index 1-5) and bare substrate cover (%, logit transformed), and the response variable is the probability of visible sponge necrosis (%) in a given quadrat. Transect is included as a random effect, nested within reef.

Table 1. Analysis of Deviance summary (Type II Wald Chi^2 tests) for GLMM model with binomial error distribution, where the predictor variables are depth (m), rugosity (index 1-5), bare substrate cover (%, logit transformed) and reef, and the response variable is probability of visible sponge necrosis (%) in a given quadrat. Transect is included as a random effect, nested within reef.

	Chi^2	*df*	*p*(Chisq)
Depth	0.03	1	0.86
Rugosity	7.45	4	0.11
Bare substrate	0.09	1	0.76
Reef	2.35	2	0.31

Appendix K. Diagnostics for Q2, Chapter 3

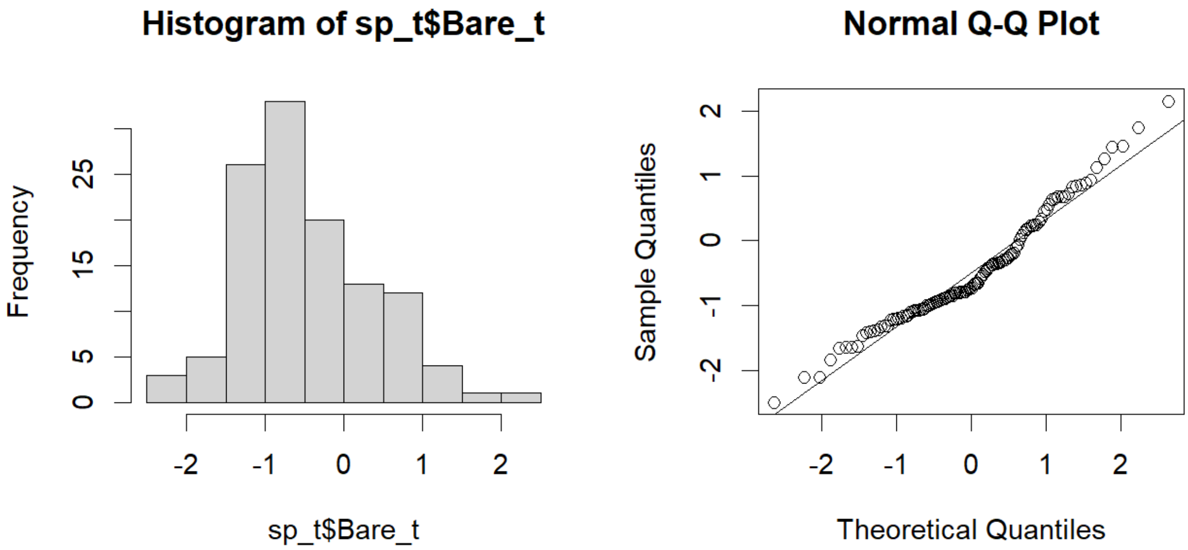


Figure 1. Diagnostic plots of raw response data for testing the assumptions normality, where bare substrate cover (%, logit transformed) is the response variable. Left: Shows an approximate bell-curve, satisfies the assumption of normality. Right: Shows a relatively straight line of data points suggesting normal distributions, satisfies the assumption of normality.

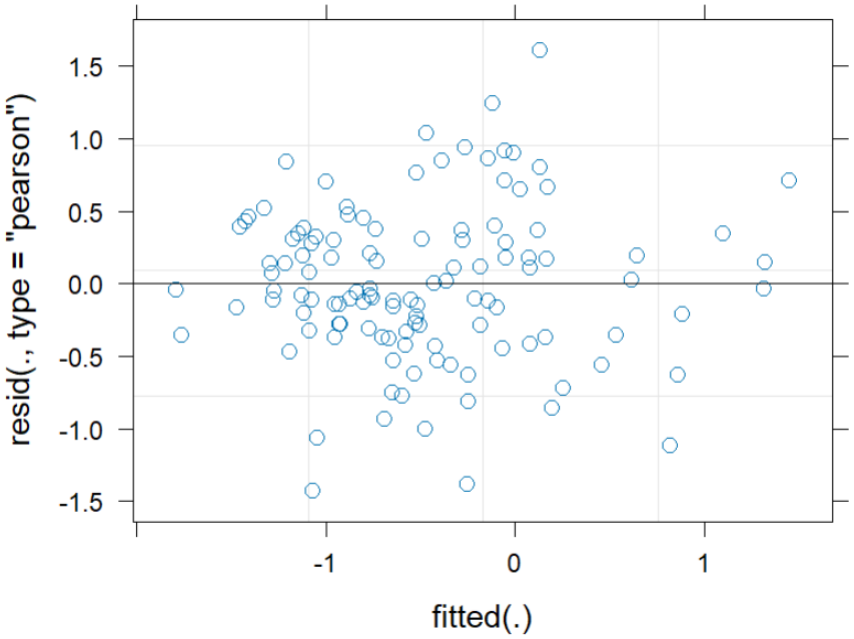


Figure 2. Diagnostic plot of residual vs fitted values for the LME model with Gaussian error distribution, where bare substrate cover (%, logit transformed) is the response variable, and depth (m), rugosity (index 1-5) and reef are the predictor variables. Transect, nested in reef, is included as a random effect. Shows no obvious patterns, satisfies assumptions of model.

Appendix L. Diagnostics for Q3, Chapter 3

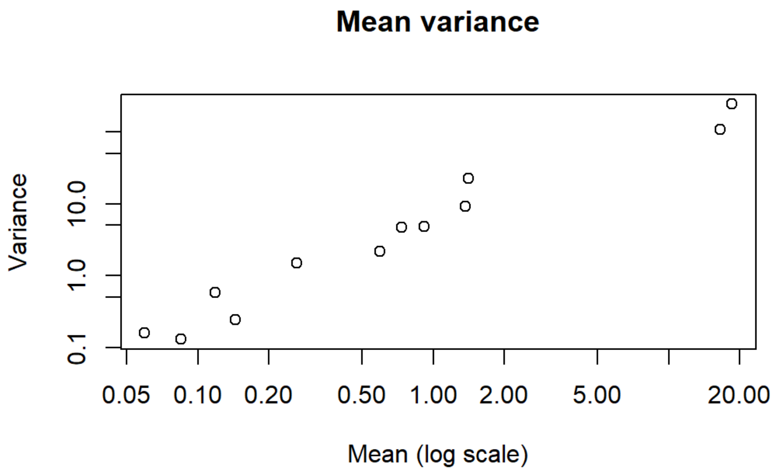


Figure 1. Mean variance relationship plot showing that variance increases as the mean increases, where mean (log scale) is the predictor and variance is the response. This is plotted based on the mvabund model, so it includes all the multivariate data.

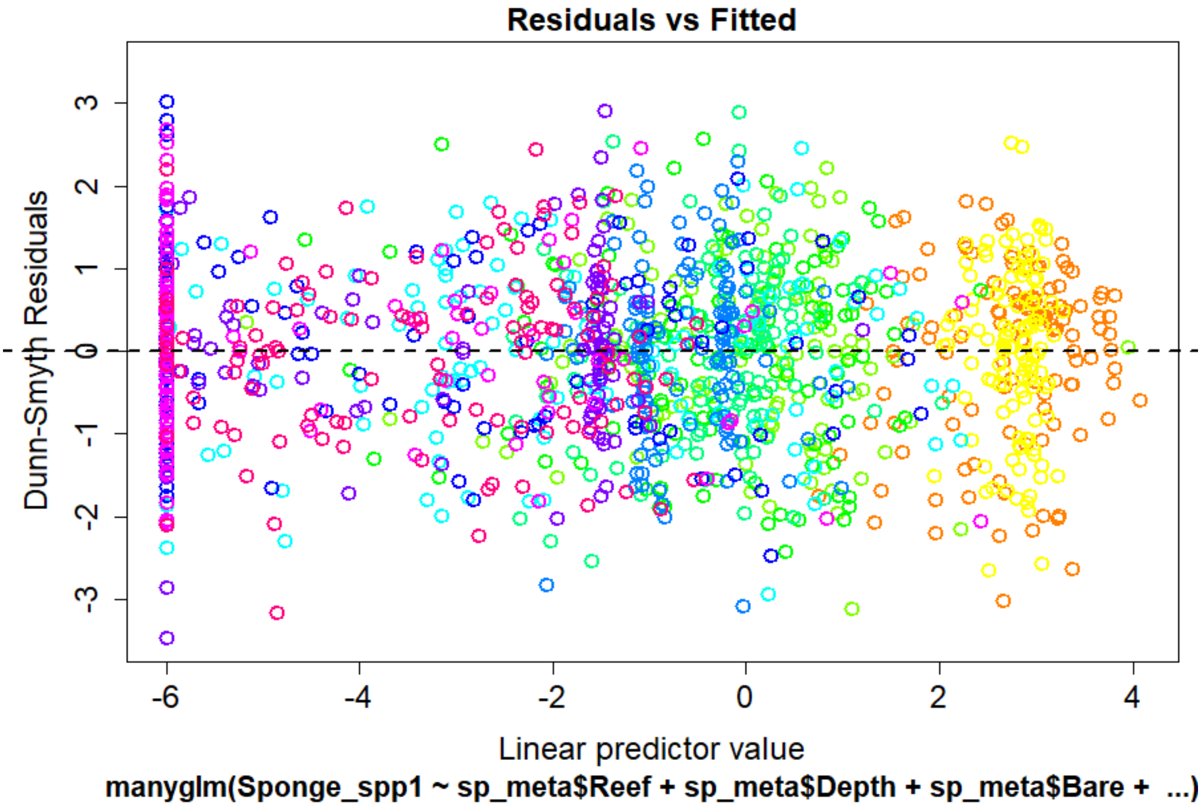


Figure 2. Residuals vs fitted diagnostic plot for the manyglm model with negative binomial error distribution, using the mvabund R package. The predictor variables are reef, depth (m), bare substrate cover (%), and reef and depth interaction, and the response variable is multivariate morphological composition of sponge assemblages. Colours correspond to the different independent variables. Shows no obvious patterns, satisfies assumptions of model.

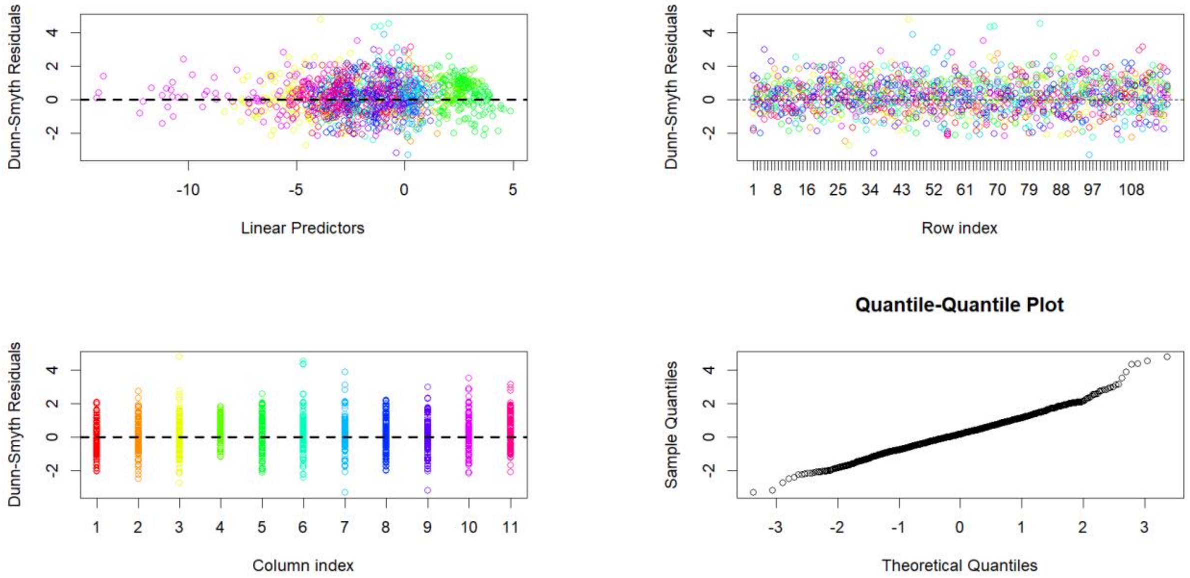


Figure 3. Residuals analysis diagnostic plots for the boral ordination with negative binomial error distribution, using the boral R package. The predictor variables are reef, depth (m), bare substrate cover (%), and reef and depth interaction, and the response variable is multivariate morphological composition (% cover) of sponge assemblages. Colours correspond to the different independent variables. Shows no obvious patterns, satisfies assumptions of model.