Subcanopy Responses to Human-Induced Disturbances:

Astrolabe/Otāiti and Motiti Reefs under the MV *Rena* and Climate Change Stressors

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Abstract

Disturbances are recognised as key drivers of ecosystem change, yet there remains limited consensus on how different disturbance types interact, particularly across trophic levels and within subcanopy communities. Existing theories often overlook the nonlinear relationships between climate-driven stressors and species interactions, underscoring the need for system-specific studies to clarify recovery mechanisms. The grounding of the MV *Rena* on Astrolabe Reef/Otāiti in 2011 resulted in New Zealand's worst maritime environmental disaster. Fourteen years later, this provides a rare opportunity to assess how legacy disturbance interacts with natural variability to influence subcanopy assemblages. This thesis investigated subcanopy dynamics at two Bay of Plenty locations: Astrolabe Reef, directly impacted by the MV *Rena* wreck, and Motiti Island, a nearby reef indirectly affected by the wreck, but directly affected by Cyclone Gabrielle, and both systems subject to fishing pressure, sedimentation, and other stressors. Biodiversity surveys, species inventories and Baited Remote Underwater Videos, were combined with manipulative clearance experiments to test environmental responses. At Astrolabe Reef, small-scale clearances were established in high and low impact zones, while at Motiti Island, large canopy removals in *Carpophyllum spp* and *Ecklonia radiata* transition zones simulated storm-driven disturbance. Quantitative assessments after eleven weeks of the clearances revealed rapid recolonisation but divergent trajectories. At Astrolabe Reef, sites nearer the wreck were dominated by turfing algae and urchins (*Centrostephanus rodgersii*), while more distant sites supported greater sponge richness and habitat heterogeneity. At Motiti Island, opportunists such as kina (*Evechinus chloroticus*) and turfing algae shifted into available space. *Carpophyllum spp*. recovered strongly and expanded downslope, contrasting with the weak recovery of *Ecklonia radiata*. These findings demonstrate that outward canopy recovery can mask deeper structural shifts in subcanopy communities. More broadly, they highlight how legacy disturbance, grazer dynamics, and climate-driven pressures interact to shape resilience pathways in temperate reefs.

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Chapter 1

General Introduction

1.1 Human-Induced Disturbances and the Changing Marine Environment

Human-induced disturbances are fundamentally reshaping Aotearoa's marine ecosystems. In recent years, a complex mix of factors have acted upon coastal rocky reef ecosystems. These factors include the rate of habitat degradation from unregulated fishing practices, pollution from urban centres, nutrient influx from rural regions and arguably most importantly sedimentation from poorly managed catchments (Airoldi, 2003). In addition to the current pressures of human associated stressors, is the longer term and much more serious occurrence of marine heat waves (Gupta et al., 2020; Smith et al., 2023), ocean acidification (Kroeker et al., 2017) and increasing cyclonic events that exacerbate all other stresses on marine systems, especially rocky coastal reefs characterised by kelp forests (Breitburg & Riedel, 2005; Keller et al., 2012; Sala et al., 2012).

Natural disturbances, such as storms, wherein wave action creates patchiness by removing dominant organisms and opening space for new colonisers (Sousa, 1984; Thistle, 1981) are to be expected and enhance the ecological dynamic of reef dwelling organisms, especially benthic species (Dayton, 1971). These events play a central role in maintaining biodiversity and influencing resilience by resetting successional trajectories and aiding recruitment (Palumbi et al., 2009; Seidl et al., 2022). Additionally, total biodiversity loss is rarely caused by natural disturbances, as they increase diversity of niches and structural heterogeneity (Seidl et al., 2022). However, anthropogenic disturbances such as oceanic CO_2 uptake and ocean acidification (Gale & Davison, 2004) influencing marine climate change now dominate many marine environments and differ from ‘past’ natural events in both frequency and scale. Stressors such as organic/inorganic contamination, eutrophication, and sedimentation can fragment habitats, reduce biodiversity, and drive long-term ecological changes (Magris & Ban, 2019; Bhuyan et al., 2025). The interactive and often unpredictable nature of these changes, especially large geographic-scale events like marine heat waves and shifts in oceanic currents can result in outcomes as varied as poleward shifts in species' ranges to the abrupt collapse of previously stable communities (Schiel et al., 2004). Substantial research has been conducted to assess how marine biodiversity is influenced by disturbance regimes

(Sousa, 1984; Dornelas, 2010), but we are now experiencing unprecedented rates and extent of change (Brierly & Kingsford, 2009; Laffoley et al., 2020; Barlow, 2021; Ross et al., 2023).

In Aotearoa, climate-driven stressors compound other stressors. Rising ocean temperatures, shifting currents, and increasingly frequent extreme weather events are altering species distributions and transforming ecosystem dynamics (MacDiarmid et al., 2012; Maxwell et al., 2018; Worm & Lotze, 2021) that are already under stress from coastal land use developments (Schiel & Battershill, 2024). These changes pose risks not only to biodiversity but also to fisheries, tourism, customary harvest, and cultural practices that depend on healthy marine systems (Pinkerton, 2017). Resilience, defined as the capacity of an ecosystem to absorb disturbance while retaining structure and function (Suding & Hobbs, 2009), is central to understanding these processes. Following disturbance, many habitats are unsuitable for immediate recolonisation by dominant species, particularly those requiring specialised substrates (Hewitt et al., 2005). Consequently, opportunistic taxa such as sea urchins often proliferate (Byrne & Andrew, 2013; Schiel, 1982), potentially shifting communities toward simplified, low-diversity states with reduced ecological stability (Scheffer et al., 2001; Thrush et al., 2009). Against this backdrop of global change, human-induced disturbances, especially severe local scale environmental impacts, are increasingly producing novel effects that defy simple predictions. These "ecological surprises" highlight the urgency of improving our understanding of recovery dynamics and thresholds of resilience in marine ecosystems.

1.2 Otāiti/Astrolabe Reef

Astrolabe Reef is located in the Bay of Plenty, approximately seven kilometres north of Motiti Island and 25 kilometres northeast of Tauranga Harbour (37°32.4'S, 176°25.7'E) (Dempsey, 2015). Situated within an archipelago of islands that stretch offshore and parallel to New Zealand's northeast coast, Astrolabe Reef rises from a depth of about 90m to a rock structure that breaks the surface at mid to low tide (Ross et al., 2016). Astrolabe reef experiences stronger wave action and currents compared to Motiti Island due to its exposed location and the deeper waters surrounding it, making it a high-energy marine environment. Only the northeastern promontories of Motiti Island come close to the conditions that Astrolabe Reef experiences. Astrolabe Reef is often affected by a large prevailing northly swell, which further influence the reefs diverse community.

Astrolabe Reef is recognised as an "Area of Significant Conservation Value" because it serves as a key haul-out site for the New Zealand fur seal, *Arctocephalus forsteri* (Dempsey, 2015). It has only recently come under protection (along with a number of the other reefs in the 'Motiti Archipelago'), and has had a complex recent history as will be discussed below. Like other reserves in north-eastern New Zealand, the Motiti Protection Area (MPA) is also influenced by the East Auckland Current, which brings in warmer, tropical waters (Figure 1). This current plays a significant role in shaping the local marine environment, potentially enhancing biodiversity by supporting species that thrive in warmer conditions. The reef is known for its diverse ecological community, including a wide variety of species such as benthic and pelagic fish, sponges, molluscs, urchins, and macroalgae (Robertson, 2014), which contribute to its importance as a unique marine habitat.

In 2021, Astrolabe Reef was designated as a marine protected area within the Motiti Protection Zone. This was after a time where it was 'effectively' protected during the Marine Vessel (MV) *Rena* salvage, then opened up again to fishing (see below). As one of the newest marine protected areas, the Motiti Protection Area faces unique challenges influenced by the *Rena* wreck and its location within an archipelago (Urlich, 2020). The new reserve adds an interesting element for comparison between Motiti and Astrolabe (Motiti Island remains open to fishing), at a time of unprecedented climatic change and pressures. Hence to some extent mindful of locational factors, discussed below there is an opportunity to examine the interactions of a number of human associated stressors (of different scales) on Astrolabe Reef such as shipwreck pollution and scouring combined with cyclonic and marine heat wave stress. An adjacent, non-protected reef system at Motiti Island offers a comparative site with broadly similar habitat may be found. Importantly, the establishment of the Motiti Protection Area also forms part of the backdrop to Astrolabe Reef's recovery, with the presumed restoration of a potential trophic cascade as reef-associated fishes such as blue cod, red moki, and leatherjackets return, influencing subcanopy communities through their interactions with kina and other grazers (Shears & Babcock, 2002; Schiel et al., 2016).

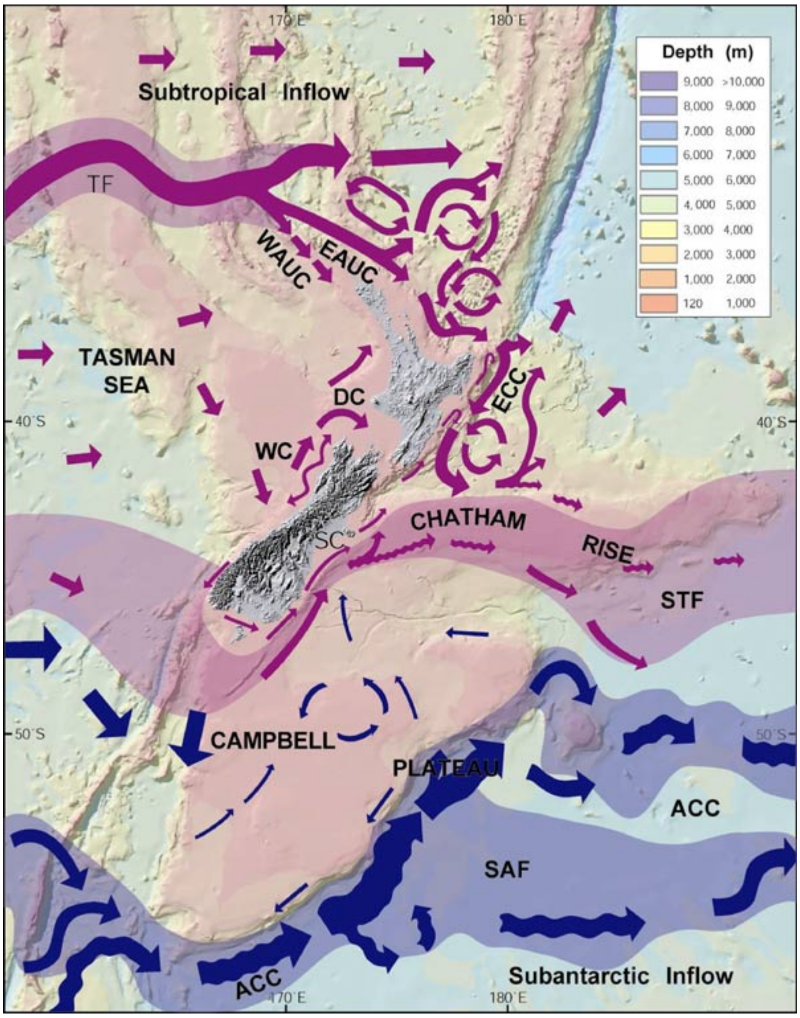

Figure 1. A depiction of prevailing currents around New Zealand. EAUC (East Auckland Current) flowing through the Bay of Plenty (Carter, 2001).

1.3 MV *Rena* Disaster

At 0214 hours on 5 October 2011, the Liberian-flagged container vessel MV *Rena*, weighing 38,788 tonnes and measuring 236 meters in length, struck Otāiti/Astrolabe Reef. The ship was traveling at a speed of 17 knots when a series of human errors caused it to hit the reef (Ministry for the Environment, 2014; Schiel et al., 2016). The vessel had changed course to approach the harbour more directly before its pilotage window closed at 0300 hours (Webby, 2014). At the time of the incident, the MV *Rena* was carrying 1,368 containers, along with 1,733 tonnes of heavy bunker fuel oil (HFO 380) and smaller amounts of other fuels and oils (Orchard et al., 2020). Among these were 121 containers with perishable goods and 32 holding dangerous goods (McLean, 2018).

The first Maritime New Zealand inspector boarded the MV *Rena* just over 3 hours after the grounding had occurred. At 0700 hours, just five hours after the grounding, the MV *Rena* grounding was declared a Tier 3 event by the Director of Maritime New Zealand, marking the highest level of action under New Zealand's Marine Oil Spill Response Strategy (Julian, 2012). The oil, cargo, and equipment were carried by ocean currents and tides, causing significant environmental effects across the Bay of Plenty region.

On 6 October, deceased oiled wildlife were first seen at sea, highlighting the environmental impact of the spill (Gartrell et al., 2019). A significant challenge in the success of the response was the delay in obtaining the ship's manifest. When it was eventually provided, many items were poorly labelled, causing confusion over whether they were dangerous or harmful. In the first five days following the wreck, calm weather allowed initial response efforts to begin, including attempts to pump oil from the vessel. However, on the fifth day, the weather worsened, bringing in 5-7m swells, and the ship began to shift position on the reef. On 12 October, the first containers were seen falling overboard. By the 13 October, approximately 350 tonnes of oil had washed up on nearby Papamoa Beach (McLean, 2018).

By 4 May 2012, the response status was downgraded from Tier 3 to Tier 2, marking the beginning of the recovery phase. Management responsibilities were then transferred to a Regional On-Scene Commander. As a result of environmental risks and safety concerns, a two-nautical-mile exclusion zone was established around the wreck site, and access to the area was restricted until 5 April 2016. At that time, the reef was reopened to fishing, with an immediate impact on targeted fish stocks. In response, an iwi collective sought and won protection status for the reef and a number of the other islands/reef systems in the Motiti Archipelago (RMLA, 2020). It is against this backdrop that this study has been designed, in order to examine the possible ramifications of both the current protection status, with a focus on the area most affected by the shipwreck. Of relevance here to the focus on the kelp forest habitat and the subcanopy benthos, ecological dynamics near and distant to where the ship grounded and where there was subsequent massive scouring by the hull and release of a mixture of contaminants, most importantly metals.

1.3.1 Historic Data

The effects of oil spills on marine communities are complex and depend on multiple factors, including the type of oil, the quantity spilled, and the remedial actions taken in response (Battershill & Bergquist, 1982; Ministry for the Environment, 2014). While oil spills have often been documented to cause lethal impacts on marine ecosystems (Saadoun, 2015; Akpan, 2022; Maurya & Gupta, 2024), not all incidents result in widespread mortality, and effects can be both direct and indirect (Schiel et al., 2016). The grounding of the MV *Rena* on Astrolabe Reef in 2011 made it extremely clear that New Zealand was not adequately prepared for a marine environmental disaster of this scale, particularly in terms of predicting and managing ecological toxin effects as evidenced in the independent review by Murdoch (2013).

The grounding of the MV *Rena* is New Zealand's worst ever maritime disaster and the second most expensive vessel wreck to recover from and manage (Schiel et al., 2016). Compared to other marine disasters internationally, the MV *Rena* event was considered relatively small in scale. For example, the BP Deepwater Horizon oil spill in April 2010 was the second-largest oil spill in human history, releasing over 800 million tonnes of oil into the Gulf of Mexico (Barron, 2012). A key distinction of the MV *Rena* disaster, however, was contamination of a mixture oils, other hydrocarbons, heavy metals, and dangerous goods, and importantly the substantial scour of an offshore reef system by the ship's hull as it broke up and slid down the reef releasing hull antifouling paint called Tributyltin (Battershill et al., 2016). Also unique, was the swift initiation of a scientific monitoring program within hours of the wreck, setting it apart from many other incidents where scientific responses were delayed and allowing for acquisition of ecological information 'before' the event fully unfolded was possible. Although initial concerns predicted catastrophic environmental consequences, long-term monitoring over the past 14 years has shown that while impacts exist, they are not as severe as initially feared, at least superficially. However, close inspection of the full dynamic of the reef, especially beneath the kelp forest cover, has not until now been carried out until now.

On the same day as the wreck, the New Zealand National Oiled Wildlife Response Team (NOWRT) was mobilised as part of the coordinated spill response, establishing an oiled wildlife treatment facility in Tauranga. In 2013, a comprehensive environmental monitoring programme was established to assess contaminant concentrations in sediments and fauna around Astrolabe Reef and Motiti Island, aiming to understand the potential for ongoing contamination linked to the *Rena*. This generated macro-scale information on the distribution and abundance of key habitat types (e.g. kelp forest, or urchin grazed areas), and the ecotoxicology of selected fish and invertebrates focusing on heavy metal accumulation or otherwise. Detailed biodiversity surveys were not carried out.

Previous surveys also examined the rate of spread/retention of metal and organic contaminants (Ross, 2023). Sediment samples collected from sites near to where the ship grounded and sank recorded the highest levels of tributyltin (TBT) detected since 2015; while these concentrations were elevated compared to recent years, they remained below the thresholds that would trigger additional monitoring or management responses. At four out of five outer reef sampling sites, TBT was also detected at concentrations ranging from 0.0028 to 6.2 mg/kg (see below and Appendix A: Figure 1). These findings indicated ongoing concern around settlement and accumulation of contaminants that may also be affecting reef communities and encrusting benthos associated with kelp forests. Ref

The most recent monitoring report, conducted by Beca Limited (2024) on behalf of the Astrolabe Community Trust, concluded that the overall ecology of Otāiti remains healthy, with an abundance of fish, plants, and invertebrate life (assessed from examining only a few reefs invertebrate species such as kina) in and around the reef and the wreck. Despite the continued presence of TBT and the isolated ecological effects of the copper clove deposit, the reef's environmental health appears stable (Ross, 2023). The monitoring results indicate no significant emerging ecological threats and confirm that no immediate actions are required to address existing issues. Although macroalgal cover in the shipwreck-affected area seems to have fully recovered, the dynamics of the subcanopy have yet to be investigated and a detailed biodiversity inventory along with associated ecological assessments has yet to be completed, hence the focus of this research.

1.4 Thesis Preface

1.4.1 Aims and Objectives

Given this context, there is a clear scientific and management imperative to look deeper—literally and figuratively, into the responses of subcanopy communities following acute human-induced disturbance events. The case of the MV *Rena* disaster, with its detailed history of monitoring, proximity to control and comparison sites (such as Motiti Island), and recent marine protection status, offers an ideal natural experiment to address this knowledge gap. While 'superficial' macroalgal recovery has been studied, subcanopy ecological responses and dynamics remain poorly understood. How do different subcanopy communities respond to the array of disturbances experienced?

This thesis is designed to fill that gap by integrating comparative, experimental, and observational approaches to analyse the structure, function, and dynamics of subcanopy communities at Astrolabe Reef post-MV *Rena* disaster. By drawing on both biodiversity surveys (herbarium and benthic encrusting invertebrate collections, and Baited Remote Underwater Video) and targeted experimental manipulations (macroalgal removal, substrate clearing near and distant to disturbance sites), and by explicitly comparing outcomes with those at Motiti Island (an adjacent location experiencing intensive fishing and other pressures), I seek to understand the mechanisms by which disturbance affects subcanopy recovery and ecosystem resilience.

By doing so, this research contributes not only to our local understanding of Astrolabe Reef but also to the broader global discourse about how best to predict, manage, and mitigate the ecological impacts of human-induced marine disasters.

1.4.2 Thesis Format

This thesis has presented as a series of publishable units, with modifications made to minimise repetition. The following chapters are structured as follows:

Chapter 2 - Explores biodiversity at Astrolabe Reef and Motiti Island, detailing methods for characterising species richness, with particular attention to herbarium and encrusting invertebrate collections and Baited Remote Underwater Video (BRUV) approaches.

Chapter 3 - Presents the results of clearance and manipulation experiments, examining the short and long-term impacts of macroalgal removal and physical substrate clearing on subcanopy community assembly, dominant species recruitment, and succession dynamics near and distant to areas of reef damage from the MV *Rena* shipwreck.

Chapter 4 – Presents the results of a larger-scale kelp transition zone clearance, replicating a larger storm event, here to further examine effects of a changing climate linked to the likelihood that a new dynamic between the major invertebrate grazers (urchins *Evechinus chloroticus* and *Centrostephanus rodgersii*) that may also be influencing recovery and resilience of the reef kelp forest ecology.

Chapter 5 - Provides a synthesis across all research elements of this project, and articulates a general discussion on the main drivers of recovery and resilience in response to a shipwreck exacerbated by significant climate change events while possibly being mitigated somewhat by protection status. A review of a three-way dynamic and offering recommendations for management of reef systems and future research.

The thesis ultimately aims to generate fundamental insights into how broad-scale disturbances interact with fine-scale ecological processes beneath the kelp canopy, highlighting the importance of subcanopy dynamics in driving long-term resilience.

Chapter 2

Biodiversity at Astrolabe Reef and Motiti Island

2.1 Introduction to Biodiversity

Biodiversity, broadly defined as the variability among living organisms from all sources, underpins the functioning and resilience of marine ecosystems (DeLong, 1996). Marine biodiversity is expressed through the richness and abundance of species, the diversity of habitats, and the complexity of ecological interactions linking primary producers to apex predators. The maintenance of biodiversity is essential for sustaining ecosystem services (Palumbi et al., 2009) such as fisheries productivity (Boehlert, 1996), coastal protection, and nutrient cycling, while also supporting cultural and recreational values for coastal communities (Ruiz-Frau et al., 2013). Paradoxically, the diversity of life in the ocean is being dramatically altered by the rapidly increasing and potentially irreversible effects of a changing climate (Sala & Knowlton, 2006; Gamfeldt et al., 2015). Anthropogenic drivers such as overfishing (Rieser, 1996; Shao, 2009, Craig, 2012), pollution and coastal habitat degradation, togeter with larger scale climate change (Worm & Lotze, 2021) are reshaping the composition and distribution of marine life at local, regional, and global scales (Cheung et al., 2009; Pawar, 2016).

The recovery of the Astrolabe Reserve is expected to be shaped by an interplay of top-down and bottom-up processes. Predator species such as snapper (*Pagrus auratus*) and rock lobsters (*Jasus edwardsii)* are anticipated to recover under protection, consistent with patterns observed in other New Zealand reserves where predator rebounds have triggered trophic cascades (Shears & Babcock, 2003; Schiel, 2013; Edgar et al., 2017). However, bottom-up limitations caused by contamination and habitat loss may constrain recovery, producing outcomes that diverge from reserves where ecosystems were less disturbed prior to protection (Posey et al., 2002). The influence of the East Auckland Current adds further complexity (Stevens et al., 2021). This current delivers warm subtropical waters that support species more typical of northern reef ecosystems, potentially enhancing biodiversity in the Motiti archipelago. Additionally, warming waters and the increasing frequency of marine heatwaves are also exerting stress on temperate reef assemblages, with impacts documented even at mesophotic depths (Donald, 2023). These dual influences highlight the unique setting of

Astrolabe Reef where anthropogenic disturbance and natural oceanographic drivers intersect to shape ecological trajectories.

The combination of predator recovery, oceanographic influences, and legacy impacts from anthropogenic disturbance at Astrolabe Reef creates a unique case study to investigate how different disturbances interact with each other.

Importantly, these drivers do not act in isolation. Changes at one trophic level or environmental driver cascade through the system, directly and indirectly shaping recovery outcomes. For instance, the resurgence of predators may restructure prey populations, but the scale of these effects is dependent on whether benthic habitats and primary producers can recover in the face of contamination and warming seas. Likewise, bottom-up stressors such as nutrient limitation or reef damage can constrain the ecological benefits of predator protection, altering long-term trajectories of recovery. The interplay of these processes emphasise why biodiversity must be viewed as a dynamic and interconnected system, where ecological, oceanographic, and anthropogenic factors continually interact. Understanding these interactions is central to predicting recovery at Otāiti and highlights the broader need for integrated approaches to marine conservation in a changing climate.

2.1.1 Aims and Objectives

The primary aim of this chapter is to establish a baseline understanding of biodiversity at Astrolabe Reef and Motiti Island within the Motiti Protection Area. This involves compiling a species inventory across multiple trophic levels and characterising the structure of local communities. A key component of this study is the comparison of biodiversity at Astrolabe Reef with that of neighbouring Motiti Island, enabling the identification of similarities and differences in community composition between the two sites. Another key aim was to assess how fish communities change depending on the proximity to the wreck, as well as different reef locations. By developing this baseline, the research provides a foundation for long-term monitoring and contributes to understanding how biodiversity patterns at Astrolabe Reef are shaped by the direct and indirect effects of human-induced disturbances.

2.2 Baited Remote Underwater Video

2.2.1 Method

This component of the study was carried out in accordance with the Department of Conservation (DOC) Baited Remote Underwater Video guidelines (Haggitt et al., 2014), the DOC Marine Monitoring Toolbox (Zintzen, 2016), and the Bay of Plenty Regional Council's 2022 BRUV report (Crawshaw, 2022). The work also followed the regional monitoring structure developed by Bay of Plenty Regional Council and forms part of a larger collaborative project.

2.2.2 Field Method

Purpose-built Department of Conservation "L-Frames" were used for all deployments (Figure 2). Each frame consisted of an L-shaped aluminium structure fitted with a GoPro Hero 11 or a GoPro Hero 8, mounted at the top of the vertical arm. A measurement scale marked at 100 mm intervals was fixed along the frame base. To maintain a stable orientation of the cameras toward the seabed, small floats were attached to the camera housing. The bait box was reloaded before each drop with 300 g of defrosted, chopped jack mackerel (*Trachurus novaezelandiae*). Surveys were undertaken on 8 November 2024 at Astrolabe Reef (sites AST3 and AST6) and Motiti Island (sites MT1 and MT2). A total of 12 deployments were conducted, with three replicates at each site. Frames were deployed between 08:47 and 13:40 NZST, and soak times ranged from 31–36 minutes, yielding approximately 30 minutes of usable footage per deployment.

Deployments were carried out in calm sea conditions with base swell <0.1 m, during daylight hours and under predominantly sunny weather. Water temperature was approximately 17–20°C, and underwater visibility ranged from 8–10 m. Depths of deployments varied between 15.1 m and 22.2 m at Astrolabe Reef (rocky reef habitats with varied topography and steep drop-offs), and between 17.3 m and 22.2 m at Motiti Island (rocky bottoms and sandy flats). Distances to the nearest reef ranged from 100 m to 240 m. Environmental conditions (tide state, current direction, swell, and visibility) were recorded at each deployment using standardised DOC marine reserve monitoring toolbox datasheets. All fish and invertebrate species observed in the footage were identified and counted, with the exception of triplefins (family *Tripterygiidae*), butterfly perch (*Caesioperca lepidoptera*), and two-spot demoiselles (*Chromis dispilus*). These taxa were excluded from analyses due to the difficulty of accurate identification (triplefins) and the high densities and schooling behaviour that made reliable counts impractical (butterfly perch and two-spot demoiselles).

For analysis, the maximum number of individuals of each species observed in a single frame (MaxN) was recorded as a measure of relative abundance. MaxN values were calculated from 30-second time bins over each 30-minute deployment, with the highest MaxN for each species retained for subsequent analysis.

Figure 2. Baited Remote Underwater Video “L” shaped frame

2.2.3 Data Analysis

2.2.3.1 Relative Abundance Method

Baited Remote Underwater Video (BRUV) deployments were undertaken at four fixed sites: AST3 and AST6 at Astrolabe Reef (protected) and MT1 and MT2 at Motiti (unprotected). Each site was sampled with three replicate deployments (total n=12) For every deployment and species, relative abundance was quantified as MaxN, the maximum number of individuals observed simultaneously in a single frame. Four common reef fishes were specified prior as indicator species for species-specific analyses: snapper *Pagrus auratus*, blue cod *Parapercis colias,* red pigfish *Bodianus unimaculatus*, and scarlet wrasse *Pseudolabrus miles*. Data were reshaped to a long format with columns for species, site (AST3, AST6, MT1, MT2), replicate (1–3), and MaxN. For the primary hypothesis test related to protection status, sites were collapsed to a two-level factor ("Reef") contrasting Astrolabe (AST3, AST6) with Motiti (MT1, MT2); a binary "Protection" indicator (protected vs unprotected) was retained for plotting.

All analyses were conducted in R (Version 2025.05.1+513). For each indicator species, relative abundance (MaxN) was modelled using a generalized linear model with log link and Poisson errors. Overdispersion was evaluated from the Pearson residual chi-square divided by residual degrees of freedom; where this exceeded ~1.5, models were refitted using a quasi-Poisson family and quasi-likelihood standard errors were used for inference. Standard diagnostic plots were inspected to assess model fit and dispersion. Effect sizes are reported as log rate differences and as back-transformed rate ratios (Astrolabe/Motiti). Because blue cod were not present at Astrolabe, which can induce separation and unstable GLM coefficients, the GLM inference for that species was complemented with an exact two-sample Poisson rate test comparing reefs. To aid interpretation at the finer spatial scale, site-level patterns were also visualised and, where appropriate, explored with Tukey-adjusted pairwise contrasts among the four sites using the "multcomp" function.

2.2.3.2 Species Richness and Diversity

For each BRUV deployment at each site (AST3, AST6, MT1, MT2), species richness was calculated as the number of species with MaxN > 0 and species diversity as the Shannon index using the vegan diversity function. Site effects on richness and Shannon diversity were tested with a one-way Gaussian GLM/ANOVA. Where useful for interpretation, a Tukey HSD post-hoc comparisons among sites with multiplicity adjustment was completed. Summary statistics are reported as mean ± SD, with n=3 deployments per site.

2.3 Results

The Baited Remote Underwater Video deployments revealed clear contrasts in fish assemblages between Astrolabe Reef and Motiti Island, reflecting both protection status and local habitat variation (Table 1). A range of reef-associated species were recorded, including predatory taxa such as snapper (*Pagrus auratus*) and red pigfish (*Bodianus unimaculatus)*, as well as benthic associates like hiwihiwi (*Chironemus marmoratus*) and leatherjackets (*Meuschenia scaber*). Notably, total abundance was highest at the protected Astrolabe sites, while Motiti sites particularly MT2 supported few or no reef fish. It should be noted that MT2 was located on a sandy flat adjacent to reef habitat, which likely accounts for the absence of reef-associated species recorded there. These observations highlight the role of habitat complexity and reserve protection in shaping community structure and provide a baseline for evaluating long-term ecological responses in the Motiti Protection Area.

Table 1. Frequency of occurrence and total abundance of species observed during Baited Remote Underwater Video (BRUV) deployments at Astrolabe Reef (AST3, AST6) and Motiti Island (MT1, MT2). "No. sites" indicates the number of sites where each species was recorded. Site totals represent the summed abundance across the three replicate deployments at each site.

Scientific name	Common name	No. sites	AST3 (n=3)	AST6 (n=3)	MT1 (n=3)	MT2 (n=3)
Pseudolabrus miles	Scarlett Wrasse	3	9	8	7	0
Pagrus auratus	Snapper	3	17	7	4	0
Parapercis colias	Blue Cod	1	0	0	2	0
Chironemus marmoratus	Hiwihiwi	2	2	0	2	0
Meuschenia scaber	Leather jacket	2	0	1	1	0
Cheilodactylus spectabilis	Red Moki	3	1	1	1	0
Bodianus unimaculatus	Red Pigfish	3	14	20	9	0
Gymnothorax prasinus	Yellow Moray	2	7	0	2	0
Hypoplectrodes huntii	Red banded perch	1	0	1	0	0
Helicolenus percoides	Sea perch	1	0	2	0	0
Scorpaena cardinalis	Scorpionfish	2	4	6	0	0
Jasus edwardsii	Crayfish	2	1	5	0	0
Upeneichthys lineat	Goat fish	2	2	2	0	0
Suezichthys aylingi	Crimson Cleanerfish	1	2	0	0	0
Lotella rhacinus	Largetooth Beardie	2	5	3	0	0
Pempheris adspersa	Big Eye	1	1	0	0	0

Bodianus flavipinnis	Yellowfin Pigfish	1	0	2	0	0
Latridopsis ciliaris	Blue Moki	1	0	1	0	0
Notolabrus fucicola	Banded wrasse	1	0	1	0	0
Macroctopus maorum	Common octopus	1	0	0	1	0
Notolabrus celidotus	Spotty	1	0	0	1	0
Total Number of Fish		4	65	60	30	0

2.3.1 Relative Abundance

Across the four indicator species, relative abundance tended to be higher at the protected Astrolabe Reef than at Motiti (Figure 3). In reef-level GLMs contrasting Astrolabe with Motiti, snapper were more abundant at Astrolabe, with an estimated log rate difference of 1.79 ± 0.83 ($p=0.05$p), equivalent to an Astrolabe/Motiti rate ratio of approximately six. Red pigfish showed a clear effect, with abundance significantly higher at Astrolabe ($p<0.001$p), corresponding to a rate ratio of about 3.78. Scarlet wrasses were also more abundant at Astrolabe (0.887 ± 0.449), a rate ratio of roughly 2.43. Blue cod were detected only at Motiti (two individuals in one of six Motiti deployments) and not at Astrolabe (zero of six deployments). As expected with these zeros, the GLM coefficients were unstable; an exact two-sample Poisson rate test indicated no evidence of a difference in rates between reefs ($p=0.50$). Full model coefficients, standard errors, p-values, and back-transformed rate ratios with 95% confidence intervals are provided in Appendix B: Table 1. Visual inspection of the abundance distributions indicates that variance structure was largely driven at the site level, with greater dispersion among local sites than between reefs overall. This suggests that local-scale variability contributed substantially to observed abundance patterns within each reef.

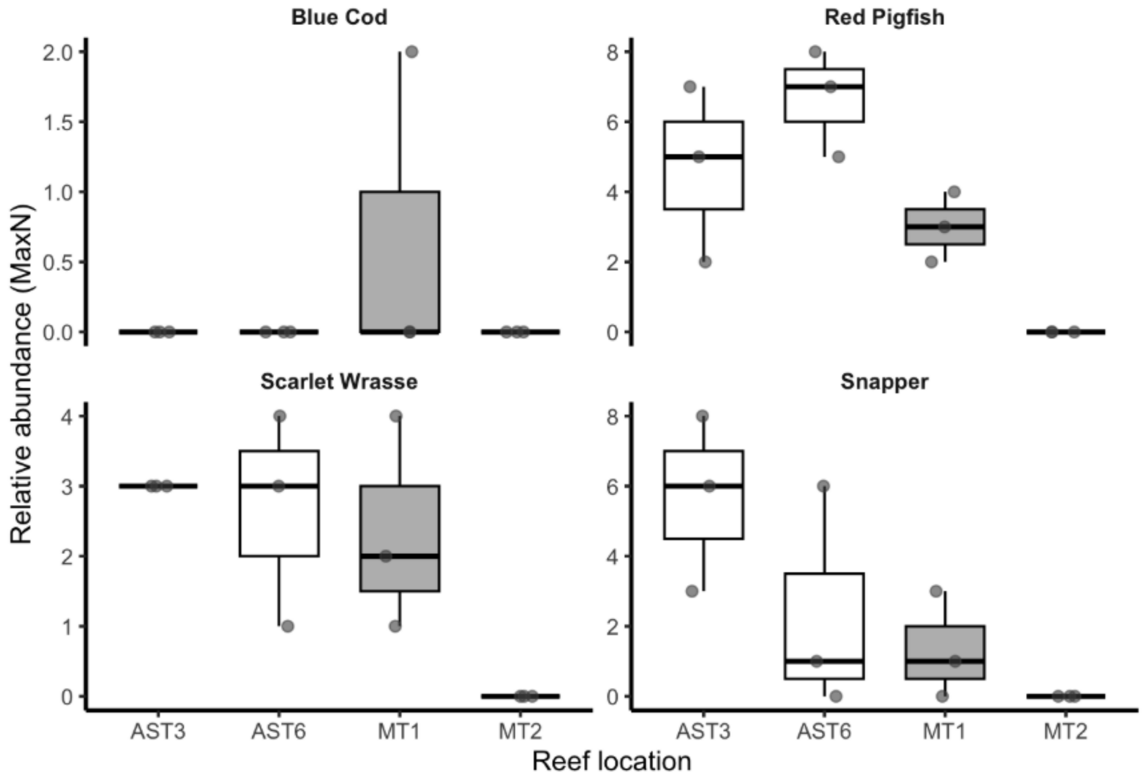

Figure 3. Relative abundance (MaxN) of four indicator fish species across reef locations AST3 and AST6 (Astrolabe; protected) and MT1 and MT2 (Motiti; unprotected). Panels are A — Blue cod (*Parapercis colias*), B — Red pigfish (*Bodianus unimaculatus*), C — Scarlet wrasse (*Pseudolabrus miles*), D — Snapper (*Pagrus auratus*). Boxes show the interquartile range (25th–75th percentiles) with the median indicated by the horizontal line; points are individual deployments jittered for clarity. Protected sites are plotted with white boxes and unprotected sites with grey, with error bars showing standard error.

2.3.2 Species Richness and Diversity

Mean species richness of fish, octopus and crayfish was calculated across each of the reef sites (Table 2, Figure 4) Mean species richness differed significantly among sites ($p = 0.001$). Richness was highest at the protected Astrolabe sites. Tukey HSD showed that MT2 was significantly lower than AST3 ($p = 0.0011$), AST6 ($p = 0.0015$), and MT1 ($p = 0.0167$); differences between AST3 and AST6 and between the Astrolabe sites and MT1 were not significant at $\alpha = 0.05$ given $n = 3$ per site.

Shannon diversity also varied strongly among sites (p = 8.0 × 10^-6), mirroring the richness pattern. Diversity was highest at Astrolabe. Tukey HSD indicated significantly lower diversity at MT2 relative to AST3 ($p < 0.001$), AST6 ($p < 0.001$), and MT1 ($p = 0.001$); contrasts among AST3, AST6, and MT1 were not significant at $\alpha = 0.05$.

Table 2. Species richness and Shannon diversity across monitored sites (mean ± SD; n=3 deployments per site).

Site	Count	Richness (Mean)	Richness (SD)	Shannon (Mean)	Shannon (SD)
AST3	3	8.33	0.58	1.93	0.02
AST6	3	8.00	3.00	1.75	0.33
MT1	3	5.33	1.15	1.52	0.21
MT2	3	0.00	0.00	0.00	0.00

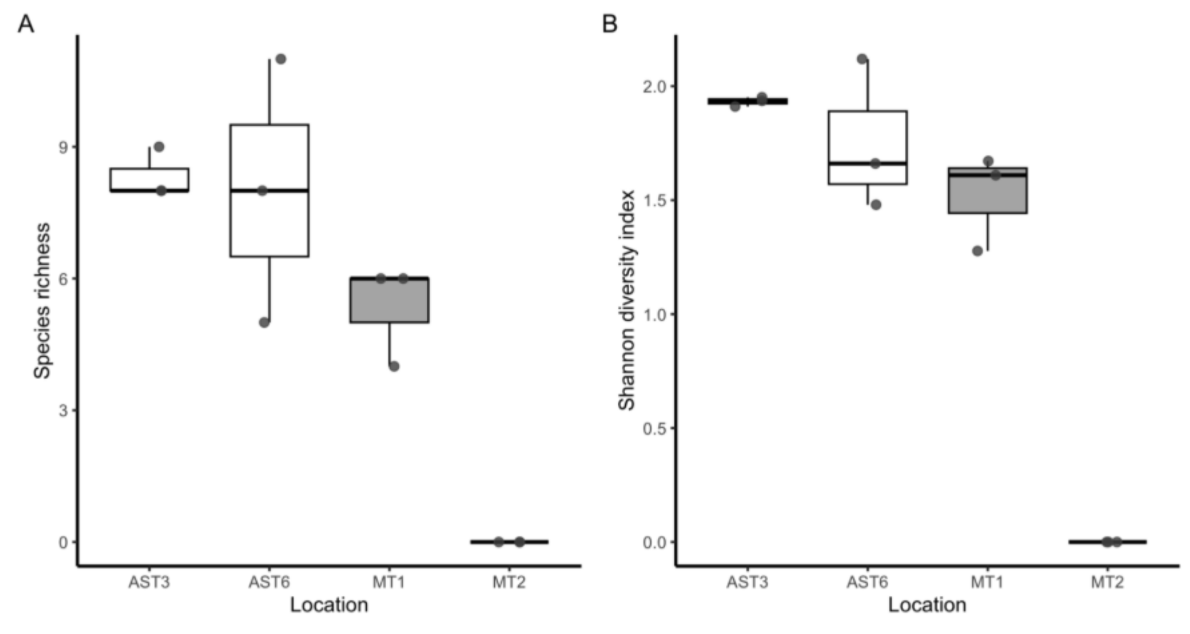

Figure 4. Boxplots of species richness (A) and Shannon diversity index (B) across the surveyed reef sites. Boxes show the interquartile range (25th–75th percentiles) with the median as a horizontal line; points are individual deployments. Protected sites are plotted in white and unprotected sites in grey. Error bars showing standard error.

2.4 Discussion

The Baited Remote Underwater Video (BRUV) surveys revealed clear differences in reef fish assemblages between Astrolabe Reef and Motiti Island, with higher relative abundance, species richness, and diversity consistently recorded at the protected Astrolabe sites. These findings are consistent with patterns from other New Zealand marine reserves, where the recovery of predatory fish following protection has been linked to increases in richness, biomass, and ecological complexity (Babcock et al., 1999; Shears & Babcock, 2002).

Relative abundance patterns across indicator species reinforce this interpretation. Key stone species, snapper (*Pagrus auratus*), scarlet wrasse (*Pseudolabrus miles*), and red pigfish *(Bodianus unimaculatus*) were all significantly more abundant at Astrolabe Reef than at Motiti, highlighting early evidence of reserve benefits despite the site's relatively recent protection. Snapper, in particular, showed a sixfold higher relative abundance at Astrolabe, suggesting predator recovery trajectories similar to those observed at long-established reserves such as Leigh. The presence of multiple large-bodied reef fish at Astrolabe further indicates that protection is already influencing local trophic dynamics. In contrast, blue cod (*Parapercis colias*) were only detected at Motiti. While this could reflect habitat differences in low-density populations, it may also highlight how species with different depth distributions and habitat preferences respond variably to protection.

Patterns of richness and Shannon diversity further emphasised these site-level contrasts. Astrolabe supported consistently higher richness and diversity than Motiti, while MT1 showed intermediate values and MT2 contained no reef-associated fish. The absence of diversity at MT2 likely reflects habitat structure, as this site was dominated by sand and lacked complex reef relief. This underscores how habitat availability acts as a bottom-up driver of biodiversity that interacts with protection status to shape ecological outcomes.

The Baited Remote Underwater Video results suggest that protection at Astrolabe Reef is already facilitating recovery of targeted fish populations and enhancing community diversity, despite the site's recent designation as part of the Motiti Protection Area. However, the variability observed among sites indicates that reserve status alone does not fully explain biodiversity patterns, and that habitat structure and species-specific ecological traits also play important roles in shaping reef fish assemblages.

2.5 Species Inventory

2.5.1 Field Method

Specimens were collected during SCUBA dives at Astrolabe Reef on the 31 January 2025 and at Motiti Island on the 2 and 3 February 2025. Two dives were undertaken at Astrolabe Reef, with subsequent collections made across multiple sites at Motiti Island.

Coordinates of all transects were recorded. Sampling was done along a 30 metre transect with a 5 metre belt on either side, within which seaweeds, bryozoans and other encrusting invertebrates were systematically collected. Additional conspicuous taxa such as octopus (*Octopus maorum*), rock lobster (*Jasus edwardsii*), and nudibranchs were photographed opportunistically and recorded in field notes to ensure a broader record of local biodiversity.

Specimens were photographed in situ using a Fujifilm XP camera set to automatic flash mode, with multiple photographs taken to capture diagnostic features from different angles. Each sample was placed in a pre-labelled plastic bag, and corresponding bag numbers and photograph codes were recorded on an underwater slate to maintain consistency between field and laboratory records. Where possible, tentative identifications were noted in the field to aid later taxonomic confirmation.

2.5.2 Sample Processing

Upon return to the laboratory, specimens were removed from their bags and assigned unique specimen codes that incorporated the collection date, location, and bag number. Each sample was then photographed *ex situ* alongside its assigned code to provide a permanent record linking field and laboratory observations. Seaweeds were pressed using a standard herbarium press and dried for long-term storage, while sponges were preserved in 70% ethanol and labelled with their specimen codes. Bryozoans and hydroids were retained in labelled containers containing 70% ethanol.

All specimens were identified to the lowest possible taxonomic level based on morphological characteristics and reference to both field and laboratory photographs. Identifications were made to species level where diagnostic features were clear, or otherwise to genus or family. All taxonomic identification was standardised against the World Register of Marine Species. A complete inventory of identified taxa is presented in the Results.

2.6 Results

Rhodophyta, Chlorophyta, Phaeophyceae, Bryozoa, Porifera, and Cnidaria were identified. Of these, 28 were present at Astrolabe Reef and 22 at Motiti Island, with 14 species were shared between sites (Table 3).

Within the *Ochrophyta,* the assemblage was broadly similar between sites, with dominant canopy-forming genera such *as Ecklonia radiata, Carpophyllum plumosum, Carpophyllum maschalocarpum, Zonaria aureomarginata*, and *Z. turneriana* present at both Astrolabe and Motiti. However, several species showed a restricted distribution*. Xiphophora chondrophylla, Colpomenia sp.,* and *Cystophora retroflexa* were only observed at Astrolabe, whereas *Distromium skottsbergii* and *Microzonia velutina, Carpomitra costata*, and one unidentified brown alga were only recorded at Motiti.

Patterns were more uneven within the Rhodophyta, with Astrolabe characterised by *Pterocladia lucida*, *Jania sp.,* and *Polysiphonia sp.*, while Motiti supported *Delisea compressa* and *Cladhymenia sp*. Both sites shared *Plocamium spp.* and an unresolved epiphytic red alga, indicating some overlap but also clear site-specific differences in red algal composition. Only Motiti hosted representatives of the *Chlorophyta*, with *Ulva sp*. recorded exclusively there. Among *Bryozoa,* three species (*Pterocella vesiculosa, Catenicella elegans, and Hornera robusta*) were restricted to Astrolabe, while *Galeopsis porcellanicus* was only observed at Motiti. In contrast, the Porifera displayed the opposite trend: *Raspailia topsenti* and *Polymastia massalis* were exclusive to Motiti, while *Latrunculia procumbens* was recorded at both sites. Cnidarian hydroids were confined to Astrolabe, with *Sertularia unguiculata* and *Sertularia* sp. both recorded there.

Overall, Astrolabe Reef supported a slightly higher taxonomic richness than Motiti Island, particularly for bryozoans and hydroids. The presence of canopy-forming brown algae at both sites indicates a degree of structural similarity, though species-level differences highlight localised variation in benthic community composition.

Table 3. Presence–absence inventory of macroalgae, bryozoans, sponges, hydroids, and unresolved taxa collected at Astrolabe Reef and Motiti Island. Species are grouped by phylum, with identifications resolved to the lowest possible taxonomic level (cf. indicates tentative identifications). “Y” denotes presence and “N” denotes absence.

Phylum	Scientific name	Astrolabe Reef	Motiti Island
Ochrophyta (Brown seaweeds)	Xiphophora chondrophylla	Y	N
	Sargassum sinclairii	Y	Y
	Carpophyllum plumosum	Y	Y
	Carpophyllum maschalocarpum	Y	Y
	Zonaria turneriana	Y	Y
	Zonaria aureomarginata	Y	Y
	Ecklonia radiata	Y	Y
	Colpomenia sp.	Y	N
	Halopteris sp.	Y	Y
	Cystophora retroflexa (cf.)	Y	N
	Distromium skottsbergii / Microzonia velutina	N	Y
	Lessonia variegata	Y	Y
	Carpomitra costata	N	Y
	Unknown brown alga	N	Y
Rhodophyta (Red seaweeds)	*Pterocladia lucida*	Y	N
	Jania sp.	Y	Y
	Polysiphonia sp	Y	N
	Plocamium	Y	Y
	Delisea compressa	N	Y
	Cladhymenia sp.	N	Y
	Unknown epiphytic red seaweed	Y	Y
Chlorophyta (Green seaweeds)	*Ulva sp.*	N	Y
Bryozoa (Ectoprocta)	*Pterocella vesiculosa*	Y	N
	Catenicella elegans	Y	N
	Hornera robusta	Y	N
	Galeopsis porcellanicus	N	Y
Porifera (Sponges)	*Raspailia topsenti*	N	Y
	Tethya burtoni	Y	Y
	Polymastia massalis	N	Y
	Latrunculia procumbens	Y	Y
Cnidaria (Hydroids)	*Sertularia unguiculata*	Y	N
	Genus Sertularia	Y	N
Unresolved / Unknowns	*Unknown*	Y	N

Opportunistic observations of other invertebrates recorded during SCUBA surveys revealed both site-specific and shared patterns in species occurrence (Table 4). At Astrolabe Reef, single individuals of *Octopus maorum* and *Goniobranchus aureomarginatus* were recorded alongside two *Jasus edwardsii,* three *Aphelodoris luctuosa*, and four *Ceratosoma amoenum.*

In contrast, Motiti Island supported a higher abundance of nudibranchs, with twelve *C. amoenum* recorded compared with only four at Astrolabe, while *A. luctuosa* and *G. aureomarginatus* were absent. Rock lobsters *(J. edwardsii*) were present at both sites but appeared slightly more abundant at Motiti (n = 3) than at Astrolabe (n = 2).

Echinoids were present in large numbers at both sites, with *Centrostephanus rodgersii* and *Evechinus chloroticus* observed in high densities.

Table 4. Opportunistic records of other invertebrate observed during SCUBA surveys at Astrolabe Reef and Motiti Island. Counts represent the number of individuals recorded per species. A dash (–) indicates no individuals were observed at that location. Due to large abundance of *Centrostephenus rodgersii* and *Evechinus chloroticus* they were recorded qualitatively as “Present” rather than counted.

Species	Astrolabe Reef	Motiti Island
Octopus maorum	1	–
Jasus edwardsii	2	3
*Aphelodoris luctuosa (*nudibranch*)*	3	–
*Ceratosoma amoenum (*nudibranch*)*	4	12
*Goniobranchus aureomarginatus (*nudibranch*)*	1	–
Centrostephenus rodgersii	Present	Present
Evechinus chloroticus	Present	Present

2.7 Discussion

It should be noted that several additional ecological observations were made during collections and surveys that provide useful context for interpreting species distributions. At Motiti Island, a wandering anemone was recorded at a depth of 10 metres. . An unidentified red alga was collected at Astrolabe Reef. Some species also demonstrated associations with other organisms: *Polysiphonia sp* were observed growing epiphytically on the sponge *Tethya burtoni,* while *Sertularia unguiculata* occurred attached to blades of *Zonaria turneriana.* In addition, morphological variation was noted in *Carpophyllum plumosum* collected at

Astrolabe, where several thalli displayed an unusual bushy form. Behavioural observations were also made among invertebrates, with eight of the twelve *Ceratosoma amoenum* recorded at Motiti found in small aggregations of two or more individuals, potentially reflecting reproductive behaviour. Additionally, extensive barrens dominated by the urchins *Evechinus chloroticus* and *Centrostephanus rodgersii* were observed at both sites.

Benthic encrusting species assemblages were representative of warm and cool temperate biodiversity for northeastern New Zealand, suggesting a mix of oceanographic current influences. Many of the species found around Astrolabe Reef in particular had affinities with assemblages found north at the Poor Knight Islands.

Chapter Three

Effects of Small Scale Environmental Impacts

Community Recovery and Early Recruitment Dynamics at High and Low Impact Sites on Otāiti/Astrolabe Reef

3.1 Introduction to Recruitment

Recruitment and succession are fundamental processes that drive the recovery and long-term stability of marine ecosystems (Palumbi et al., 2008). The success of recruitment, as measured by the settlement and survival of new individuals, depends on a complex combination of direct and indirect factors both physical and biological. Recruitment of species that should be 'native' to a particular habitat, is a critical factor for successful recovery following major disturbances (Adjeroud et al., 2017). These include physical impact disturbances, chemical contamination, and various deleterious biological interactions, all of which can influence growth and survival during the early life stages of marine organisms. Recruitment is a multidimensional process, involving a series of stages from larval supply and settlement, to post-settlement survival and growth (Fogarty et al., 1991). Each of these stages can be affected by a variety of environmental conditions. For example, physical disturbances such as storms, sedimentation, or mechanical damage from human activities can alter the structure of the reef and the availability of suitable habitat for new settlers. Chemical factors, including contaminants, can directly impact larval viability or indirectly affect recruitment. Contaminants can influence recruitment in subtle but significant ways (Johnston & Mayer-Pinto, 2015). For example, some compounds may repel larvae or juvenile organisms from settling in contaminated areas (Araújo et al., 2020), even if those contaminants are not directly lethal. This avoidance behaviour may result in altered spatial distribution patterns, reduced local biodiversity, and hindered recolonisation of disturbed habitats (Araújo et al., 2020). Biological interactions also play a critical role. Competition for space, predation on newly settled juveniles, and the presence or absence of key facilitators (such as crustose coralline algae) can all influence the outcome of recruitment events. The recent increase of *Centrostephanus rodgersii* and their altered behaviours adds another layer of complexity to recruitment and competition for space on reef systems. While these dynamics are particularly relevant for understanding changing species interactions, disturbances more broadly can also create windows of opportunity for invasive or range-extending species to establish and further modify habitat structure (Occhipinti-Ambrogi & Savini, 2003; Altman & Whitlatch, 2007). All of these factors are at play at Astrolabe Reef.

The research focus for this thesis centres on Astrolabe Reef, a system where the interplay of physical disturbance, chemical contamination, and shifting biological interactions converge in unique and complex ways. Unlike many reefs affected by a single dominant stressor, Astrolabe represents a case where multiple simultaneous pressures act together to shape ecological outcomes. The catastrophic grounding of the MV *Rena* introduced a combination of physical damage to reef structure, the chronic release of contaminants such as tributyltin (TBT) and copper, and the potential for long-term trophic disruptions through impacts on grazers and benthic recruitment (Ross et al., 2016; Dempsey et al., 2016). These influences occur alongside existing ecological challenges, such as competition for space, altered grazing behaviour from *Centrostephanus rodgersii*, and the ever-present background of natural disturbances such as storms and sediment resuspension. Taken together, Astrolabe Reef provides a rare opportunity to study how diverse stressors interact to influence recovery trajectories in a temperate reef ecosystem. Importantly, this chapter foregrounds the immediate localised impacts of the MV *Rena* disaster, while recognising that these processes are embedded within broader environmental pressures, including marine heatwaves, intensifying cyclone activity, and sedimentation, which will be addressed in subsequent chapters.

3.1.1 Tributyltin and Copper

For over 40 years, Tributyltin (TBT) based antifouling paint was used to protect ship hulls from biofouling. However, in 1990, the International Maritime Organisation (IMO) recommended strategies to eliminate TBT from biofouling paints due to its high toxicity to marine organisms. After about 20 years of using TBT-based antifouling paints, it was discovered that TBT had severe negative effects on marine life (Kotrikla, 2009). For instance, off the south coast of England, TBT concentrations as low as 1 ng/L were causing imposex in the dogwhelk, *Nucella sp.* Thain and Waldock (1986) described TBT as the most toxic substance ever deliberately introduced into the marine environment. Even concentrations as low as 2 ng/L were found to affect shell calcification in *C. gigas* (Evans, 1999a). As a result of its devastating impact on marine ecosystems, the use of TBT in antifouling paints was banned in 2008. Despite being certified as a TBT-free vessel, the MV *Rena* still had layers of TBT beneath its more modern antifouling paint.

In addition to TBT contamination, the MV *Rena* disaster led to the release of approximately 23,000 kg of granulated copper, remnants of earthquake-damaged electrical wiring stored in a container on board (Ross et al., 2016). This copper, originating from copper wiring that had been cut into 1-3mm lengths following the Christchurch earthquake, was deposited on the northeastern slope of Astrolabe Reef at a depth of approximately 30–45 meters. While copper is an essential micronutrient for marine organisms, in excessive amounts, it can become highly toxic (Kong, 2022). The elevated concentrations of copper can cause severe physiological impacts, including reductions in growth rates, immune responses, reproduction, and survival (Lee et al., 2010; Bagheri et al., 2024; Zalewksa et al., 2024). Exposure to sediments holding elevated levels of copper has been linked to sublethal reproductive effects in organisms like the amphipod *Melita plumulosa* (Gale et al., 2006; Campana et al., 2012; Podlesinska, 2024). Despite considerable efforts by salvors to recover the copper, much of it remains beneath the hull of the sunken stern.

Ross (2023) documents the monitoring effects to provide further insight into the persistence and distribution of both TBT and copper at the site. During the 2023 sediment analysis, the highest TBT concentrations were recorded at site 2622 (4.9 mg/kg). Since 2013, TBT levels within the former debris field have fluctuated, ranging from a mean of 2.78 mg/kg in 2014 to 0.09 mg/kg in 2021, without a clear trend of decline. While fewer samples now show extremely high concentrations, notable spikes continue to occur. In 2023, the mean TBT concentration in outer reef samples (1.16 ± 0.85 mg/kg) surpassed those from 2021 and 2020, due to the elevated reading at site 2622 These results highlight the lingering presence of TBT in sediment, especially in zones closest to the wreck (Ross, 2023). Sediments at Astrolabe contained elevated levels of TBT, copper, PAHs, zinc, diuron, fluoride, nickel, and tin compared to reference sites Motiti and Tuhua. Among these, PAHs, copper, and TBT were present at concentrations exceeding the ANZECC Interim Sediment Quality Guideline (ISQG) values (Ross, 2023).

Similarly, elevated copper levels remain a concern in the vicinity of the known copper deposit. In 2023, water column samples from sites G18/G19, located directly above the deposit revealed persistently high copper concentrations, due to ongoing oxidation of the copper clove (see Appendix A: Figure 1). This plume of contamination was largely localised, with copper concentrations returning to background levels within 20 m of the source. Sediment copper concentrations ranged from 1 to 360 mg/kg in 2023, slightly lower than those recorded in 2020 and 2021. The highest levels outside of G19 were found at site E14 (360 mg/kg), in close proximity to the source. These consistent results across multiple years suggest no significant new release of copper but confirm the long-term persistence of contamination within the affected area (Ross, 2023).

Although these results have been returned largely from sediment monitoring programs at the base of reef promontories, the likelihood that sediments are disturbed and resuspended into the water column during storms is high. This increases the potential for contaminants to directly influence reef encrusting benthos. The effects of TBT and copper are not limited to encrusting taxa: grazers and other mobile invertebrates can also be impacted through bioaccumulation, physiological stress, or behavioural changes. Such effects may in turn alter grazing pressure, recruitment success, and competitive interactions across the benthic community. In this way, legacy contamination from the MV *Rena* has the potential to shape not only the composition of subcanopy assemblages, but also the broader trophic dynamics of rocky reef and kelp forest ecosystems. This ecological context provides the foundation for the aims of this chapter.

3.1.2 Aims

The aim of this chapter is to evaluate differences in community structure and succession on rocky reef walls at high- and low-impact sites associated with the MV *Rena* wreck. In addition, a clearance experiment was designed to assess whether proximity to the wreck continues to influence settlement and recruitment processes.

The following null hypotheses were tested:

1. There is no ecological difference in recruitment patterns or community composition between the high- and low-impact sites.
2. There is no difference in settlement, recruitment, or resultant biodiversity in newly created space between high- and low-impact sites.

To test these hypotheses, the study employed two levels of control: (i) baseline quadrats taken across each wall to provide a measure of background diversity, and (ii) control photoquadrats placed adjacent to clearance plots, which allow assessment of localised changes occurring independently of the manipulations.

Accordingly, the analysis is structured around three research questions:

1. Does overall community composition differ between high- and low-impact sites from the MV *Rena* wreck?
2. Does species richness differ between high- and low-impact sites from the MV *Rena* wreck?
3. Is settlement, recruitment, and subsequent biodiversity in newly created space (i.e., clearance plots mimicking storm disturbance and patch creation) affected by proximity to the wreck?

3.2 Methods

3.2.1 Survey Sites

To assess the ongoing disturbance resulting from the MV *Rena* grounding, two contrasting vertical wall sites were selected at Astrolabe Reef for comparative analysis (Figure 5). The 'high impact' site lies near the main wreckage of the MV *Rena* as it lies across the lower depths of Astrolabe Reef where evidence of both physical scarring and nearby shipwreck debris remains apparent. This site is located directly above an unidentified section of the wreck still embedded within the reef structure, potentially contributing to elevated contaminant levels and altered sediment chemistry due to leaching and debris breakdown (sites recommended by Phil Ross, UoW, MPI).

In contrast, the 'low impact' site is situated in a relatively sheltered area of Astrolabe Reef, well removed from the direct influence of the grounding and associated debris. This site shows no visible physical disturbance and lacks known contaminant sources in close proximity, providing a comparative baseline for assessing natural conditions and potential dispersal effects. Reef wall slope and geological structure are very similar, although the reef aspect is a little different which will be taken into account.

In addition to the high and low impact sites, two forms of control plots were established to provide essential context for interpreting the clearance experiments. The first set of controls comprised general quadrats taken randomly across each reef wall prior to the initiation of the experiment. These "baseline controls" offered a broader description of biodiversity and community composition across the walls, enabling assessment of whether the two sites were fundamentally similar or exhibited pre-existing differences in species richness, functional group cover, or structural complexity. These baseline images also allow for later comparison with post-experimental data to identify any broad-scale changes independent of the manipulations.

The second set of controls were “adjacent controls,” consisting of images taken on the top left of each clearance. These were also revisited after 14 weeks and provided a fine-scale comparison of natural variation at the same spatial and temporal scale as the clearance treatments.

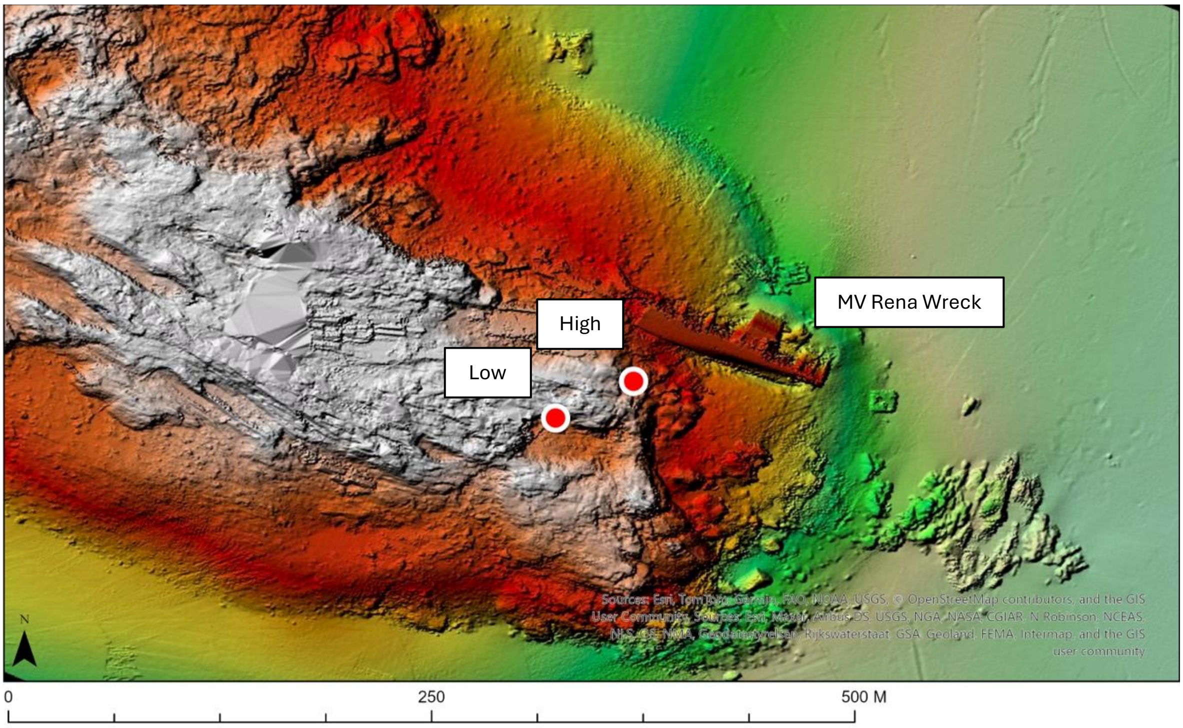

Figure 5. Bathymetric map of Astrolabe Reef / Otāiti showing the location of the MV *Rena* wreck and study sites used in clearance experiments. Red dots indicate the positions of high and low impact sites relative to the wreck.

3.2.2 Field Methods

3.2.2.1 Background to kelp forest biodiversity near and distant to the Rena

On the 31st of February 2025, two vertical wall sites (15–18 m depth) at Astrolabe Reef were surveyed, high and low impact. Photographic quadrats were taken randomly across both walls and analysed. In addition, a biodiversity inventory was created for both sites, near and distant to the wreck (Chapter 2).

3.2.2.2 Clearance Experiment

In order to examine whether the presence and proximity of the shipwreck is still influencing the reef environment a clearance experiment mimicking severe storm disturbance and scouring creating bare space was conducted. At each site, a team of three SCUBA divers conducted a standardised clearance procedure along a near-vertical rocky reef face.

Four 25cm² clearances were made at each site using the backs of hammers, chisels, and wire brushes to remove macroalgal, epifaunal and as much encrusting cover from the substrate as was possible. Each replicate was spaced at least 2 metres apart along the wall at a depth of between 14 and 18m. A numbered yellow tag was hammered into the top-left corner of each cleared area to allow for long-term relocation and monitoring. 25cm² square photo quadrats were taken of each replicate following clearance for subsequent image analysis (see figure 6). A photo was taken to the right of each cleared area as a control.

After 14 weeks, the sites were revisited, and each of the previously cleared areas was relocated using the yellow markers (Figure 6). A 25cm² quadrat was carefully repositioned so the tag appeared in the top-left corner, ensuring consistent orientation between time points. Multiple photographs were taken of each replicate to ensure image clarity and avoid issues from blurring or poor visibility. The monitoring is designed to continue for at least a year, but further assessment was outside the scope (time wise due to poor weather in the planned early winter sampling period) of this thesis. See figure 7 for the study design.

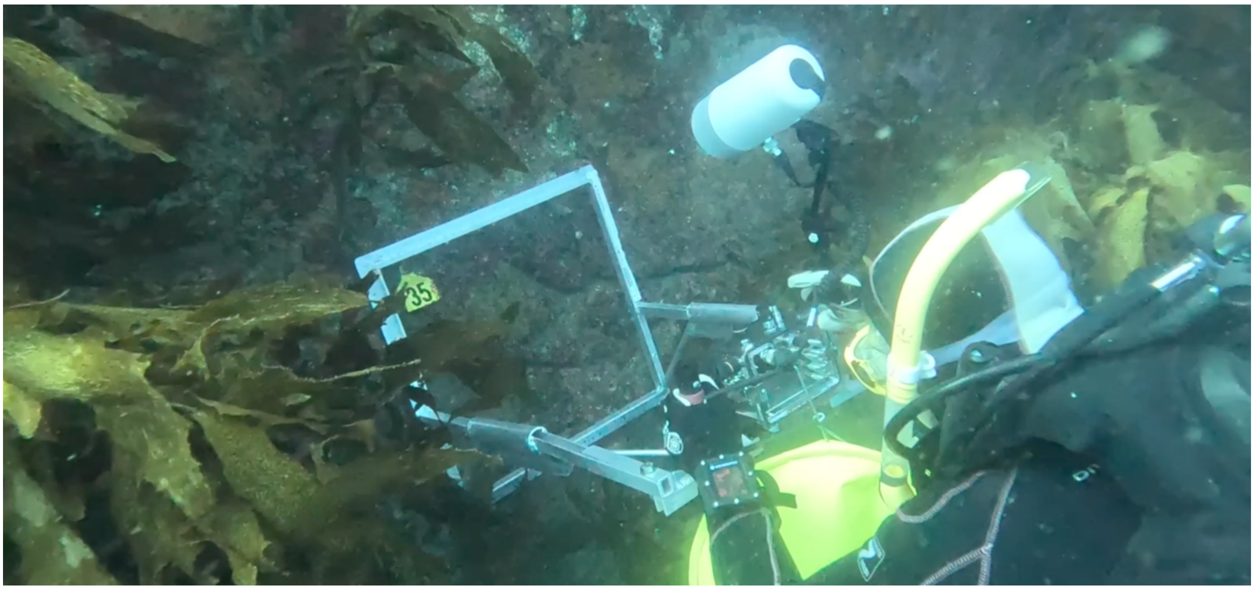

Figure 6. An example of one of the clearances at the Low impact zone 14 weeks following the clearances using the photo quadrat.

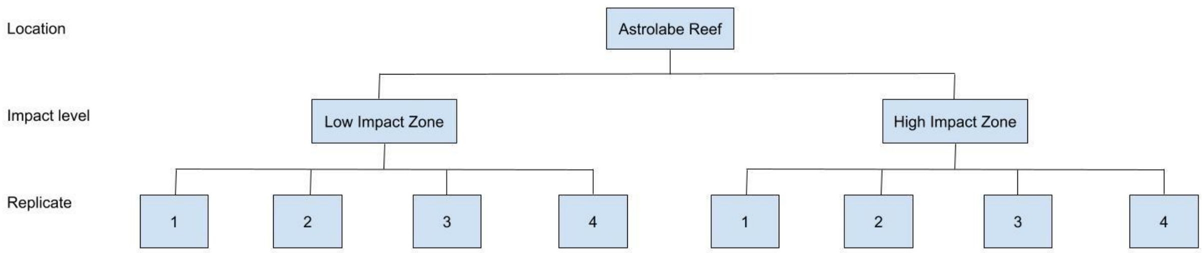

Figure 7. Project design with the high and low impact zones with four replicates at each site. Design for both the clearance and control plots.

3.2.2.3 Post-Collection Analysis

Photographic data collected during the initial survey and the 11-week follow-up were processed and analysed to quantify changes in benthic community composition. Prior to analysis, all images were standardised through minor adjustments to saturation and contrast using photo-editing software, Lightroom (Version 8.4).

Image analysis was conducted using ImageJ (Version 1.54g), a widely used software platform for biological image processing. For each 25cm² quadrat image, all features were carefully outlined using the freehand polygon selection tool. This involved manually tracing the precise boundaries of each feature with the tool to accurately capture the complex shapes and irregular edges of benthic organisms and substrate types. The meticulous outlining ensured high resolution spatial representation of each component within the quadrat, enabling precise quantification of percent cover and detailed analysis of community structure.

For the purpose of this study, each outlined feature was assigned to a specific category, including *Centrostephanus rodgersii,* macroalgae, turfing algae, sponges, coralline crustose algae (CCA), and other. The category 'other' consisted of blur, unidentifiable species or bryozoans. Individual sea urchins, either *Centrostephanus rodgersii* or *Evechinus chloroticus* were identified to facilitate targeted analysis of grazing pressure and potential ecological impacts. Percent cover was calculated for each functional group within each individual photograph. Subsequently, averages of the four replicate quadrat photographs were computed for each site, providing representative averages of benthic composition and organism abundance and diversity at both the high and low impact locations.

3.2.2.4 Species Richness

To further explore biodiversity differences, sponge species richness was quantified as the number of distinct sponge types present per replicate quadrat. All species were identified when possible, but due to some blurred photos taken during the frequent swell-surge moments, identification to species level (or even genus) was not possible for some.

<u>Sponge Species Richness</u>

To further explore biodiversity differences, sponge species richness was quantified as the number of distinct sponge types present per replicate quadrat. As above, all species were identified when possible. Based on photographic analysis, five operational taxonomic units of sponges were distinguished. For each replicate quadrat, sponge richness was calculated as the number of these species present with greater than 0% cover.

Sponges were selected as a focal group due to their well-documented sensitivity to environmental stressors and their ability to absorb heavy metals and other toxins directly from the water column (Chidugu-Ogborigbo et al., 2025). As such, they are widely regarded as useful biomonitors of environmental health in marine ecosystems (Aljahdali & Alhassan, 2023).

3.2.2.5 Statistical Analysis

All statistical analyses were conducted in R Studio (Version 2025.05.1+513), and significance was evaluated at the $\alpha = 0.05$ level. To assess differences in subcanopy community composition between high and low impact sites at Astrolabe Reef, both multivariate and univariate statistical approaches were used.

To evaluate differences in subcanopy community composition between treatment groups before canopy clearances were conducted (Day Zero), a permutational multivariate analysis of variance (PERMANOVA) was performed using the “adonis2” function in the “vegan” package. Bray–Curtis dissimilarities were computed from square-root transformed percent cover data for each functional group to reduce the influence of dominant taxa. The analysis compared low- versus high-impact sites across replicate quadrats, using 999 unrestricted permutations to estimate significance. F-statistics, R^2 values, and permutation-based p-values were reported.

To evaluate differences in subcanopy community composition between treatment groups after the 14 weeks, separate permutational multivariate analyses of variance (PERMANOVA) were conducted for the control and clearance datasets using the “adonis2” function in the vegan package in R. Percent cover data for each benthic group were square-root transformed prior to analysis to reduce the influence of dominant taxa. Bray-Curtis dissimilarity matrices were computed for each dataset, and PERMANOVA was used to compare subcanopy communities between impact levels (high vs low) within each treatment type. Each test used Monte Carlo p-value estimation with 999 unrestricted permutations (by = "margin"), and significance was evaluated at $\alpha = 0.05$. F-statistics, R^2 values, and Monte Carlo p-values were reported for each comparison.

To further evaluate differences in the percent cover of individual benthic groups, non-parametric Wilcoxon rank-sum tests were conducted using the “wilcox.test()” function in R Studio. These tests compared the distributions of percent cover for sponges, turfing algae, crustose coralline algae (CCA), *Centrostephanus rodgersii* and the “Other” category between the two sites. This approach was selected due to the small sample size ($n = 4$ per site) and non-normal distribution of the data.

To investigate differences in benthic community composition across treatment types and impact levels at Astrolabe Reef, multivariate analyses were conducted using square-root ($\sqrt{x}$)

transformed percent cover data for six functional groups: Sponges, Brown Turfing Algae, Crustose Coralline Algae, *Centrostephanus rodgersii,* Seaweeds, and Other. The square-root transformation was applied to reduce the influence of dominant taxa and improve the normality of the data distribution prior to ordination. Principal Components Analysis (PCA) was used to visualise patterns in community structure. Principal Components Analysis was conducted separately for control and clearance datasets using the rda() function from the vegan package in RStudio (version 2025.05.1+513). The analysis was performed on scaled data, and both site scores (representing individual samples) and species scores (indicating functional group contributions) were extracted. Ggplot2 was used to generate PCA plots, with 68% confidence ellipses added to illustrate treatment group dispersion. Species vectors were overlaid to represent the direction and strength of each functional group's contribution to the primary components.

<u>Statistical Analysis of Species Richness</u>

To evaluate differences in species richness among site types, a Shapiro-Wilk normality test was first conducted to assess the distribution of the data. The test indicated a significant departure from normality ($p < 0.05$), and therefore, a non-parametric Kruskal-Wallis rank sum test was used to compare species richness across site types (Low Control, High Control, Low Clearance, High Clearance). Statistical significance was evaluated at $\alpha = 0.05$.

<u>Sponge richness method</u>

Differences in sponge richness between High and Low impact sites were tested using a Wilcoxon rank-sum test due to small sample size ($n = 4$ per site) and potential non-normality of the data. A boxplot was generated to visualise sponge richness distributions at each site using ggplot.

3.3 Results

3.3.1 Does overall community composition differ between high and low impact sites from the MV *Rena* wreck?

At the beginning of the experiment, prior to the clearances, the high and low impact sites displayed broadly similar benthic community structures, dominated by turfing algae, sponges, crustose coralline algae, and patches of brown macroalgae. Despite this general similarity, several distinctions were apparent. At the low-impact site, 100% of replicates contained bryozoans, whereas only 50% of replicates at the high-impact site showed their presence. The long-spined sea urchin *Centrostephanus rodgersii* was observed exclusively at the high impact site (Appendix C: Figure 1). In contrast, the low-impact site featured approximately 20 metres from the clearance plots, a dense ~30 × 30 m aggregation of the colonial anemone *Parazoanthus elongatus* (Appendix C: Figure 2), contributing to the distinctiveness and complexity of the surrounding habitat. These observations provided a clear ecological baseline from which to assess subsequent changes following canopy clearance.

Quantitative comparisons (Figure 8) support these observations, showing that although both sites were composed of the same dominant functional groups, their relative abundances differed. Turfing algae and seaweeds were more abundant at the high-impact site (40% and 20% mean cover, respectively), while sponges were markedly higher at the low-impact site (60% compared with 20%). Coralline algae were present at both sites, with slightly greater mean cover at the high-impact site, while *Centrostephanus rodgersii* occurred only at the high-impact site (~1.5% cover). Overall, the low-impact site exhibited greater sponge dominance and invertebrate complexity, whereas the high-impact site was characterised by higher turfing algae and seaweed cover together with the presence of urchins. These differences, while modest, highlight the contrasting ecological baselines against which clearance responses could be assessed.

A PERMANOVA based on Bray–Curtis dissimilarities found no significant difference in overall community composition between the low- and high-impact sites at Day Zero (adonis2: $F = 2.35$, $R^2 = 0.37$, $p = 0.10$), (Appendix D: Figure 1) While the low-impact site tended to have higher sponge cover and the high-impact site supported greater turfing and brown macroalgal cover, these differences were not statistically significant.

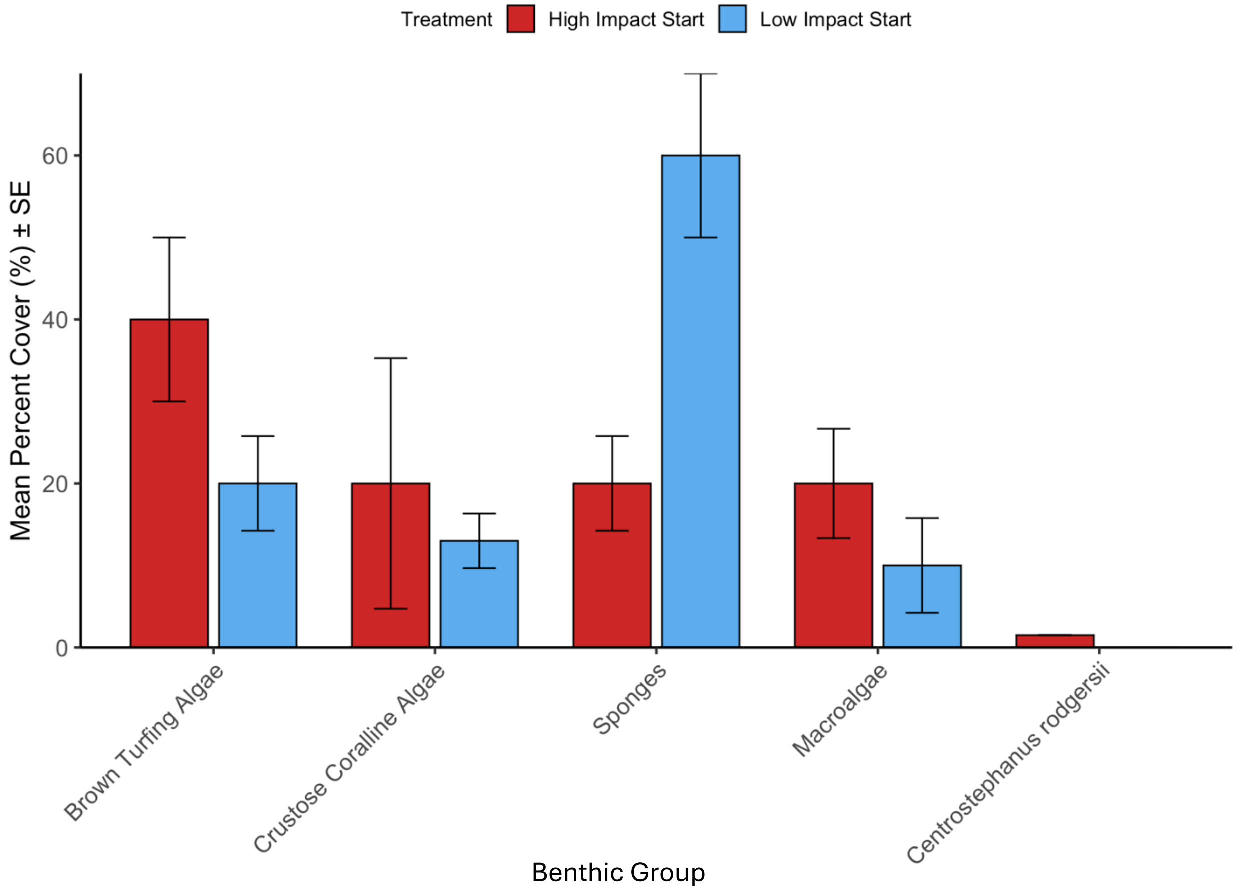

Figure 8. Mean percent cover (± SE) of major benthic functional groups at the start of the experiment (Day Zero) at low- and high-impact sites.

3.3.2 Does overall community composition differ between high and low impact sites from the MV *Rena* wreck after 14 weeks of clearances?

A two-way ANOVA showed no significant effect of Impact, Treatment, or their interaction on total benthic cover ($p > 0.05$), confirming that both clearance and their adjacent control plots were fully recolonised within the monitoring period (Appendix D: Table 2). To test whether recovery trajectories differed, a three-way ANOVA was performed comparing control plots adjacent to clearance areas across Impact (High vs. Low), Treatment (Control vs. Clearance), and Functional Group (sponges, turfing algae, crustose coralline algae, seaweeds, and "other").

This analysis revealed no significant effects of Impact ($p = 0.855$), Treatment ($p = 0.753$), or their interactions (all $p > 0.05$), (Table 5). In contrast, there were highly significant differences among functional groups ($p < 0.001$), indicating strong variation in how space was occupied on the reef walls regardless of site or treatment. Post-hoc Tukey HSD tests confirmed that brown turfing algae had significantly higher cover than all other groups ($p < 0.001$). In comparison, sponges, seaweeds, crustose coralline algae (CCA), and “other” taxa clustered at consistently lower cover values, while *Centrostephanus rodgersii* occurred only at very low abundance and did not differ significantly from these subordinate groups (Appendix D: Figure 3).

Table 5. Results of a three-way ANOVA testing the effects of Impact (High vs. Low), Treatment (Control vs. Clearance), and Functional Group (sponges, turfing algae, crustose coralline algae, macroalgae, *Centrostephanus rodgersii*, and “Other”) on benthic percent cover at Astrolabe Reef after 14 weeks.

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact	1	10	10	0.033	0.855
Treatment	1	31	31	0.100	0.753
Group	5	23218	4644	15.181	<0.001
Impact × Treatment	1	9	9	0.028	0.867
Impact × Group	5	1872	374	1.224	0.307
Treatment × Group	5	2605	521	1.703	0.145
Impact × Treatment × Group	5	1426	285	0.932	0.465
Residuals	72	22024	306		

3.3.2.1 Clearance Plots after 14 weeks

After eleven weeks of clearances visual inspection of benthic percent cover patterns (Figure 9) revealed differences in community composition between high and low impact zones at Astrolabe Reef. Clearance plots were dominated by brown turfing algae at both sites, with higher mean cover at the high impact site (68.0%) compared to the low impact site (48.1%). However, this difference was not statistically significant (Wilcoxon, $p = 1.000$). Sponges recruited to very similar levels across treatments, with no detectable difference ($p = 1.000$). Crustose coralline algae (CCA) showed moderately higher recruitment at the low impact site

(23.0%) compared to the high impact site (13.8%), but this difference was not significant (p = 0.665). *Centrostephanus rodgersii* was observed only in the high impact clearances (1.5%) and absent from the low impact site, although overall cover was very low and not statistically different (p = 0.453). Seaweed cover was minimal in both treatments, with 0.7% at the high impact site and 0% at the low impact site, and this difference was not significant (p = 0.453). The "Other" category was more variable at the low impact site (22.6%) compared to the high impact site (17.0%), but again the difference was not statistically significant, though it approached marginal levels (p = 0.112). Overall, Wilcoxon tests confirmed no statistically significant differences between clearance plots at high and low impact zones (Table 6).

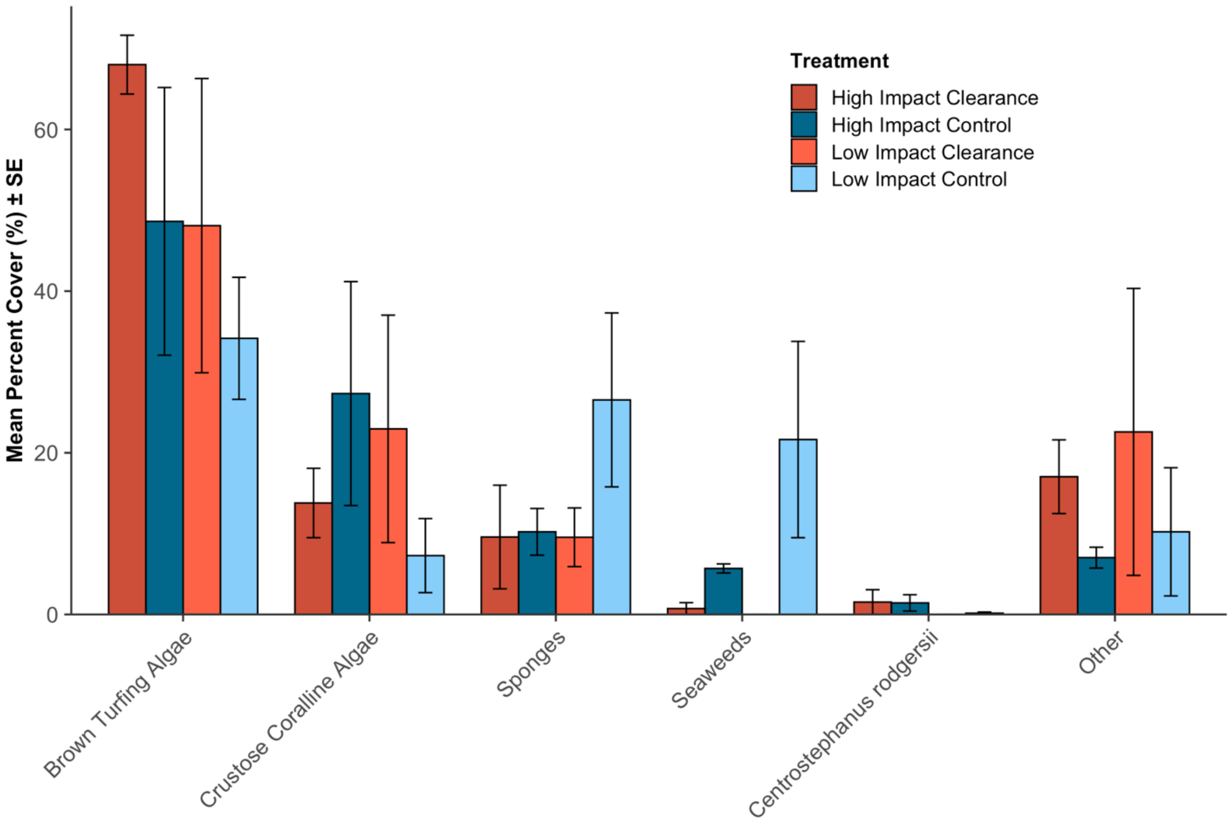

Figure 9. Mean Percent Cover (± SE) of all benthic species groups across treatments at high and low impact sites following the MV *Rena* disaster at Astrolabe Reef after 14 weeks of the clearances. Treatments include control and clearance plots at both high and low impact zones. Bars represent mean percent cover, and error bars denote standard error.

3.3.2.2 Control Plots after eleven weeks

After eleven weeks, the control plots adjacent to the clearance plots exhibited broadly similar benthic community composition between high and low-impact sites, with substantial overlap in the dominant functional groups (Table 6). Mean cover was higher at the high impact site (48.6%) compared to the low impact site (34.2%), but this was not significant ($p = 0.343$). Sponge cover was more abundant at the low impact site (26.5%) than at the high impact site (10.2%), although the variation was high and the difference not statistically significant ($p = 0.343$). Crustose coralline algae showed greater average cover in the high impact controls (27.3%) compared to the low impact site (7.3%), but the difference did not reach statistical significance ($p = 0.114$). Seaweed cover was slightly higher at the low impact site (21.6%) compared to the high impact site (5.7%), but this was not significant ($p = 0.343$). *C. rodgersii* was present only in the high impact controls (1.4%) and almost absent at the low impact site (0.15%), but this difference was also not significant ($p = 0.408$). The "Other" category showed moderate representation at both sites, averaging 10.2% at the low impact site and 7.0% at the high impact site, but this was not significant ($p = 0.486$). Despite some apparent variation in percent cover among groups, Wilcoxon results consistently indicated a high degree of overlap in community structure between control plots at high and low impact zones.

Table 6. Wilcoxon Rank-Sum Test Results for Individual Benthic Groups in the clearances after 14 weeks and control plots adjacent to the clearances.

Treatment	Benthic Group	W Statistic	p-value
Clearance	Sponges	8	1.000
	Brown Turfing Algae	8	1.000
	Crustose Coralline Algae	10	0.665
	Centrostephanus rodgersii	10	0.453
	Seaweeds	10	0.453
	Other	14	0.112
Control	Sponges	4	0.343
	Brown Turfing Algae	12	0.343

Crustose Coralline Algae	14	0.114
Centrostephanus rodgersii	11	0.408
Seaweeds	4	0.343
Other	11	0.486

3.3.2.3 Multivariate Analysis for Community Composition Analysis

Permutational Multivariate Analysis of Variance (PERMANOVA) was used to test for differences in benthic community composition between high and low impact sites within each treatment type (control and clearance), based on Bray–Curtis dissimilarities (Table 7).

For the clearance treatment, there was no significant difference in benthic community composition between high and low impact sites ($F_{1,6} = 0.63$, $R^2 = 0.113$, $p = 0.767$), with the model explaining 11.3% of the total variation. Similarly, for the control treatment, no significant differences were observed between impact levels ($F_{1,7} = 1.45$, $R^2 = 0.194$, $p = 0.257$), though the model accounted for 19.4% of the total variation. These findings suggest that within each treatment type, the localised impact of the MV *Rena* grounding did not result in statistically distinct multivariate subcanopy communities.

Table 7. PERMANOVA results testing for differences in benthic community composition between high and low impact sites within control and clearance treatments at Astrolabe Reef after 14 weeks. Analyses were based on Bray–Curtis dissimilarities with 999 permutations.

Treatment	Source	Df	Sum of Squares	R^2	F-value	p-value
Clearance	Model	1	0.04477	0.11265	0.6348	0.767
	Residual	5	0.35262	0.88735		
	Total	6	0.39739	1.00000		
Control	Model	1	0.18749	0.19444	1.4482	0.257
	Residual	6	0.77679	0.80556		

Total	7	0.96428	1.00000

PERMANOVA analyses revealed no statistically significant differences in benthic community composition between any of the treatment group comparisons at Astrolabe Reef (Table 8). Comparisons between control and clearance treatments at both low and high impact sites showed modest F-values (F = 1.35 and F = 1.31, respectively) and low R^2 values (0.18 for both), with non-significant p-values ($p = 0.204$ and 0.281). Similarly, differences between clearance treatments across impact zones (F = 1.08, $R^2 = 0.15$, $p = 0.413$) and between control plots across impact zones (F = 1.45, $R^2 = 0.19$, $p = 0.253$) were not significant. These results suggest that neither impact level nor clearance treatment alone significantly influenced overall benthic community structure during the sampling period.

Table 8. Summary of PERMANOVA Results Comparing Benthic Community Composition Between Treatment Groups at Astrolabe Reef/Otāiti

Comparison	F	R^2	p-value	Significant
Low Control vs Low Clearance	1.35	0.18	0.204	-
High Control vs High Clearance	1.31	0.18	0.281	-
Low Clearance vs High Clearance	1.08	0.15	0.413	-
Low Control vs High Control	1.45	0.19	0.253	-

3.3.2.4 Principal Component Analysis for Community Composition

A Principal Component Analysis (PCA) revealed distinct patterns in benthic community structure between high and low impact sites for both clearance and control treatments (Figure 10). For the clearance treatments, the first two principal components explained 66.0% of the total variance (PC1 = 37.4%, PC2 = 28.6%). Samples from high and low impact sites clustered separately, indicating divergent community composition. High impact clearance sites were more strongly associated with *Centrostephanus rodgersii,* brown turfing algae and sponges, while low impact sites were more closely aligned with crustose coralline algae and "Other" taxa. Seaweeds also showed some influence on the low impact group.

In contrast, the control treatment PCA explained 65.1% of the total variance (PC1 = 42.4%, PC2 = 22.7%). Clear separation between high and low impact sites persisted, with high impact controls again showing stronger associations with *Centrostephanus rodgersii* and brown turfing algae. Low impact control sites were associated with seaweeds, crustose coralline algae, and "Other" taxa. Species vectors suggest that turfing algae and *C. rodgersii* were primary drivers of community differences between impact levels, particularly at high impact sites.

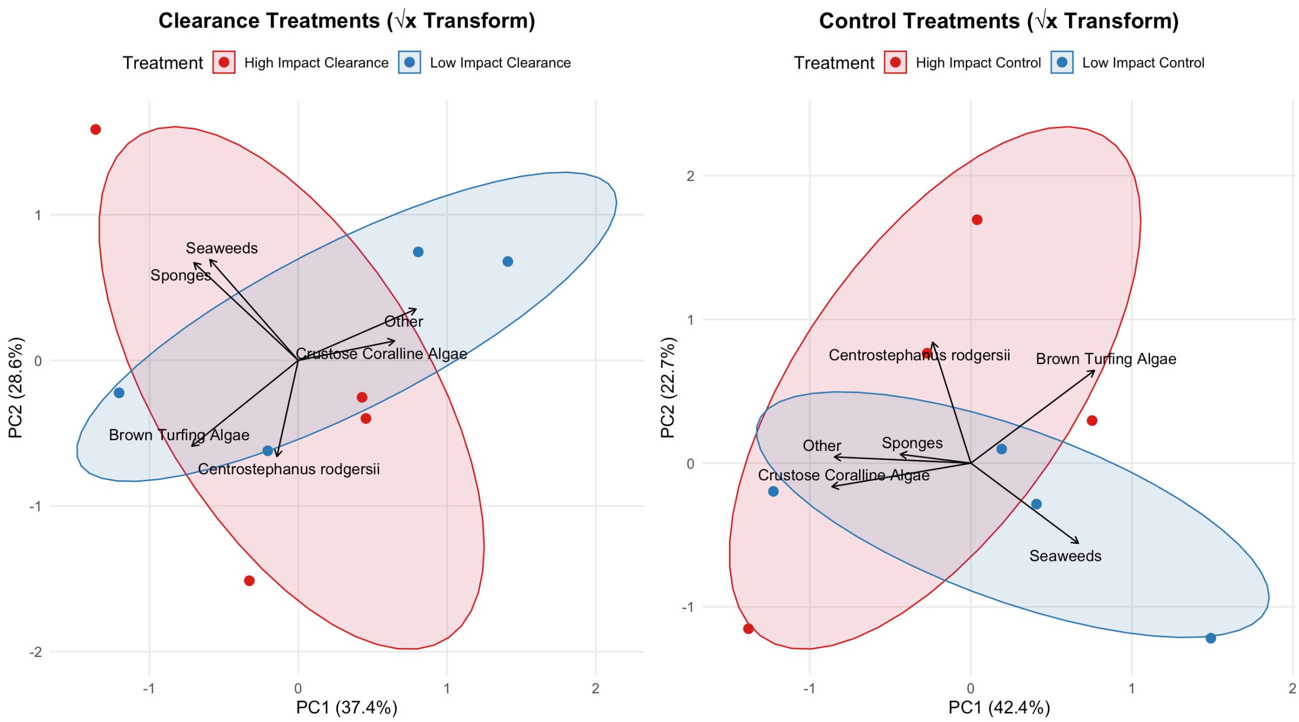

Figure 10. Principal Component Analysis (PCA) of functional group percent cover across high and low impact sites at Astrolabe Reef following square root (√x) transformation. Left: Clearance treatments; Right: Control treatments. Ellipses represent 68% confidence intervals for each treatment group.

3.2.3 Does species richness differ between high and low impact sites from the MV *Rena* wreck after 14 weeks of clearances?

Species richness varied across the four treatment types at Astrolabe Reef: High Impact Control, High Impact Clearance, Low Impact Control, and Low Impact Clearance (Figure 11). The Low Impact Control plots exhibited the highest overall species richness, with 22 unique species observed across all replicates. High Impact Control plots also had relatively high richness, with 16 species, followed by High Impact Clearance (14 species), and the lowest richness recorded at Low Impact Clearance plots, which contained only 9 species in total.

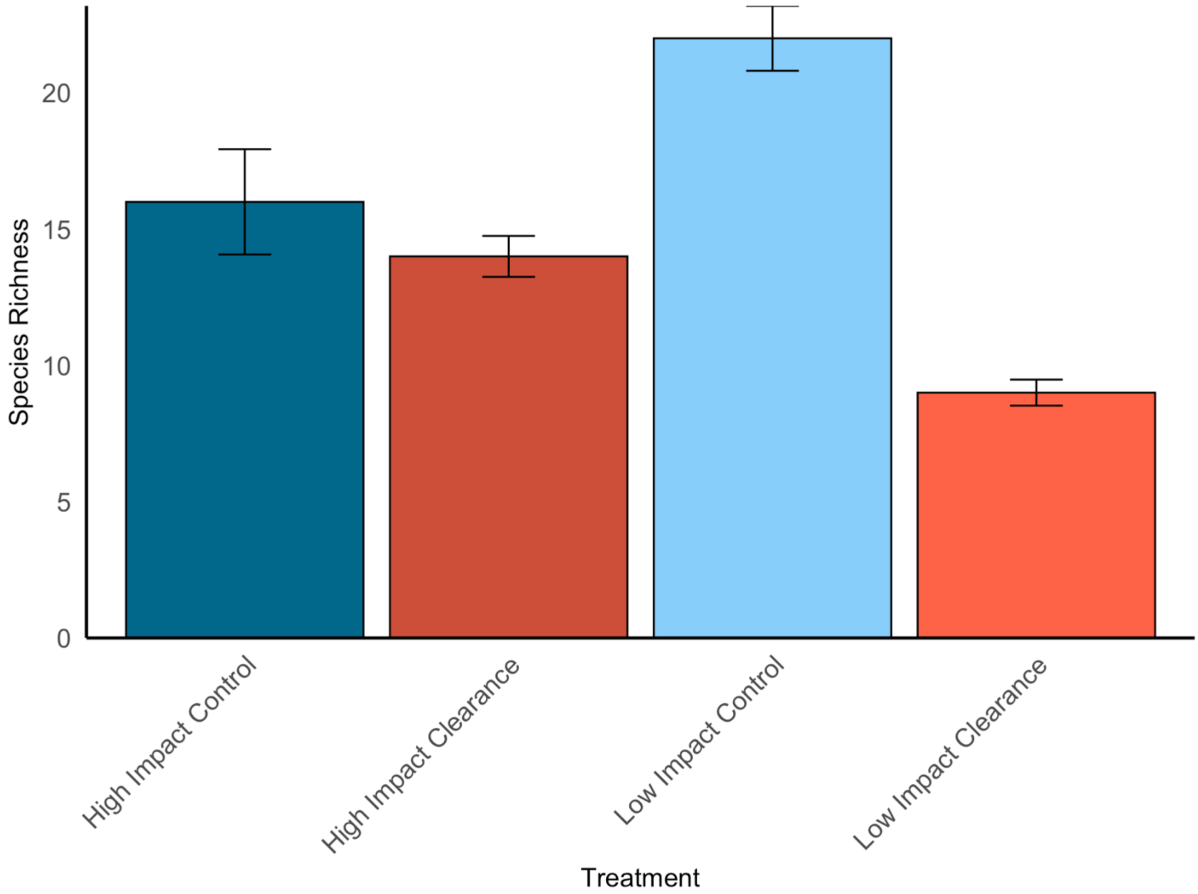

Figure 11. Total species richness (± SE) summed across all the replicates at High and Low impact sites at Astrolabe Reef. Treatments included High Impact Control, High Impact Clearance, Low Impact Control, and Low Impact Clearances.

When examined per replicate, species richness was highest in the High Impact Control plots, with a mean of approximately 10 species per replicate. In contrast, the Low Impact Clearance plots had the lowest mean species richness, averaging around 5.5 species per replicate (Figure 12). Both clearance treatments, regardless of impact level, had reduced richness compared to their respective control plots, suggesting that the act of canopy removal may have a negative influence on subcanopy community composition.

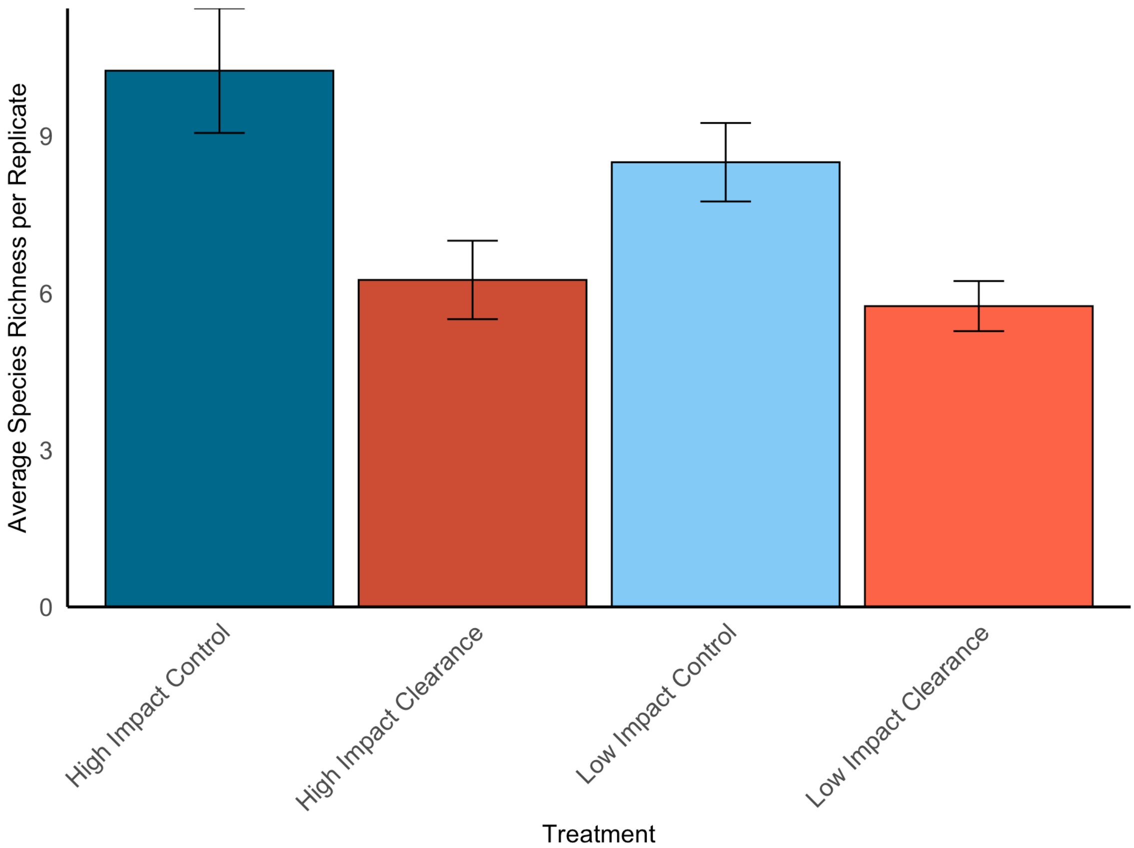

Figure 12. Average species richness (mean number of species per replicate ± SE) at Otāiti / Astrolabe Reef. Values represent the average species counts across individual replicates within each treatment (High Impact Control, High Impact Clearance, Low Impact Control, Low Impact Clearance).

3.3.2.1 Sponge Species Richness

After 14 weeks of clearances sponge species richness varied notably across impact levels and treatments (Figure 13). The highest species richness was observed in the low impact control plots, with a mean of 7 visually identifiable sponge types per replicate (± SE). In contrast, both high impact control and high impact clearance plots exhibited the lowest species richness, each with 3 species per replicate. Low impact clearance plots showed intermediate richness SE), indicating a potential reduction due to disturbance. These patterns suggest that sponge communities at the high impact site may still be influenced by legacy effects from the MV *Rena* grounding, and that experimental clearance may further suppress sponge recolonisation, particularly in the less disturbed areas.

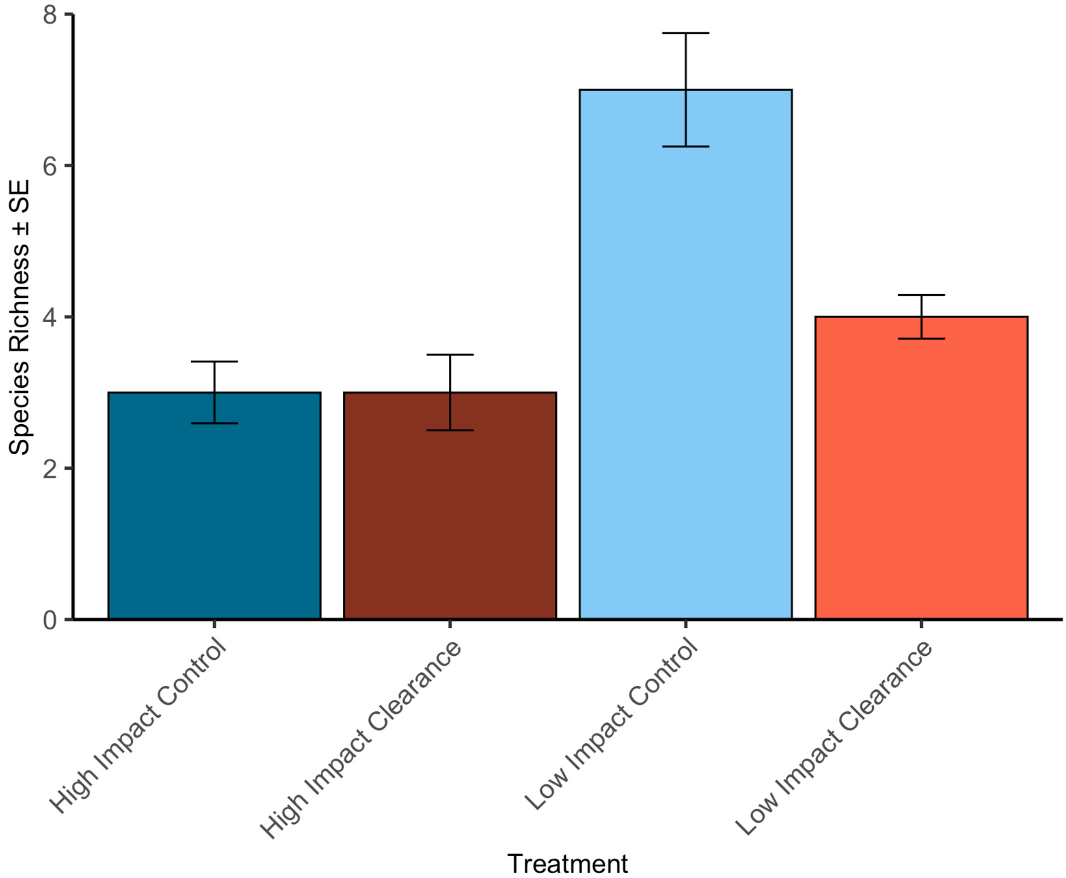

Figure 13. Sponge species richness (± standard error) across treatment groups at Astrolabe Reef / Otāiti after 14 weeks of clearances.

3.4 Discussion

3.4.1 Biodiversity Following a Disturbance

High biodiversity is widely recognised as a key factor in enhancing ecosystem resilience and recovery following disturbance (Oliver et al., 2015). More diverse systems often contain a broader range of functional traits, life histories, and species interactions, which can buffer against environmental stress and support faster recovery trajectories (Oliver et al., 2015). This functional redundancy means that even if some species are lost or impacted, others can maintain critical ecological processes. Such diversity-driven resilience is particularly important in dynamic or disturbed environments, where the ability of an ecosystem to resist or rebound from change depends heavily on the diversity of species and their adaptive capacities. These principles form the basis of the insurance hypothesis, which suggests that biodiversity provides a safeguard against ecosystem collapse by ensuring that some species can persist or recover under stress (Leary & Petchey, 2009; Lamy et al., 2019).

Although the High Impact Control site had a higher average species richness per replicate (mean = 10), the Low Impact Control site showed the highest total species richness across all replicates (22 species in total). This suggests that while each individual quadrat at the Low Impact Control had fewer species on average, different species were found in different replicates, indicating greater replicate-to-replicate variation and higher spatial heterogeneity. In contrast, the High Impact Control replicates likely contained a more consistent subset of species, pointing to a more homogeneous community structure. This difference implies that the Low Impact site supports a wider range of microhabitats or ecological niches, reflected by greater species turnover among replicates, whereas the High Impact site appears to be dominated by a smaller and more uniform subset of species. Increased spatial heterogeneity and species diversity are widely linked to greater ecological resilience by reducing vulnerability to localised disturbance.

This pattern is consistent with multiple other disturbance studies showing that populations with homogeneous distributions tend to have better bet-hedging capacity than those with more heterogeneous distributions, potentially enhancing resilience to localised stressors (Wang et al., 2020).

Similarly, research following the Deepwater Horizon oil spill found that higher biodiversity, particularly taxonomic diversity, reduced the negative effects of oil exposure on coastal ecosystems, largely through the presence of resistant or fast-recovering species (Zerebecki et al., 2022). These findings reinforce the idea that community structure and diversity patterns are critical to understanding and predicting ecosystem responses to disturbance.

3.4.2 Community Composition and Early Succession Patterns

Fourteen years after the large-scale disturbance caused by the MV *Rena* grounding, physical scarring, chemical contamination, and remnant wreckage remain evident at Astrolabe Reef. Despite these ongoing stressors, PERMANOVA and Bray–Curtis dissimilarity analyses revealed no statistically significant differences in overall benthic community composition between high and low impact zones across both control and clearance treatments. This suggests that early-stage recruitment processes may be functioning similarly across sites during the 11-week recovery period.

In contrast, Principal Component Analysis (PCA) revealed biologically meaningful distinctions between sites. High impact communities, both in control and clearance plots, were more closely associated with *Centrostephanus rodgersii* and brown turfing algae, while low impact sites were more aligned with crustose coralline algae (CCA), seaweeds, and the "Other" category. The recruitment of *C. rodgersii* and turfing algae into the high impact site is noteworthy, as both are considered opportunistic species that readily colonize newly available space following disturbance (Harris et al., 2015; Burek et al., 2018; Christie et al., 2019). Their dominance may reflect reduced competition at the high impact site, where fewer sensitive or specialist taxa appear to establish.

The widespread presence of brown turfing algae across all treatments reflects patterns observed in similar canopy clearance experiments globally. Following disturbance, turf species often recolonise rapidly due to their fast growth rates, tolerance of fluctuating environmental conditions, and ability to outcompete slower-growing or more sensitive taxa (Kennelly, 1987; Benedetti-Cecchi et al., 2001). Their ability to dominate early successional stages can suppress the recovery of canopy-forming macroalgae and encrusting invertebrates, potentially leading to alternative stable states locked in by turf dominance (Connell & Russell, 2010). Similar dynamics have been documented in Tasmania, where turfing algae persisted while canopy-forming fucoid exhibited limited or delayed recovery (Edgar et al., 2004; Flukes et al., 2014).

3.4.3 Sponge Richness

Sponge species richness patterns further supported ecological divergence between sites. The Low Impact Control site showed the highest sponge richness, while the High Impact Clearance site showed the lowest. Although the Kruskal-Wallis test did not yield statistically significant differences, the visual patterns of richness and spatial variability suggest that the absence of contamination at the low impact site support higher sponge diversity and more compositional heterogeneity (Wulff, 2012; Pawar, 2017).

These patterns are consistent with the concept of facilitation, where canopy-forming macroalgae such as *Ecklonia radiata* create more suitable conditions for subcanopy species by modifying light regimes, stabilising sediment, and reducing competition with turf algae (Bruno et al., 2003; Thomsen et al., 2010). In a related New Zealand study, *Ecklonia radiata* removal led to a sharp increase in turf algae and a concurrent decline in sponges like *Crella incrustans*, driven by both direct and indirect stress pathways (Cardenas et al., 2016). In this experiment, sponges were especially sparse in clearance plots, with higher richness at undisturbed low impact controls, likely reflecting both the loss of canopy buffering and increased competitive dominance of turfing algae. Turfing algae may rapidly occupy space but support low biodiversity, while sponges and other encrusting invertebrates although lower in cover can be key contributors to filter-feeding capacity, habitat structure, and trophic connectivity (Robertson et al., 2017; Coppock et al., 2024).

3.4.4 Recruitment Dynamics and Functional Trajectories

Despite difference in species identity and richness, all cleared plots reached full benthic coverage within 14 weeks, indicating rapid colonisation regardless of impact level. High impact plots were primarily colonised by turfing algae and *C. rodgersii,* while low impact plots had greater representation of seaweeds, corallines, and sponges. These differences may reflect variation in larval supply, substrate quality, and post-settlement survival factors commonly observed to influence early successional trajectories (Fogarty et al., 1991).

Importantly, the presence of *C. rodgersii* exclusively at high impact sites is ecologically significant. This species has been strongly implicated in the formation of barrens across southern Australasia and can maintain degraded reef states via grazing feedback loops (Andrew & Underwood, 1989; Babcock et al., 1999). Its presence may be a relic of predator depletion or altered trophic dynamics, which continue to influence recruitment and community structure. A study from Leigh, New Zealand have shown that marine reserves with high predator biomass suppress urchin numbers, allowing for macroalgal recovery and higher biodiversity (Shears & Babcock, 2003).

Together, these observations suggest that physical disturbance is only part of the recovery equation. Long-term ecological trajectories are shaped by the interplay of legacy effects, species interactions, and habitat structure, which can either reinforce or resist recovery.

3.5 Conclusions

The findings of this experiment, add to the growing evidence that disturbances influence recruitment and biodiversity at different scales. Greater biodiversity prior to the disturbance can strongly influence ecosystem outcomes. Enhancing biodiversity is therefore essential to withstand increasing anthropogenic impacts, making it vital to understand these unique interactions between species and different disturbances.

This experiment provides early evidence that benthic communities at Astrolabe Reef are recovering along broadly similar trajectories, regardless of impact history. However, the species richness, community structure, and functional composition suggest subtle but ecologically meaningful differences. High impact zones appear more dominated by opportunistic, early-successional taxa, while low impact sites support a more diverse and variable assemblages, likely facilitated by intact canopies and reduced legacy stress.

These results emphasise the importance of canopy-forming macroalgae in supporting subcanopy biodiversity, particularly for sensitive taxa like sponges. Continued legacy effects from the *Rena* disaster, especially chemical contaminants and altered grazer dynamics, may still shape reef recovery in the long term. As such, ongoing monitoring and restoration efforts must consider both the biological interactions and environmental filters that influence succession in these complex, dynamic reef systems

Finally, the intention of this study was to return to the reef in winter to record an additional set of data on the patterns of change (or otherwise) at all sites on Astrolabe Reef in order to create a trajectory of responses. Severe weather conditions through the period of availability for field work precluded this however. Hence the findings reported above represent a snapshot of the dynamics occurring at this reef.

Chapter Four

Large Scale Environmental Stressors

Recruitment Responses to Canopy Removal in *Ecklonia radiata* and *Carpophyllum spp*. Transition Zones

4.1 Background

Storm-driven canopy loss was a leading cause of mortality for the small kelp *Ecklonia radiata* in temperate Australasia through physical swell and wave surge turbulence (Thomson et al., 2004). With the increasing frequency and intensity of storms linked to climate change, understanding the mechanisms and consequences of canopy removal is critical for predicting population and community responses in macroalgal-dominated systems (Norderhaug et al., 2020). In relatively recent times however, other factors are taking their toll on the health of kelp forests throughout Australasia. These include urchin outbreaks (Johnson et al 2023, 2024), marine heat waves (Schiel et al., 2024), and stress induced by sediment turbidity in the water column now termed ‘marine dark waves’ (Thorel et al., 2025). These phenomena are largely caused by interacting stressors associated with climate change and the increasing frequency of severity of cyclonic events that additionally impact on the land leading to catastrophic levels of coastal sedimentation (Orchard et al., 2025).

Kelp forests dominate shallow-water rocky habitats across much of the world’s temperate coastline (Steneck et al., 2002). Kelps inhabit highly dynamic wave-exposed environments, where wave-driven dislodgement can reshape reef biodiversity and functioning (De Bettignies et al., 2015). As foundation species, they support high primary productivity, enhance secondary production (Krumhansl & Scheibling, 2012), and provide habitat for a diverse associated flora and fauna (Steneck et al., 2002; Smale et al., 2013). Canopy-forming kelps and fucoid strongly influence their environment by altering light availability (Wernberg et al., 2005), modifying water flow, regulating sedimentation rates (Eckman et al., 1989), and providing shelter from physical disturbance (Connell, 2003). Less studied is the kelp ‘subcanopy’, the encrusting benthos of plants and animals that form much of the high biodiversity associated with kelp forests and which contribute to the trophic cascade and carbon flux.

The formation of clearings in kelp forests through physical and biological disturbance has been widely documented. Large-scale canopy loss may be driven by physical factors such as storms and El Niño events (Dayton et al., 1999; Norderhaug et al., 2020) or biological factors including grazing by sea urchins (Paine & Vadas, 1969; Ayling, 1981; Kimura & Foster, 1984). In some cases, clearings are colonised by dense aggregations of sea urchins, creating extensive “barren grounds” (Leinaas & Christie, 1996; Wing et al., 2022; Miller & Shears, 2023). Where urchins are absent, the substratum in clearings is dominated by red and brown turfing algae (Filbee-Dexter & Scheibling, 2015), which have been shown to inhibit canopy kelp recruitment (Kennelly, 1987; Layton et al., 2019; Farrell et al., 2025). Several mechanisms have been proposed to explain this suppression, including physical obstruction of settlement surfaces, chemical deterrents, and post-settlement competition for space and resources (Fletcher & Fletcher, 1975; Dayton et al., 1984; Reed & Foster, 1984; Schiel & Foster, 1986). Experimental studies in New South Wales have further demonstrated that even after turf is removed from clearings during peak kelp settlement, recruitment remains low, suggesting that turf may leave lingering effects on the substratum that continue to inhibit settlement (Kennelly, 1987; Farrell et al., 2025). Such feedbacks may reinforce shifts from canopy-forming kelps to turf-dominated states, reducing the likelihood of natural recovery without intervention.

As above, in addition to storm damage and direct human disturbance, macroalgal canopies are increasingly threatened by episodic sedimentation events from terrestrial runoff, sometimes referred to as "marine darkwaves" (Thoral et al., 2025). These events deposit large amounts of fine sediment on the reef, which can smother fucoids and kelps and reduce light penetration (Schiel et al., 2006; Kawamata et al., 2011; Bishop, 2025). Such conditions can hinder the recruitment of canopy-forming species, shift competitive balances toward turf algae, and slow or prevent recovery after disturbance. The interaction between natural disturbances, such as storms, and human-induced pressures, including fishing pressure and sedimentation, is becoming increasingly important to understand for effective reef management (Levin, 2000; Smale et al., 2020; Edwards et al., 2010). With climate change projected to increase the frequency and severity of storm events in New Zealand, the combined effects of these pressures may push ecosystems past recovery thresholds, particularly in ecotones where species composition is finely balanced.

4.1.1 Macroalgal Forests: *Ecklonia radiata* and *Carpophyllum spp*.

Macroalgal forests in New Zealand are often dominated by two key canopy-formers: *Ecklonia radiata*, a medium-sized kelp typically found on deeper reef slopes and one of the most widespread kelps globally, dominating temperate reefs, and *Carpophyllum* species, which dominate shallower, more wave-exposed habitats (Schiel, 1988; Schiel, 1990; Hurd et al., 2004; Buchanan, 2011). At Motiti Island and Astrolabe Reef, the *Carpophyllum* assemblage is primarily composed of *C. plumosum, C. flexuosum, and C. maschalocarpum,* which together provide significant structural complexity and ecosystem services. The transition zone between *Carpophyllum* species and *Ecklonia radiata* dominated habitats supports species from both assemblages, acting as a biodiversity hotspot where ecological processes from both zones overlap (Kerr & Grace, 2005) (Figure 14). Because of this, disturbances in the transition zone may have disproportionate effects on local biodiversity and can act as focal points for shifts in community structure. These mixed-canopy zones are vulnerable to shifts toward alternative, less productive states such as turf algae or kina (*Evechinus chloroticus*) barrens. The recent invasion of the long-spined sea urchin *Centrostephanus rodgersii* at Astrolabe Reef and Motiti Island represents an additional pressure on canopy-forming species, as its grazing can prevent macroalgal recovery and accelerate the transition toward urchin barrens (Kerr et al., 2025).

Figure 14. Image of an *Ecklonia radiata* and *Carpophyllum spp* transition zone at 10m depth.

4.1.2 Urchin Dynamics

Kelp–urchin–predator dynamics are a defining feature of temperate reefs in Aotearoa (Kerr et al., 2025). When urchins are lightly regulated by predators, they can overgraze kelp and lock reefs into low-diversity “barrens” (Shears & Babcock, 2002; Miller & Shears, 2023). Two species matter most in this system: the native kina (Evechinus chloroticus), long implicated in localised kelp loss, and the warm-affiliated *Centrostephanus rodgersii*, whose regional expansion and behavioural shift (less cryptic, more active grazing) raise the risk of persistent barrens (Balemi & Shears, 2023). Classic narratives emphasise top-down control by apex predators, especially large snapper (*Pagrus auratus*) and rock lobsters (*Jasus edwardsii*), acting mainly on subadult and adult urchins (Field, n.d.; Kerr et al., 2025). Equally important, but often under-stated, is life-stage control by benthic foragers (blue cod, leatherjackets, moki, some wrasses) that forage on the seafloor and remove newly settled and small juvenile urchins before they join the grazing front.

This framing is essential for interpreting the study area. At Motiti (unprotected), historical fishing pressure has reduced both apex predators and benthic foragers, weakening control across both urchin life stages. At Astrolabe (protected), predator recovery is underway but appears functionally uneven: apex predators are returning, yet some benthic foragers, such as blue cod, remain scarce, leaving a potential recruitment bottleneck for *Evechinus chloroticus* and *Centrostephanus rodgersii*.

The BRUV results (Chapter 2) support this ecological dynamic. At Astrolabe Reef, relative abundance of several predators was higher (e.g., snapper, scarlet wrasse, red pigfish), and crayfish were recorded only at Astrolabe Reef. In contrast, key benthic feeders showed mixed or low signals: blue cod were seen only at Motiti Island, leatherjackets were present but sparse, and red and blue moki were rare across sites. One Motiti Island survey site (MT2) recorded no fish during our deployments, highlighting the patchiness and overall depletion there. Taken together, these data point to stronger top-down pressure at Astrolabe Reef than at Motiti Island, but also to an incomplete restoration of the benthic-foraging guild that is critical for suppressing urchin recruits.

This context sets up the interpretation of Chapter 4: where benthic feeders are under-represented and stressors persist (e.g., near the MV *Rena*), early successional space is disproportionately captured by turfing algae, *C. rodgersii* can persist or appear locally, and subcanopy species(CCA, sponges) remain lower, conditions that favour urchin–turf feedbacks over kelp recovery.

4.1.3 Aims and Objectives

To investigate these dynamics, we examined how the removal of canopy-forming macroalgae in the *Carpophyllum spp – Ecklonia radiata* transition zone influences species recruitment, community composition, and the potential for ecosystem state shifts. The study aimed to determine which species would dominate recolonisation following canopy disturbance, whether *Ecklonia radiata*, *Carpophyllum spp*, or other opportunistic taxa—and to assess whether small-scale disturbances in mixed-species zones could act as tipping points, leading either to dominance by a single canopy-former or to less productive states such as turf algae or urchin barrens. The experiment mimicked large scale kelp destruction now occurring with violent storms to examine prevailing ecological dynamics between two seaweed characterised zones (*Ecklonia* versus *Carpophyllum* forests), while additionally monitoring the prevailing urchin dynamics.

This experiment also extended the disturbance assessments carried out with clearances around the MV *Rena* (Chapter 3). The eastern location of Motiti Island, used for kelp canopy clearance treatments, provides a habitat broadly comparable to Astrolabe Reef, allowing discussion of small- and large-scale clearance effects (within the limits described) and enabling closer examination of urchin responses. Large-scale clearance experiments could not be undertaken at Otāiti due to its marine protection status.

Unlike many disturbance studies that simplify designs by testing only the presence or absence of a single dominant species and recording responses of a limited set of community components, this experiment assessed recovery across the full benthic community while also tracking the species-specific responses of *Carpophyllum* and *Ecklonia radiata* as they recolonised newly available space. The study further considered how canopy removal interacts with environmental stressors such as elevated sedimentation and wave action to influence the stability and resilience of this mixed-canopy zone. Understanding these interactions is critical for predicting ecological responses to future climate-driven disturbances and for guiding the management of temperate reef ecosystems dominated by macroalgal canopies.

4.2. Methods

4.2.1 Site Selection and Experimental Design

Field work was conducted on 5 February 2025 at two contrasting locations on Motiti Island. The first site, MT1 (37°36.973′S, 176°26.374′E), was located on the more exposed eastern side of the island, while the second site, MT2 (37°37.468′S, 176°24.191′E), was situated on the sheltered northwestern coastline. These locations were selected to capture differences in environmental exposure, with the eastern site subject to higher swells and wind, and the western site relatively protected (Figure 15). At each location, two adjacent replicates were selected, resulting in four study sites in total. The eastern location was chosen to be as similar to the Astrolabe location as possible in terms of habitat, reef aspect and exposure.

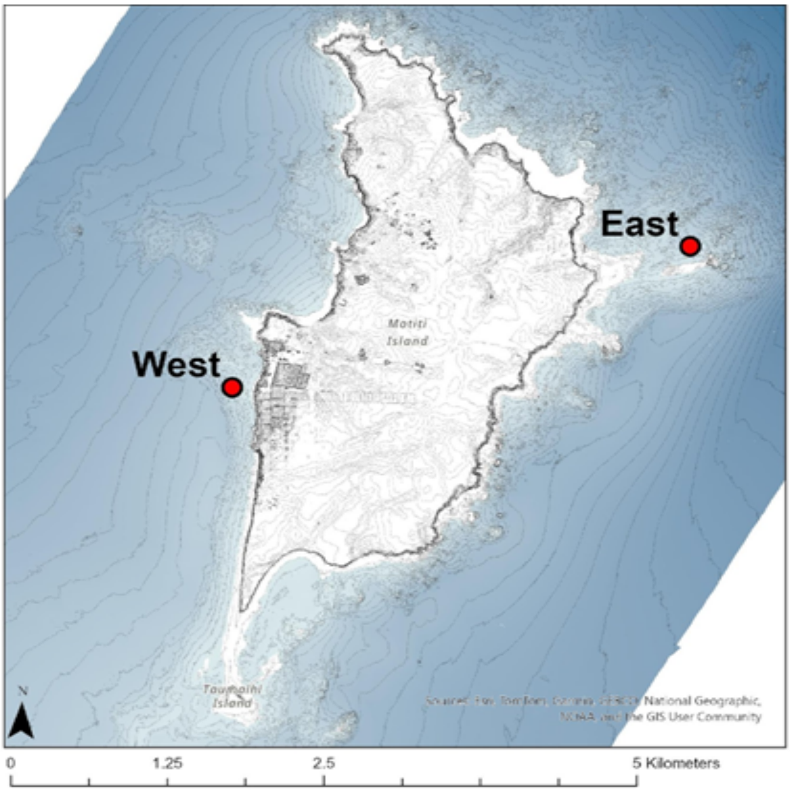

Figure 15. Map of Motiti Island, Bay of Plenty, New Zealand, showing the locations of the two study sites: West (more sheltered) and East (more exposed).

4.2.2 Field Method

Within each site, divers identified a transition zone between two dominant canopy-forming macroalgal genera, *Carpophyllum spp*. and *Ecklonia radiata*. On the 5 February 2025, a 16m^2 metre experimental plot was established spanning the boundary between these two habitat types (Figure 16). All canopy-forming individuals of *Carpophyllum spp*. and *E. radiata* within the quadrat were cut at the holdfast, simulating canopy clearance. Sites were permanently marked with yellow identification tags fixed to the substrate for relocation.

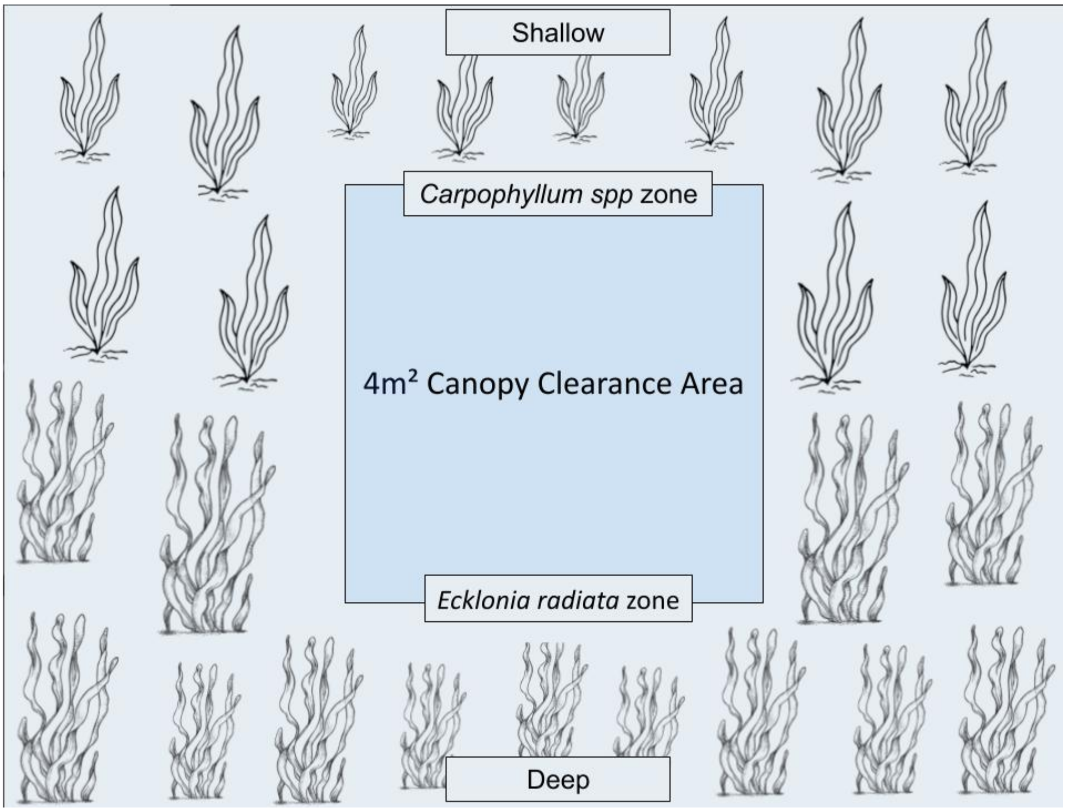

Figure 16. Example of the 4 m² canopy clearance area spanning the transition between *Ecklonia radiata* (bottom) and *Carpophyllum spp*. (top) zones.

Photographs were taken to document the initial benthic community prior to manipulation. After an 11-week recovery period, post-clearance sampling was conducted. At each site, twenty photographic quadrats were collected from the cleared plots, ten within the *Carpophyllum spp*-dominated zone and ten within the *Ecklonia radiata*-dominated zone. An additional twenty photographs were taken in adjacent undisturbed areas approximately 5-10m away (10 each in *Carpophyllum* and *Ecklonia* zones) as controls, following the same habitat breakdown. This yielded forty images per site and 160 images across all four sites.

To assess grazer responses to canopy clearance, three key invertebrate grazers, *Evechinus chloroticus* (kina), *Centrostephanus rodgersii*, and *Cookia sulcata*, were quantified within the 4x4 metre clearance plots at East and West sites. Surveys were conducted immediately before clearance and repeated 14 weeks afterwards. Grazer abundance was determined through direct counts of individuals within each plot. Divers systematically searched the entire 4 × 4 m area, recording the number of individuals of each species. Counts were performed by the same observer across all surveys to minimise observer bias.

4.2.3 Image Analysis

Photographic quadrats were analysed to quantify benthic community composition using CoralNet, a machine learning–based annotation platform. A manually annotated subset of images from the study was used to train the algorithm. Each image was overlaid with ten randomly generated points, and the organism or substrate under each point was identified to the lowest practicable taxonomic level (Figure 17). Classifications included dominant macroalgae (*Carpophyllum spp*., *Ecklonia radiata*), turfing red algae, crustose coralline algae (CCA), encrusting and tubular sponges, bryozoans, ascidians, and sand/rubble. All organisms were identified to species level where possible; otherwise, points were classified as "unknown." For statistical analysis, sponges, bryozoans, ascidians, sand, and shadowed areas were grouped into a broad "Other" category. The resulting community composition data were summarised by functional group and visualised to provide an overview of treatment and site differences.

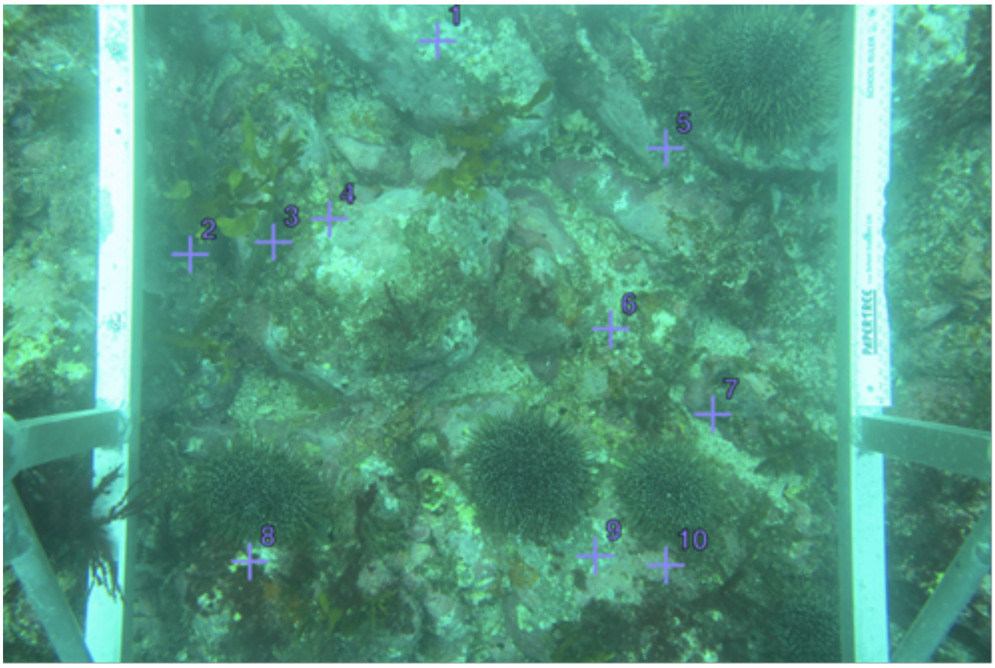

Figure 17. Example of 10 randomly generated points within the kelp canopy clearances using a 50x50cm quadrat. Screenshot acquired from CoralNet.

4.2.4 Data Analysis

4.2.4.1 Community Composition

To examine changes in benthic functional group composition across treatments, the images analysed from the canopy clearance experiment were plotted. Plots were assigned to one of four treatment types based on habitat (*Carpophyllum spp* or *Ecklonia radiata*-dominated) and treatments (Clearance or Control). Percent cover values for each functional group were summarised by calculating mean ± standard error (SE) within each treatment group and region. These values were visualised using grouped bar plots, allowing for comparisons across site (East vs. West), habitat type, and clearance treatment. Functional groups included crustose coralline algae (CCA), *Ecklonia radiata*, *Carpophyllum spp*, other macroalgae, turfing algae, and herbivore grazers. Analyses were conducted in R (version 2025.05.1+513) using the tidyverse and ggplot2 packages.

Mean abundances (± SE) were then calculated for each species by site and time, based on replicate plots. Statistical analysis was performed using two-way ANOVA, testing for the effects of site (East vs. West), time (Before vs. After clearance), and their interaction on grazer abundances. Data were inspected for normality and homogeneity of variances prior to analysis, and no transformations were required.

4.2.4.2 - Significance testing approach

To assess species-specific recolonisation following canopy removal, mean percent cover and standard error (± SE) were calculated for *Ecklonia radiata* and *Carpophyllum spp*. across habitat and treatment combinations. Data were reshaped into long format, and Wilcoxon rank-sum tests were used to compare clearance versus control plots for each species within each habitat type. P-values were adjusted using the Benjamini–Hochberg false discovery rate method, and significance was assessed at $p < 0.05$, $p < 0.01$, and $p < 0.001$. Analyses were performed in R (version 2025.05.1+513) using the dplyr, tidyr, and rstatix packages.

4.2.4.3 PERMANOVA and NMDS Ordination- Methods

To test for differences in community composition between species *(Ecklonia radiata* and *Carpophyllum spp*.) across experimental factors after 14 weeks, a permutational multivariate analysis of variance (PERMANOVA) was performed using the Bray–Curtis dissimilarity metric. The model included Site (East vs. West), Zone (Clearance vs. Control), and Habitat (*Carpophyllum*- vs. *Ecklonia*-dominated zones) as fixed factors, with all interactions tested.

Prior to analysis, replicates with zero cover for both species were excluded. The analysis was conducted in R (version 2025.05.1+513) using the adonis2() function in the vegan package with 999 permutations. Statistical significance was assessed at $\alpha = 0.05$.

To visualise patterns in community composition, a non-metric multidimensional scaling (NMDS) ordination was performed using the metaMDS() function in vegan, based on Bray–Curtis dissimilarity. The ordination was constrained to two dimensions ($k = 2$) and run with 100 random starts to ensure convergence on a stable solution. Samples with zero total cover were removed prior to analysis. Metadata (Zone, Habitat, and Site) were then appended to NMDS scores for plotting. A new column ('Region') was created by merging East1/East2 and West1/West2 to simplify visual interpretation. Ellipses representing 95% confidence intervals around Zone × Habitat groupings were added to visualise treatment effects within each region.

4.3 Results

<u>Pre-clearance Comparisons</u>

Prior to canopy removal, habitat zones reflected their defining canopy species: *Carpophyllum*-dominated plots were characterised by high cover of *Carpophyllum spp*., while *Ecklonia*-dominated plots were characterised by high cover of *Ecklonia radiata*. Within each zone, clearance and control plots were established in areas of similar composition, with no evident differences between treatments before manipulation. This ensured that any subsequent divergence between clearance and control plots represented post-clearance dynamics rather than pre-existing variation. East and West sites also showed comparable starting conditions, providing a consistent baseline for interpreting treatment effects.

4.3.1 *Ecklonia radiata* and *Carpophyllum spp* transition zone after 14 weeks

Overview of General Functional Group Composition

After 14 weeks of recovery, functional group composition showed clear treatment effects at both East and West sites (Figure 18).

At the East site, *Ecklonia radiata* maintained the highest cover in *Ecklonia* control plots (44 ± 2.57%), but was strongly reduced in clearance plots (2 ± 2.57%). *Carpophyllum* controls averaged 14 ± 1.75% cover, compared with 8 ± 1.75% in clearances. Crustose coralline algae

(CCA) was a dominant group, peaking at 52 ± 2.63% in *Ecklonia* clearances and 45 ± 2.63% in *Carpophyllum* clearances, while controls were consistently lower (22–31%). Herbivore grazers remained relatively low (<5%) in controls but increased to 5 ± 0.61% in *Carpophyllum* clearances. Other macroalgae averaged 27–30% across treatments, with slightly higher values in clearance plots.

At the West site, treatment effects were similar but often more pronounced. *Ecklonia radiata* cover was highest in *Ecklonia* controls (23 ± 1.84%), intermediate in *Carpophyllum* controls (20 ± 1.84%), and lowest in clearances (0–2 ± 1.84%). *Carpophyllum spp*. cover was reduced in clearance plots (4.5 ± 1.70%) compared with controls (15 ± 1.70%). CCA dominated in Ecklonia clearances (59.5 ± 3.53%) and *Carpophyllum* clearances (42 ± 3.53%), compared with only 22.5 ± 3.53% in *Ecklonia* controls. Herbivore grazers were again rare in controls (<1%), but reached 2 ± 0.13% in *Carpophyllum* clearances and 0.5 ± 0.13% in *Ecklonia* clearances. Other macroalgae showed a similar pattern, with higher values in clearance plots (17.5 ± 1.25%) compared to controls (7.5 ± 1.25%).

Overall, canopy removal consistently reduced the cover of dominant canopy species, particularly *Ecklonia radiata*, while promoting CCA, turfing algae, and other macroalgae. These changes were more pronounced at the West site, where *Ecklonia* controls reached nearly 60% cover and clearance treatments showed the strongest successional shifts.

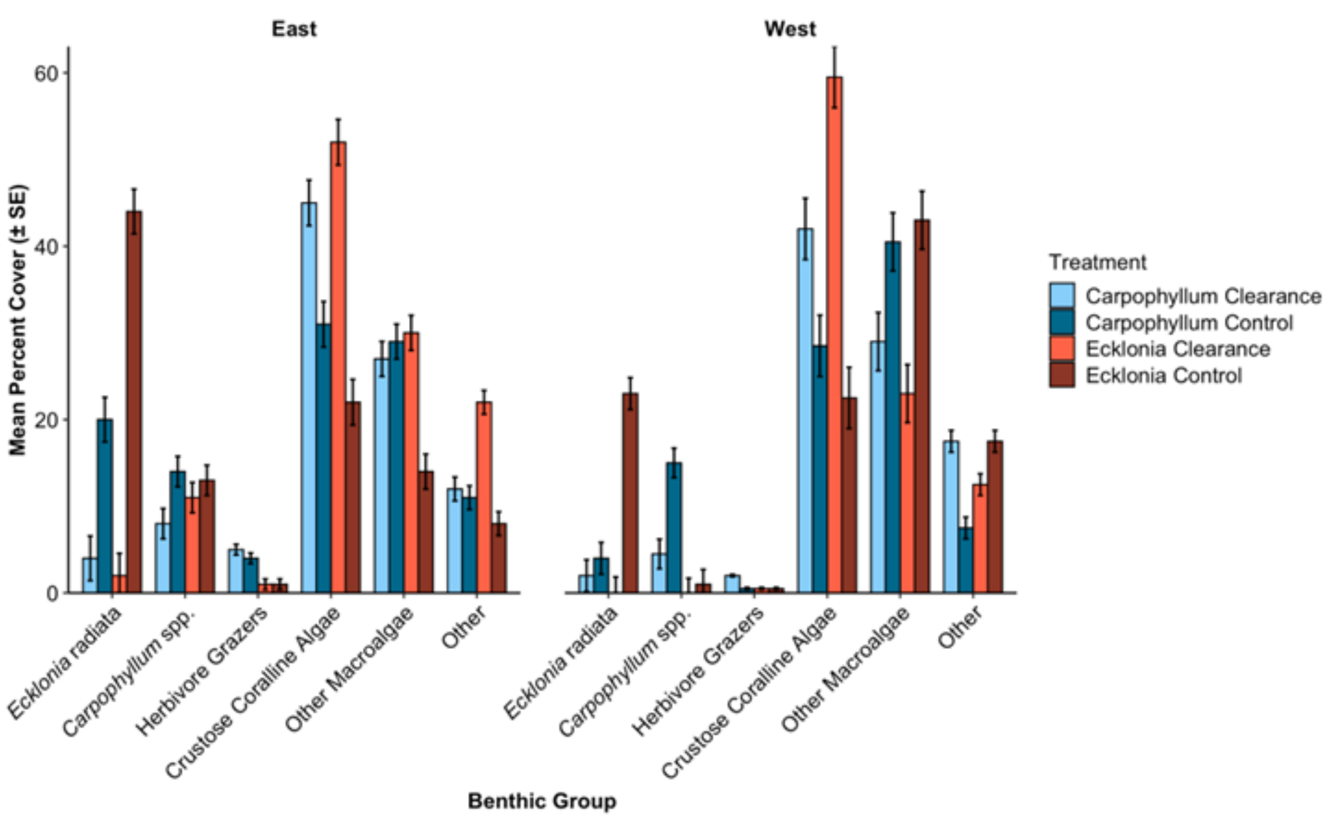

Figure 18. Mean percent cover (± standard error) of benthic functional groups 14 weeks after canopy clearance across East and West regions, under four treatment conditions: *Carpophyllum spp* Clearance, *Carpophyllum spp* Control, *Ecklonia radiata* Clearance, and *Ecklonia radiata* Control.

4.3.2 Species-Specific Recolonisation Patterns

At the West site, *Carpophyllum spp*. maintained high cover in *Carpophyllum* zones, dominating both clearance and control plots (Figure 19). Wilcoxon tests confirmed that *Carpophyllum* was significantly reduced by clearance relative to controls (p.adj = 0.015), yet it still remained the dominant canopy taxon across both treatments (Table 9). *Ecklonia radiata*, meanwhile, recruited opportunistically into *Carpophyllum* clearances (p.adj = 0.0001). In *Ecklonia* zones, however, *E. radiata* strongly dominated control plots but was almost absent from clearance plots, which were instead dominated by crustose coralline algae. This was supported statistically, with *Ecklonia* cover significantly higher in controls than in clearances (p.adj = 1.28×10^{-9}).

At the East site, *Carpophyllum* also shifted into *Carpophyllum* clearances, while *Carpophyllum* controls supported a more balanced composition, with both *Carpophyllum* and

Ecklonia present at moderate cover. In *Ecklonia* zones, *E. radiata* dominated controls, whereas clearances were colonised primarily by CCA rather than by recovering *Ecklonia.* This asymmetry was reflected in Wilcoxon results: *Ecklonia* cover was significantly reduced in clearances compared to controls (East1: $p = 9.82 \times 10^{-6}$; East2: $p = 4.13 \times 10^{-5}$), while *Carpophyllum* did not show significant recruitment into *Ecklonia* habitats ($p > 0.7$).

Overall, these results demonstrate an asymmetrical recolonisation dynamic. *E. radiata* retained dominance only in its own control plots, while *Carpophyllum spp*. was more opportunistic, able to persist after clearance in its own habitat and, in some cases, expand into *Ecklonia* zones. However, clearances in *Ecklonia* habitats were not recolonised by either canopy species and were instead dominated by CCA, suggesting a shift towards early successional, non-canopy assemblages.

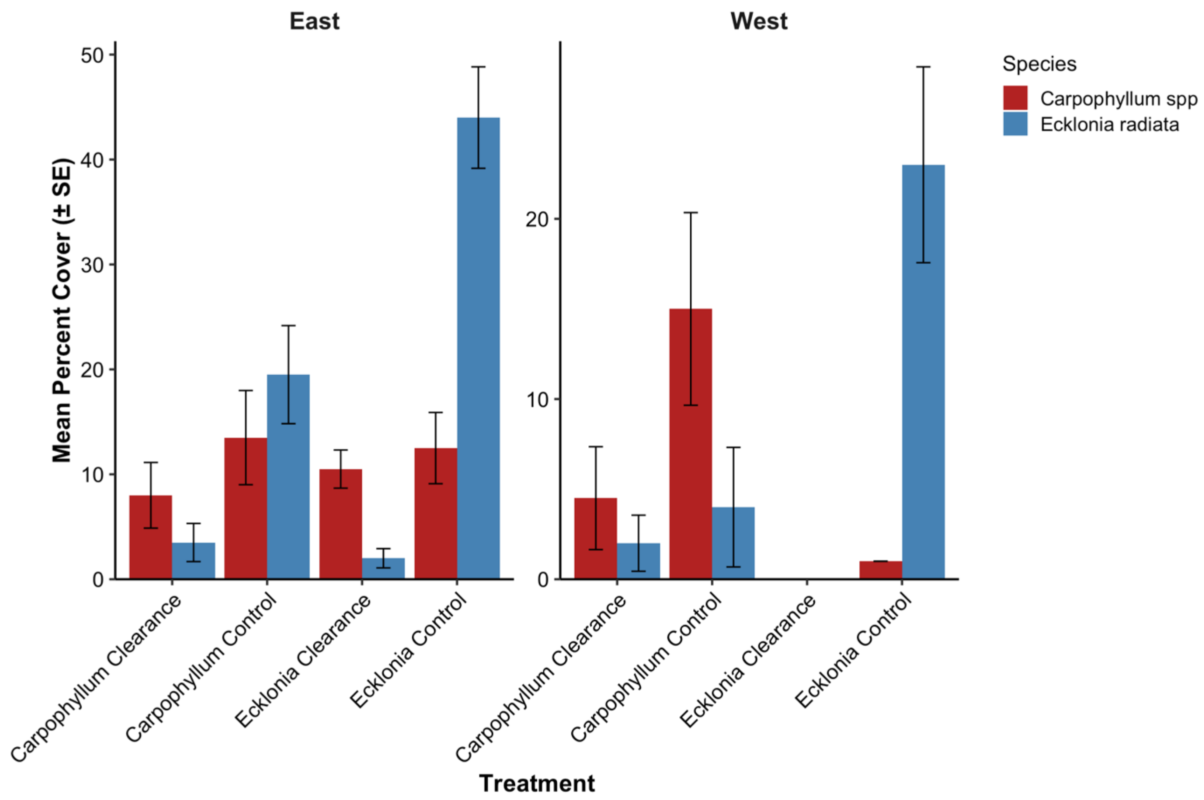

Figure 19. Mean percent cover (± SE) of *Ecklonia radiata* and *Carpophyllum spp*. across clearance and control treatments at East (left plot) and West (right plot) sites on Motiti Island after 14 weeks (5 February 2026 – 15 May 2026).

Table 9. Summary of species-specific recruitment responses to canopy clearance in *Carpophyllum spp* - and *Ecklonia radiata* -dominated habitats at Motiti Island. Mean cover of *Ecklonia radiata* and *Carpophyllum spp*. in clearance and control plots was compared using Wilcoxon rank-sum tests, with p-values adjusted using the Benjamini–Hochberg method. Significance codes: ns = not significant; * $p < 0.05$; *** $p < 0.001$; **** $p < 0.0001$.

Habitat zone	Species recruiting in	p.adj	Significance
Carpophyllum spp zone	*Carpophyllum spp*	0.015	*
Carpophyllum spp zone	*Ecklonia radiata*	0.001	***
Ecklonia radiata zone	*Carpophyllum spp*	0.742	ns
Ecklonia radiata zone	*Ecklonia radiata*	1.28E	****

4.3.3 Multivariate Community Composition Analysis

PERMANOVA and nMDS ordination

PERMANOVA revealed that community composition was strongly influenced by Zone ($F = 16.29$, $R^2 = 0.138$, $p = 0.001$), with clearance plots differing significantly from controls (Table 10). Habitat type also had a significant effect ($F = 5.04$, $R^2 = 0.043$, $p = 0.013$), reflecting differences in recruitment between *Carpophyllum*- and *Ecklonia*-dominated zones. A significant Site × Habitat interaction ($F = 3.89$, $R^2 = 0.099$, $p = 0.002$) indicated that the influence of habitat type varied between East and West sites. In contrast, there was no overall effect of Site ($F = 0.86$, $R^2 = 0.022$, $p = 0.534$) and no Site × Zone interaction ($F = 0.79$, $R^2 = 0.013$, $p = 0.518$), suggesting that the effects of canopy clearance were broadly consistent across locations. The Zone × Habitat interaction was marginal ($F = 2.46$, $R^2 = 0.021$, $p = 0.073$), suggesting a weak dependence of clearance effects on the original habitat type.

These patterns were visually supported by the NMDS ordination (Appendix E: Figure 1), which showed clear separation between Clearance and Control groups, particularly within the West region. In the East region, treatment groups overlapped more, suggesting weaker effects of clearance. Points were grouped by Zone and shaped by Habitat, but little separation was observed between habitat types, aligning with the PERMANOVA results. Ellipses for Clearance plots were more dispersed than those for Control plots, indicating greater variability in recruitment composition following canopy removal.

Table 10. PERMANOVA results (Bray–Curtis dissimilarity) for the effects of Site, Zone, and Habitat on benthic community composition.

Term	Df	Sum of Squares	R^2	F	p-value	Significance
Site	3	0.4482	0.02176	0.86	0.534	
Zone	1	2.8464	0.13816	16.29	0.001	***
Habitat	1	0.8809	0.04276	5.04	0.013	*
Site × Zone	2	0.2766	0.01342	0.79	0.518	
Site × Habitat	3	2.0376	0.09890	3.89	0.002	**
Zone × Habitat	1	0.4295	0.02085	2.46	0.073	
Site × Zone × Habitat	1	0.4062	0.01972	2.33	0.111	
Residual	76	13.2770	0.64444			
Total	88	20.6023	1.00000			

Overall, the analysis shows that clearance treatments and background habitat type were the primary drivers of variation in community composition, while East vs West site differences were minor and only apparent when interacting with habitat identity.

4.3.4 Grazer counts

Before the clearances, East and West showed a similar community composition between *Evechinus chloroticus, Centrostephanus rodgersii,* and *Cookia sulcata* (Figure 20). After the clearances a clear difference in abundance at the East and West site was observed. A higher number of *Evechinus* and *Cookia sulcata* at the East site over the West site, at the West site (more sheltered site), more *Centrostephenus rodgersii* was observed.

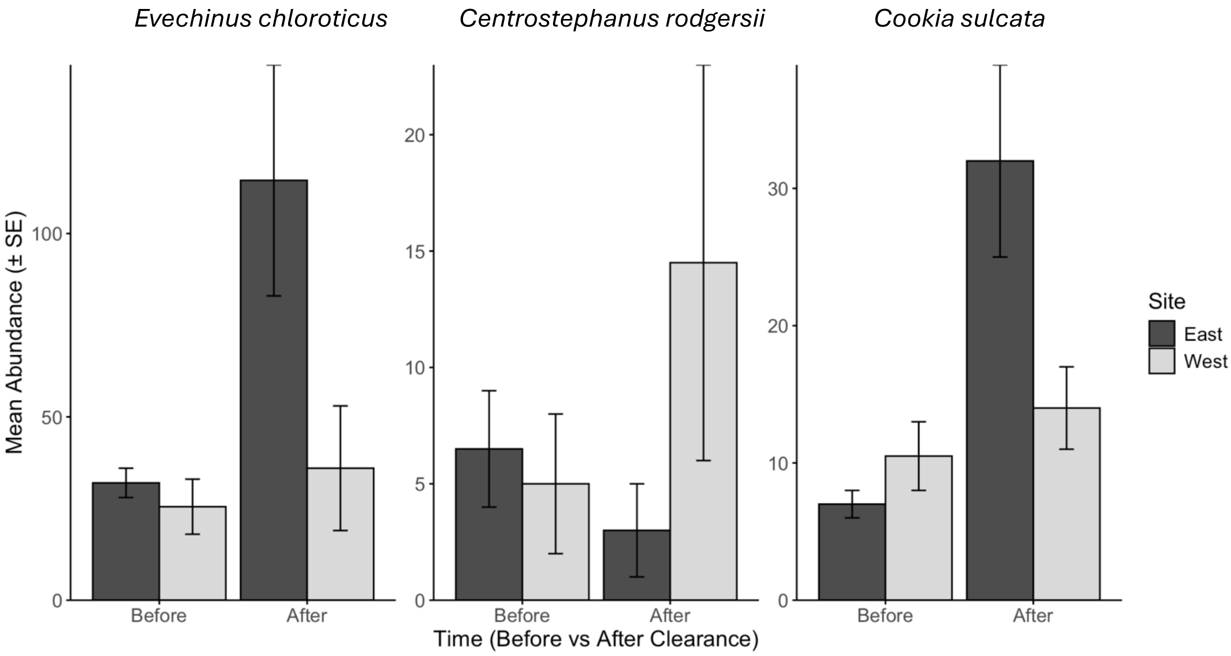

Figure 20. Mean abundance (± SE) of grazing invertebrates *Evechinus chloroticus, Centrostephanus rodgersii,* and *Cookia sulcata* within 4 × 4 m canopy clearance plots at East and West sites, surveyed before and 14 weeks after clearance. Bars represent site-specific means from replicate plots, with error bars showing standard error.

Analysis of variance revealed species-specific responses of grazing invertebrates to canopy clearance (Table 1). For *Evechinus chloroticus,* there was no significant effect of site ($F_{1,4}$ = 5.34, p = 0.082) or time ($F_{1,4}$ = 6.39, p = 0.065), although both factors were marginally non-significant and suggestive of higher abundances at the East site and after clearance. No significant site × time interaction was detected ($F_{1,4}$ = 3.83, p = 0.122).

For *Centrostephanus rodgersii*, no significant differences were observed with respect to site ($F_{1,4}$ = 1.09, p = 0.355), time ($F_{1,4}$ = 0.39, p = 0.565), or their interaction ($F_{1,4}$ = 1.85, p = 0.246), indicating that abundances remained relatively stable across sites and between survey periods. In contrast, *Cookia sulcata* showed a significant effect of time ($F_{1,4}$ = 12.45, p = 0.024), with abundances increasing after canopy clearance. Although the main effect of site was not significant ($F_{1,4}$ = 3.22, p = 0.147), a near-significant site × time interaction ($F_{1,4}$ = 7.08, p = 0.056) suggests that increases were stronger at the East site compared to the West site

Table 11. Results of two-way ANOVA testing the effects of site (East vs West), time (Before vs After clearance), and their interaction on grazer invertebrate abundances within 4 × 4 m canopy clearance plots. Significant effects ($p < 0.05$) are in bold, and trends ($0.05 \leq p < 0.1$) indicate marginal differences.

Species	Factor	F	p-value
Evechinus chloroticus	Site	5.34	0.082
	Time	6.39	0.065
	Site × Time	3.83	0.122
Centrostephanus rodgersii	Site	1.09	0.355
	Time	0.39	0.565
	Site × Time	1.85	0.246
Cookia sulcata	Site	3.22	0.147
	Time	12.45	0.024
	Site × Time	7.08	0.056

4.4 Discussion

Consequences of habitat disturbance and recovery to recruitment of subcanopy species, e.g., urchin, are increasingly important to understand in the context of both climate-driven and human-induced pressures. The interaction between large storm systems and human disturbances, such as fishing pressure, is becoming a critical focus for management. This study further considered how canopy removal interacts with environmental stressors such as increased sedimentation and reduced light availability, both of which can influence the stability and resilience of the *Carpophyllum spp – Ecklonia radiata* transition zone.

A previous study by Schiel (1990) provides important context for interpreting these findings. In north-eastern New Zealand, Schiel (1990) demonstrated that adult canopies of both *Ecklonia radiata* and fucoid species strongly suppress recruitment beneath them, with recovery dynamics heavily influenced by the timing of canopy removal. Schiel's experimental clearances showed that summer removal of *E. radiata* often facilitated early recruitment of *Carpophyllum spp* and *Sargassum sinclairii,* while winter removals tended to favour *E. radiata* recruitment. In *Carpophyllum spp* stands, seasonal timing was equally important, summer removals resulted in rapid fucoid recovery, whereas winter removals produced low recruitment of both fucoids and kelps. These results indicated that invasion of other canopy species often required not just the removal of adults but also the repeated removal of their recruits.

Interestingly, the present study, conducted in summer, contrasts with these historical patterns. Instead of fucoid dominance following summer canopy loss, *Ecklonia radiata* exhibited comparatively higher recruitment and growth rates in cleared plots. This difference may reflect site-specific conditions at Motiti Island, such as differences in hydrodynamics, grazer pressure, or light and sediment regimes, which could mediate competitive outcomes. For example, the more open hydrodynamic environment at the East site of Motiti could enhance *Ecklonia radiata* spore dispersal and settlement success, even during periods when fucoid propagules are seasonally abundant (which was seen evident in the *Ecklonia radiata* control site, higher *E. radiata* there and higher recruitment in the clearance). This suggests that, while seasonal reproductive cycles remain a strong driver of canopy recovery potential, localised environmental conditions can override expected recruitment patterns, reinforcing the need for spatially explicit management approaches.

Habitat-specific differences in recruitment patterns highlight the importance of background community composition in determining post-disturbance outcomes. *Carpophyllum spp* recruited readily into *Ecklonia radiata*-dominated habitats, likely reflecting its broad dispersal capabilities and tolerance to a range of light and sediment conditions (Wernburg et al., 2019). In contrast, *Ecklonia radiata*. recruitment into *Carpophyllum spp* habitats was minimal, consistent with its more limited dispersal range and greater sensitivity to microhabitat requirements for germling establishment. Interestingly, the opposite dynamic has been observed in other studies, where mixed-canopy systems tend to shift toward *Ecklonia radiata* dominance following disturbance, with fucoids failing to recover without sustained propagule input or favourable settlement conditions (Edgar et al., 2004; Schiel & Lilley, 2011). The significant Site × Habitat interaction detected suggests that regional factors, possibly hydrodynamics, sedimentation rates, or local grazer densities, influence the relationship between habitat identity and recruitment success. The East and West regions at Motiti Island differ in exposure and sediment regimes, which influence settlement success, and post-settlement survival. Such spatial variability is important for predicting resilience, as habitats in more sheltered or depositional environments may recover differently from those in more wave-exposed settings (Toohey et al., 2004).

The short-term recruitment patterns in this experiment show how disturbance, habitat type, and location work together to shape subcanopy communities. Canopy removal changed the composition of benthic communities at both sites, but the size and type of change depended on the habitat that was there beforehand. This supports earlier research showing that the effects of removing canopy-forming seaweeds are strongly influenced by the species already present before the disturbance (Kennelly, 1987; Schiel & Foster, 2006). The strong effect of clearance treatments suggests that small-scale canopy loss can rapidly shift competitive balances, opening space for opportunistic colonisers. This is consistent with successional theory, where early colonists, often turfing algae and filamentous species, dominate in the initial recovery phase (Connell & Russell, 2010). The observed increases in herbivore grazers within the clearance plots may further influence these trajectories, as grazing pressure can both limit canopy recruitment and promote the persistence of low-lying algal states (Ling et al., 2015). Such feedback can lock systems into alternative stable states, as documented in other temperate reef systems in Eastern New Zealand and Tasmania (Shears & Babcock, 2003; Johnson et al., 2012).

Chapter 5

General Discussion

5.1 Justification of this research

This research was undertaken to better understand how subcanopy communities respond to disturbance in temperate reef ecosystems, using Astrolabe Reef and Motiti Island as case studies. Much of the monitoring and literature on recovery following disturbances focuses on conspicuous canopy formers or fish assemblages, yet the processes occurring beneath the canopy are equally, if not more, important for resilience. Subcanopy assemblages contain a diversity of taxa that contribute to ecological stability, productivity, and long-term recovery trajectories. By investigating how these assemblages respond under different disturbance contexts, legacy contamination at Astrolabe Reef and canopy removal at Motiti, this research provides insights into the mechanisms that drive resilience and vulnerability. The work is justified in that human-induced disturbances are becoming increasingly frequent and complex, and understanding their interactions with natural variability is critical for anticipating ecosystem futures.

5.2 Collective Findings

5.2.1 Dominance of Opportunistic Species

Firstly, when the two experiments are considered together, several broad patterns become clear. First, disturbances tend to reinforce the dominance of opportunistic species, whether turfing algae or urchins, that can colonise rapidly and tolerate stress. These groups thrive because they are physiologically and ecologically adapted to exploit newly available space, altered light regimes, and reduced competition following disturbance events.

In the clearance experiments at Motiti, *Evechinus chloroticus* and *Centrostephanus rodgersii* demonstrated increases in abundance within disturbed plots, particularly in the 4 × 4 metre clearances where removal of canopy-forming macroalgae opened up large areas of bare substratum (Chapter 4). This pattern was consistent with the smaller-scale 25 × 25 cm high-impact quadrats at Astrolabe Reef (Chapter 3), where *Centrostephanus rodgersii* was frequently observed occupying available space in the clearances. Their persistence and expansion into disturbed habitats reflects a broader pattern documented across temperate reef ecosystems worldwide. In many cases, disturbance regimes can drive a transition from productive kelp beds to simplified ‘urchin barrens,’ even without a corresponding increase in sea urchin density (Konar et al., 2013; Carnell & Keough, 2016; Carnell & Keough, 2020)

Alongside echinoid expansion, turfing algae also colonised rapidly, particularly in clearance plots where crustose coralline algae (CCA) and small filamentous forms often replaced canopy-forming macroalgae. This response is well documented in the literature. Turf assemblages are recognised as some of the earliest colonisers following physical or biological disturbance (Kennelly, 1987; Connell, 2003). Their rapid establishment not only pre-empts recolonisation by slower-growing canopy formers such as *Ecklonia radiata* but can also trap sediments and alter boundary layer light and nutrient conditions, reinforcing their dominance and inhibiting the recovery of structurally complex habitats (Airoldi, 2003; Layton et al., 2019).

In both the Astrolabe and Motiti contexts, this feedback loop between disturbance, urchin presence, and turf proliferation suggests the potential for alternative stable states. Once turfing algae or grazers establish, they can suppress canopy recovery either directly through grazing pressure or indirectly by changing substratum conditions. This dynamic helps explain why some clearance plots, particularly in *Ecklonia*-dominated zones, showed limited canopy recruitment and instead shifted towards assemblages dominated by CCA and urchins.

Together, these results highlight that opportunistic taxa, both grazers and algal turfs, are not simply transient responders to disturbance, but may be key drivers of long-term community trajectories. Their ability to rapidly exploit newly disturbed space means that repeated disturbances (e.g., storms, sedimentation events, or anthropogenic stressors) could lock reef systems into simplified states, reducing biodiversity and functional resilience.

5.2.2 Dominant Macroalgae shift into Available Space

Secondly, canopy species differ markedly in resilience: *Carpophyllum spp* demonstrated strong recovery capacity, whereas *Ecklonia radiata* were much less able to re-establish following disturbance. The contrasting recolonisation dynamics between *Ecklonia radiata* and *Carpophyllum spp*. point to deeper ecological processes than a simple difference in recovery capacity, potentially due to the time of year. While *Ecklonia radiata* was comparatively slow to re-establish, *Carpophyllum* demonstrated a strong ability to expand downslope into zones historically dominated by *Ecklonia radiata*. This downward shift of *Carpophyllum spp* into deeper water reflects more than opportunistic colonisation, it may be symptomatic of the broader phenomenon of "marine darkwaves," in which increased sedimentation and turbidity reduce light penetration and alter depth-related habitat boundaries. In this context, the apparent resilience of *Carpophyllum spp* is tied to its capacity to track shifting light environments, while *Ecklonia radiata* appears more constrained in its depth distribution. These dynamics highlight how disturbance interacts with climate-driven processes to restructure canopy composition not only horizontally across habitats, but also vertically along depth gradients. This finding emphasises the importance of considering water clarity and light availability in predicting long-term trajectories of mixed-canopy reefs in the Bay of Plenty and beyond.

5.2.3 Invertebrate Indicator Species

Thirdly, small or cryptic taxa also proved to be sensitive indicators of stress. The near absence of nudibranchs across both study sites consistent with their near extinction at a number of reefs in this region including Astrolabe Reef in previous years (Gris et al., 2023) highlights subtle but ecologically significant shifts. Similarly, bryozoans were generally sparse, with the notable exception of *Pterocella vesiculosa,* which was highly abundant at Astrolabe Reef.

Overall, the experiments reinforce that resilience is strongly linked to biodiversity. Sites with greater species richness and functional diversity demonstrated stronger buffering capacity, while simplified assemblages remained more vulnerable to further disturbance.

5.3 Limitations

It is important to acknowledge several limitations of this study. The limited sample size (n = 4 replicates per site) constrained statistical power, potentially reducing the ability to detect more subtle ecological differences between high and low-impact sites (Chapter 3). The relatively short monitoring duration (14 weeks) further restricted the interpretation of recovery trajectories, as longer-term dynamics such as differences in growth rates, competitive interactions, or environmental filtering may only become evident over extended timelines. Continued monitoring of clearance plots (as originally planned – see above) would therefore be essential to determine whether the patterns observed here represent transient recovery responses or signal a genuine change in benthic assemblages 14 years after the MV *Rena* grounding.

Seasonal variation was not fully accounted for in this short-term experiment, and future work should incorporate repeated surveys across seasons to capture recruitment pulses, growth cycles, and other temporal fluctuations. Field constraints, such as depth, weather conditions, and limited underwater visibility, occasionally prevented the identification of organisms to species level, which may have reduced taxonomic resolution. In addition, logistical barriers prevented further revisits to the sites, limiting the ability to add an additional temporal layer of monitoring that could have provided greater insight into recovery trajectories.

It should also be noted that eDNA samples were collected during this study from water below the subcanopy, above the canopy, and within the sediment. These results were not available at the time of writing but will be analysed and published in future work. Incorporating eDNA into this framework has strong potential to complement visual survey methods by capturing cryptic diversity and microbial community dynamics associated with disturbance responses.

5.4 Future research

Seasonal assessments of clearances

Future work should include repeated assessments of clearance plots across different seasons to capture temporal variation in recruitment, growth, and community composition. Seasonal monitoring would help to identify whether patterns observed in short-term experiments persist across annual cycles or if recovery trajectories differ depending on the timing of disturbance events.

Species-specific clearance experiments and regional comparisons

Targeted clearance experiments focusing on individual species would provide greater resolution into species-specific recovery dynamics. Comparative studies at other northeast New Zealand reefs would further test the generality of these patterns and identify whether the processes observed at Astrolabe Reef and Motiti Island are consistent across the wider Bay of Plenty and beyond.

Fine-scale monitoring of environmental drivers

To better understand the mechanisms shaping post-disturbance recovery, future studies should integrate fine-scale monitoring of environmental variables, such as turbidity, current speed, and sedimentation rates, before and after canopy clearances. Linking these physical drivers with biological responses would improve predictive capacity for resilience in mixed-canopy reef systems.

Expanded replication and site coverage at Astrolabe Reef

Repeating the clearance experiment at Astrolabe Reef with additional replicates and broader site coverage would strengthen statistical power and allow for a more comprehensive assessment of variability across impact zones. This would help determine whether the differences observed in this study are consistent across the wider reef system.

Environmental DNA analysis

Environmental DNA (eDNA) samples collected from seawater above and below the subcanopy, as well as from sediment at Astrolabe Reef and Motiti Island, are awaiting analysis. This data has the potential to complement traditional survey methods by capturing cryptic taxa associated with disturbed and recovering habitats. Writing up and integrating these results will add an important layer of resolution to our understanding of disturbance responses. This would also add another element to the species inventory at Motiti Island and Astrolabe Reef.

5.5 Conclusion

This thesis emphasises the complexity of disturbance ecology. Human-induced and natural stressors interact in ways that defy simple prediction, producing ecological trajectories that depend on context, biodiversity, and legacy effects. Outward signs of recovery, such as the return of canopy cover, can mask deeper structural changes in subcanopy assemblages that prevent recovery and resilience. Recognising and addressing these complex dynamics is critical for effective management. The broader lesson is that biodiversity and climate cannot be managed in isolation: they are intertwined, and resilience depends on understanding this connection.

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Appendices

Appendix A: Site references for Chapter 1

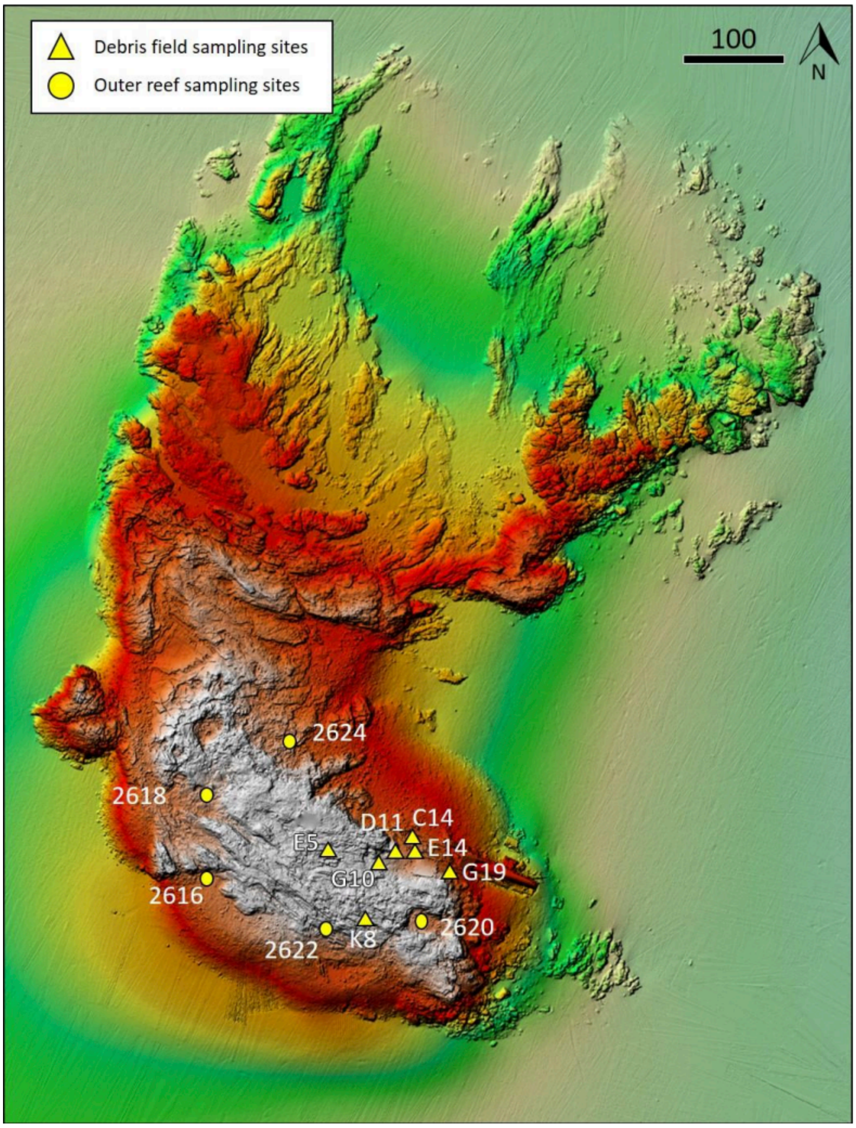

Figure 1: Bathymetry of Otāiti showing position of sampling sites. Debris field sites are marked by triangles and outer reef sites by circles. From the physical environment report (Ross, 2023)

Appendix B. Relative abundance of key stone indicator species

Table 1. Results of generalized linear models testing relative abundance of keystone indicator species between Astrolabe Reef and Motiti Island. Estimates (± SE) are shown for richness and selected fish species (Snapper, Red Pigfish, Scarlet Wrasse, and Blue Cod).

Response variable	Coefficient	Estimate	Std. Error	z value	p-value	Significance
Richness	(Intercept)	2.526	0.200	12.629	< 0.001	***
	ReefMotiti	-1.022	0.389	-2.628	0.009	**
Snapper	(Intercept)	1.946	0.267	7.281	< 0.001	***
	ReefMotiti	-1.540	0.636	-2.421	0.0155	*
Red Pigfish	(Intercept)	2.015	0.258	7.804	< 0.001	***
	ReefMotiti	-1.322	0.563	-2.349	0.019	*
Scarlet Wrasse	(Intercept)	1.253	0.378	3.314	0.001	***
	ReefMotiti	-0.560	0.627	-0.893	0.372	ns
Blue Cod	(Intercept)	-19.3	6666	-0.003	0.998	ns
	ReefMotiti	19.3	6666	0.003	0.998	ns

Appendix C. Nearby Biodiversity Assessment at High and Low Impact Sites

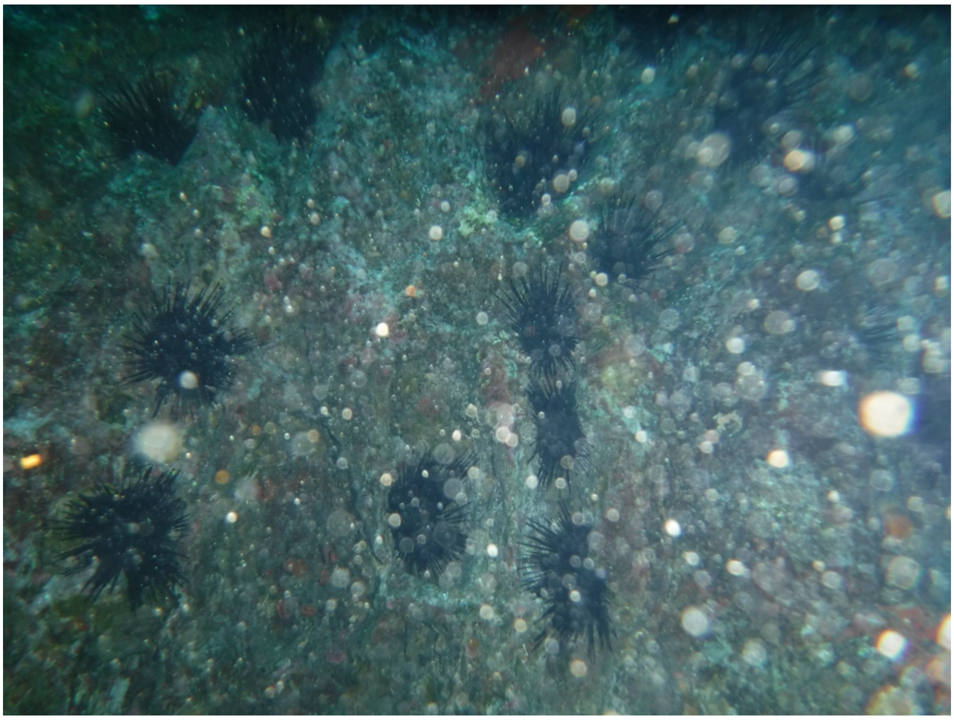

Figure 1. Wall of *Centrostephanus rodgersii* 20 metres away from the high impact site at Astrolabe Reef.

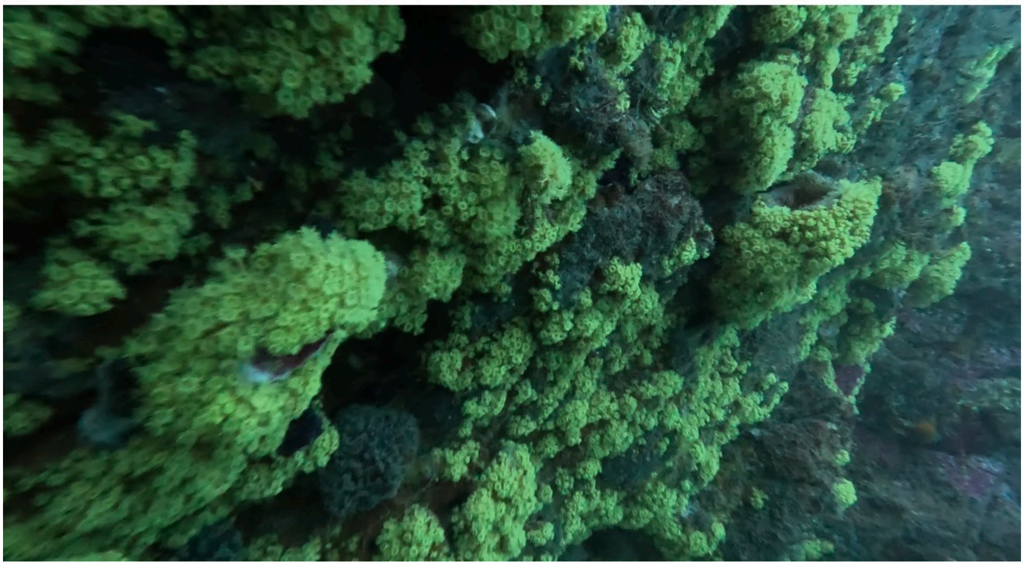

Figure 2. Dense aggregation of Parazoanthus elongatus 20 metres away from the low impact site at Astrolabe Reef.

Appendix D. Supplemental Tables for Chapter 3

Table 1. Results of PERMANOVA testing for differences in community composition between low- and high-impact sites at Day Zero (Bray–Curtis dissimilarities, 999 permutations).

Source	Df	Sum of Squares	R^2	F	p-value
Treatment	1	0.15213	0.371	2.354	0.100
Residual	4	0.25850	0.630		
Total	5	0.41063	1.0000		

Table 2. Results of two-way ANOVA testing the effects of Impact (High vs Low) and Treatment (Control vs Clearance) on total benthic cover at Astrolabe Reef

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact	1	10.2	10.2	0.018	0.892
Treatment	1	30.6	30.6	0.055	0.815
Impact × Treatment	1	8.6	8.6	0.015	0.901
Residuals	92	5115	556		

Table 3. Pairwise post hoc comparisons of functional group percent cover 14 weeks following the canopy clearances at Astrolabe Reef. Differences in mean percent cover (with 95% confidence intervals and adjusted p-values) are shown for all functional group contrasts.

Comparison	Difference	95% CI (lwr, upr)	p adj

C. rodgersii – Turf algae	-48.95	-67.05, -30.85	<0.001
CCA – Turf algae	-31.89	-49.99, -13.78	<0.001
Other – Turf algae	-35.51	-53.61, -17.40	<0.001
Seaweeds – Turf algae	-42.71	-60.82, -24.61	<0.001
Sponges – Turf algae	-35.75	-53.86, -17.65	<0.001
CCA – *C. rodgersii*	17.06	-1.04, 35.17	0.076
Other – *C. rodgersii*	13.44	-4.66, 31.55	0.263
Seaweeds – *C. rodgersii*	6.24	-11.87, 24.34	0.914
Sponges – *C. rodgersii*	13.20	-4.91, 31.30	0.282
Other – CCA	-3.62	-21.73, 14.48	0.992
Seaweeds – CCA	-10.82	-28.93, 7.28	0.504
Sponges – CCA	-3.87	-21.97, 14.24	0.989
Seaweeds – Other	-7.20	-25.31, 10.90	0.852
Sponges – Other	-0.25	-18.35, 17.86	1.000
Sponges – Seaweeds	6.96	-11.15, 25.06	0.869

Appendix E. Community Composition Analysis in Chapter 4

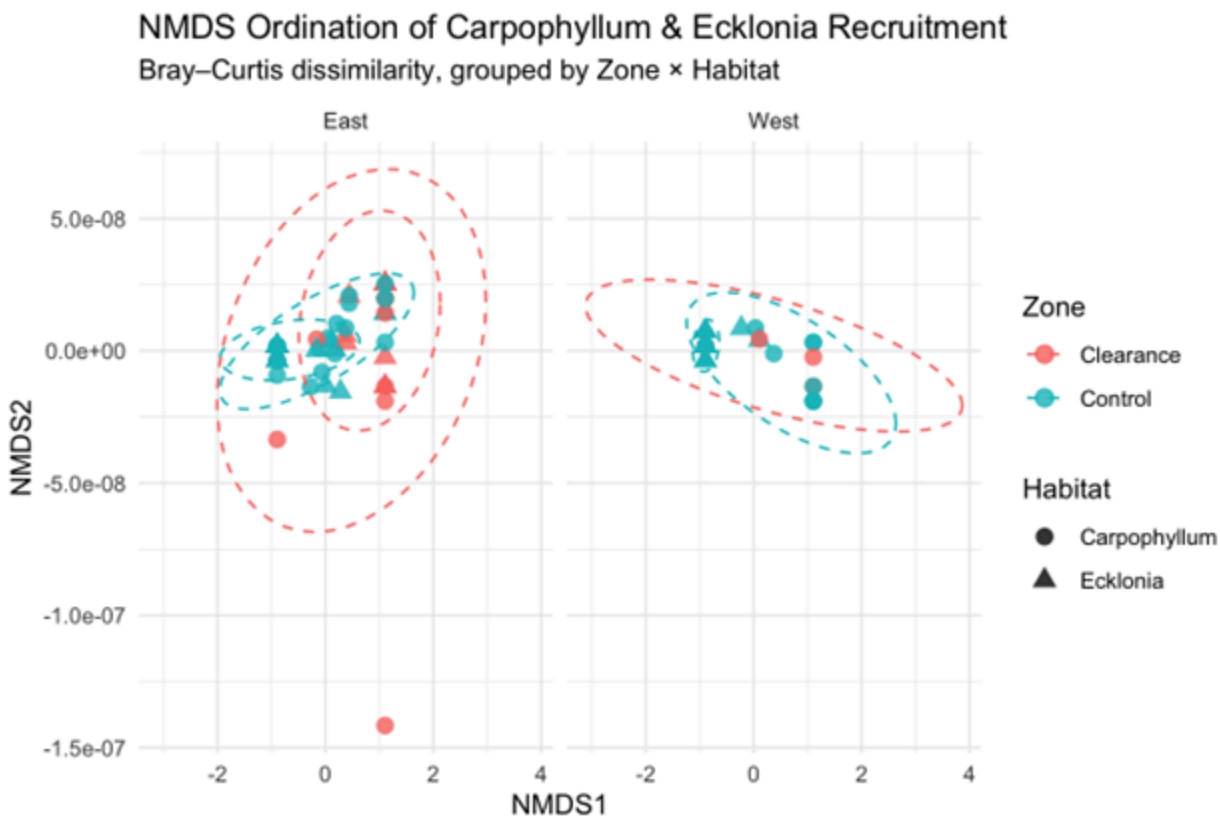

Table 1. Non-metric multidimensional scaling (NMDS) plot showing community composition of recruitment samples based on Bray–Curtis dissimilarities. Points represent replicate quadrats, with shape denoting habitat type (*Carpophyllum* or *Ecklonia*) and colour denoting treatment zone (Clearance or Control). Ellipses represent 95% confidence intervals for Zone × Habitat groupings. Data are faceted by Region (East vs. West). Clustering patterns show a separation between clearance and control treatments and some variation between habitat types, particularly in the West.