SETTLEMENT DYNAMICS AND GROWTH OF MARINE ORGANISMS ON ARTIFICIAL HABITATS

BY

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ABSTRACT

Coastal marine habitats are some of the most productive environments in the world. These habitats are also highly important for the economic, social, and cultural functioning of numerous countries, and are therefore vulnerable to stressors from the increasing level of human activity at the interface between land and sea. Many major urbanised coastal environments, including Wellington, have manipulated over half of their shorelines to support and protect coastal cities and towns, and their continuing growth. Temperate rocky reefs are some of the most affected habitats facing the highest levels of cumulative human impacts.

Artificial marine habitats are becoming a more frequent feature in coastal environments, contributing to numerous recent ecosystem management strategies around the world. It is crucial to understand factors that influence their performance as viable habitats for a range of species in order to effectively implement them as environmental mitigation or restoration strategies. Marine reef organisms typically exhibit complex life cycles defined by a period of pelagic larval development before recruiting to benthic habitat where they will continue to develop until they reach adulthood. In this thesis, I evaluated the effects of additional-three dimensional structure, proximity of an artificial reef to a natural reef, and time on the communities recruiting to artificial habitats.

In Chapter Two, I conduct a Before-After-Control-Impact-Paired Series (BACIPS) design to study the establishment of subtidal communities on two small artificial islands. I addressed the questions:

1) Does the addition of three-dimensional structure increase the densities of fish and invertebrate species across trophic groups on an artificial marine habitat?
2) Does the addition of three-dimensional structure on an artificial marine habitat shape community assemblages?
3) How does size structure of fish and invertebrate communities vary between an artificial habitat with additional three-dimensional structure and an artificial habitat without additional structure?

My results, from surveys conducted across a nine-month period, revealed no relationship between either treatment and any of the metrics studied, elucidating the lack of effect that additional structure seemed to have on the communities on these artificial habitats. However, I highlight the potential for alternative factors to be driving changes in these communities.

In Chapter Three, I evaluated the recruitment dynamics and community assemblages of the 24 artificial reef units I constructed under varying treatments. I investigated the questions:

1) Does the presence of supplemental structure and the location of an artificial marine habitat increase the abundance of fish and invertebrate species?
2) Does the placement of an artificial reef and the presence/absence of additional structure shape community composition?
3) Does the placement and design of artificial reefs influence the growth of a common species occupying them?

The effects of either structure or reef proximity were significant in shaping recruitment dynamics for a range of species including spotty wrasses (*N. celidotus*), variable triplefins (*Forsterygion varium*), kina (*Evechinus chloroticus*), cat's eye snails (*L. smaragda*), and top-shells (*Trochidae spp.*). Species diversity on artificial marine habitats were not significantly influenced by any treatment. Despite this, communities on bare substrate units were found to be significantly dissimilar to units on the natural reef edge by principal coordinates analysis. Size distributions of five focal species exhibited varying responses to each treatment, highlighting the species-specific nature of responses to structural complexity. I found no obvious relationship between structure or reef proximity on the growth of the *F. lapillum* individuals collected. This could demonstrate the potential of artificial reefs to provide viable habitats that support healthy populations of a common rocky reef species. However, given the limited sample size, further study is required in this area on a broader range of species to understand ecosystem-wide effects.

Overall, this thesis emphasizes the array of responses that marine reef organisms can have to artificial habitats based on their life history traits. It highlights the species- and spatial scale-specific nature of such responses, and the importance of acknowledging these factors when implementing environmental mitigation and/or restoration strategies that include the use of artificial reefs. Recruitment dynamics and community assembly are highly complex processes, and my research contributes to a meaningful increase in understanding of these procedures in the context of artificial marine habitats within temperate environments.

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1. GENERAL INTRODUCTION

1.1. Human Influences on Coastal Marine Environments

Coastal habitats consist of some of the most productive environments in the world, however they are particularly vulnerable to the impacts of human influences due to their position at the interface of land and sea (Costanza et al., 1997; Gunderson et al., 2008; Crain et al., 2009). Despite representing less than 15% of the Earth's land surface, coastal areas hold more than half of the human population (Mercader et al., 2017; Komyakova et al., 2019). Coastal areas are crucial to the economic, social, and cultural functioning of many countries (Airoldi et al., 2005). The high, and increasing, levels of human activities on the land-sea interface places immense pressure on coastal marine ecosystems through a multitude of stressors (Airoldi et al., 2005; Crain et al., 2009; Mercader et al., 2017; Komyakova et al., 2019, 2021). Invasive species, pollution, overfishing, and climate change are some of the most damaging human impacts on coastal habitats (Halpern et al., 2008; Crain et al., 2009; Mercader et al., 2017; Komyakova et al., 2019, 2021).

Coastal hardening – the installation of engineered structures to the shoreline – is a common practice worldwide to protect coastal populations of people, support economic endeavours, and reclaim land to sustain growing coastal cities (Airoldi & Beck, 2007; Dafforn et al., 2015; Ferrario et al., 2016; Gittman et al., 2016; Bishop et al., 2022). Many major urbanised coastal environments, including those in New York, Sydney, Hong Kong, and Wellington, consist of shorelines that are more than 50% armoured, or 'hardened' (Land, Air, Water Aotearoa (LAWA) - Wellington Harbour; Gittman et al., 2016; Bishop et al., 2022). The proliferation of coastal infrastructure, ports, harbours, and coastal defences, has been a significant cause in the loss of natural coastal habitats around the world (Halpern et al., 2008; Crain et al., 2009; Williams et al., 2016; Mercader et al., 2017; Russell, 2020; Bishop et al., 2022).

A global review by Halpern et al. (2008) found that rocky reefs ecosystems are facing the highest levels of cumulative human impacts. Artificial structures such as sea walls, wharves, and transport infrastructure generally provide habitats that are of a poorer quality as compared to the natural habitats they replaced (Moschella et al., 2005; Russell, 2020; Evans et al., 2021; Bishop et al., 2022). Topographic heterogeneity is important for the recruitment of marine organisms to natural reefs as it generates variation in the physical environments, crevices, hides, and different textures offer refugia from predation and other physical impacts (Moschella et al., 2005; Evans et al., 2021; Bishop et al., 2022). Reducing the heterogeneity of a reef environment is known to impact the survival of recruits, and can therefore influence the abundance of organisms due to the decrease in resource availability (Lavender et al., 2017; Mercader et al., 2017). This can often cause distinct assemblages to develop in urbanised coastal habitats as compared to those within natural rocky reefs, which often include increased abundances of invasive species (Glasby et al., 2007; Lavender et al., 2017). Glasby et al. (2007) found that non-indigenous species were more common on artificial structures (such as pontoons and pilings) than native species. In comparison, native species were more common on natural reefs than invasive species (Glasby et al., 2007).

1.2. Complex Marine Life Cycles

Many taxa, including insects, amphibians, and fish, have evolved life cycles that are complex and involve multiple ontogenetic stages (Werner & Gilliam, 1984; Wilbur, 1980). Wilbur (1980) describes a complex life cycle as a life history that includes an abrupt ontogenetic change that affects the morphology, physiology, and behaviour of an individual, therefore affecting the habitat that individual occupies. Individuals that exhibit complex life histories experience different pressures (for example predation and competition) through different life stages (Werner & Gilliam, 1984). Most reef fish and invertebrates display complex life cycles (Bae et al., 2022; Fontes et al., 2009; Leis et al., 2013; Shima & Swearer, 2010; Steele, 1997); their bipartite life cycles are defined by the dispersal of planktonic eggs or larvae into pelagic waters, where they will live for up to several months developing. They will then return to benthic habitats where they will continue to develop from juvenile recruits into their adult forms.

The pelagic stage of the life cycle has consequences for the distribution and genetic connectivity of many marine species and can result in fluctuations in population sizes and community assemblages (Fontes et al., 2009; Leis et al., 2013; Shima & Swearer, 2010; Steele, 1997). Larvae are highly vulnerable throughout the first days of development, especially from predation, therefore mortality rates tend to peak soon after hatching (Litvak & Leggett, 1992). Transition from the pelagic stage to adult habitat, termed ‘settlement’, is influenced by various factors, both biotic and abiotic (Levin, 1994; Fontes et al., 2009, 2011; Bae et al., 2022). Larval characteristics including size, condition, and growth rate are considered key factors of individual performance after settlement (Fontes et al., 2011). Environmental variables such as food availability, temperature, predation, and currents can all affect recruitment, in addition to larval behaviour and habitat choice (Levin, 1994; Fontes et al., 2009, 2011; Bae et al., 2022).

Many studies have highlighted the importance of structural complexity for the recruitment of juveniles fish and invertebrates to benthic habitats. The presence of macroalgae can therefore be vital to the settlement process due to its canopy-forming properties which increases the amount of available habitat for larval recruits (Carr, 1989, 1991, 1994; Anderson, 1994; Levin, 1994). Carr (1989) demonstrated how the structure of algal assemblages had a strong influence on the composition of recruits on a temperate reef, particularly the association between canopy-forming species and understory species. In further studies, the spatial and temporal recruitment of species such as kelp bass and rockfish can be strongly influenced by the variation in densities of macroalgae, especially *Macrocystis pyrifera* (Carr, 1991, 1994). Similarly, research by Anderson (1994) and Levin (1994) consider the variation in macroalgae abundance, distribution, and structure a significant factor in the distribution and density of several temperate reef fishes over both small and large scales. More recent studies have found comparable results with canopy-forming macroalgae being important nursery habitat for juvenile fishes and adult fish assemblages, increasing density of reef fish and species diversity in most cases (Vega Fernández et al., 2009; Pérez-Matus & Shima, 2010; James & Whitfield, 2023). Substrate type has also been acknowledged as a notable variable influencing the recruitment of numerous juvenile temperate reef fish and invertebrate species (Carr, 1991; Bulleri, 2005; Siddik et al., 2019; Bae et al., 2022).

1.3. Artificial Marine Habitats as Tools for Marine Mitigation and Restoration

Artificial marine habitats, commonly termed artificial reefs, can be widely defined as submerged structures positioned on the seafloor to mimic certain features of a natural reef, and alter physical, biological, or economic parameters of a marine resource (Jensen, 2002; Layman & Allgeier, 2020). Numerous different types of structures have been used to create artificial reefs, ranging from polyvinyl chloride pipes, tyres, and derelict ships to fish aggregating devices, and purpose-designed concrete modules (Sherman et al., 2002). The construction of artificial reefs has been historically centred in Japan and the United States of America (Bohnsack & Sutherland, 1985). However, there has been a steady increase in the use of artificial habitats worldwide as both restoration tools, and for economic endeavours (Sherman et al., 2002). In Europe, as well as Japan, concrete is the leading material used in artificial reef construction (Pickering et al., 1999). Whereas other areas, including Australia, the Philippines, and the United States, have historically been more focused on using materials of opportunity such as cleaned oil and gas platforms or tyres (Pickering et al., 1999).

Artificial structures can provide space for sessile biota to colonise, alter water currents, and provide complex habitat, and they have commonly been used to attain varying outcomes (Carr

& Hixon, 1997; Sherman et al., 2002; Ramm et al., 2021). Until recently, the primary purpose for most artificial reefs has been to enhance both recreational and commercial fisheries (Pickering et al., 1999; Hunter & Sayer, 2009; Komyakova & Swearer, 2019). This practice has a long history; some reefs built in Japan with the intention of enhancing fisheries can date back at least 300 years (Komyakova et al., 2019). Many studies have now recognised the potential negative impacts of the increased fishing pressure and efficiency on these reefs (Carr & Hixon, 1997; Baine, 2001; Komyakova et al., 2019).

Environmental mitigation, or habitat restoration, are more recent developments in the use of artificial marine habitats (Pickering et al., 1999). They can be used to create additional habitat and enhance existing habitat by providing alternative adult habitat for fish and invertebrate species, and acting as spawning grounds or juvenile nurseries that support the replenishment of populations (Geist & Hawkins, 2016; Komyakova et al., 2019). Positive impacts such as increased fish abundances, species richness, and species diversity have been reported as outcomes of artificial reef implementation in several studies (Hunter & Sayer, 2009), and due to the proliferation of human influences on the coast caused by urban sprawl, artificial habitats are becoming a common tool to mitigate the loss of habitat (Wu et al., 2019; Vivier et al., 2021).

1.4. Evaluating the Success of Artificial Marine Habitats

The efficacy of artificial marine habitats as a fisheries management and restoration tool has been a topic of debate for decades, and one of the most important discussions surrounds the attraction versus production potential of these artificial habitats (Pickering & Whitmarsh, 1997; Osenberg et al., 2002). The attraction-production debate seeks to interpret whether the implementation of artificial habitats is more likely to create new habitat and produce biomass, or simply redistribute (attract) existing biomass from nearby natural habitats (Morton & Shima, 2013; J. A. Smith et al., 2016). The argument against artificial habitats is that they attract fishes and other organisms that otherwise would have settled and grown on natural habitats at similar rates if the artificial habitat was absent, and thus they detract from the productivity of natural habitats (Pickering & Whitmarsh, 1997; Osenberg et al., 2002). There is evidence, however, that artificial habitats can – in certain contexts – help to increase overall biomass of fish and invertebrates at both the artificial habitat itself, as well as surrounding natural habitats (Wilson et al., 2001; Osenberg et al., 2002; Cresson et al., 2014; Roa-Ureta et al., 2019).

One manifestation of the attraction-production issue, particularly when implementing artificial habitats, is the formation of ‘ecological traps’. Ecological traps occur when settlement cues, used by animals to select adult habitat, become dissociated with the quality of the habitat, causing habitats of inferior quality to be selected (Hale & Swearer, 2016). This can cause the animals to have lower fitness than if they were to occupy other available habitats (Hale & Swearer, 2016). There has been a historical lack of studies on ecological traps in the marine environment, with most studies being based in terrestrial systems (Hale & Swearer, 2016; Swearer et al., 2021). Artificial reefs are frequently used to enhance fisheries and restore coastal habitats, however the habitats have the potential to form ecological traps and reduce their inhabitant's fitness, thus it is important that studies include fitness metrics to determine the effect of artificial habitats (Swearer et al., 2021).

Restoration efforts should result in self-sustaining ecosystems that require no ongoing maintenance and continue to produce their own populations (Hale & Swearer, 2017). Many artificial reef deployments have failed to achieve the goals specified before deployment, and this is usually a result of inappropriate design for the desired goals (Pickering & Whitmarsh, 1997; Hackradt et al., 2011; Komyakova & Swearer, 2019). Baine (2001) found that only 50% of case studies were successful in their objectives. The ecological processes that underlie the performance of artificial habitats in comparison to natural reefs are still not entirely understood (Ferrario et al., 2016; Komyakova & Swearer, 2019). Monitoring, in particular long-term monitoring, have previously been rare on artificial habitats and they did not always include comparisons against quantitative goals (Ramm et al., 2021). The importance of comparing artificial reef outcomes to natural reefs has been highlighted by many studies in the past couple of decades, and it remains important to understand the restoration potential of artificial reefs going forward (Carr & Hixon, 1997; Pickering & Whitmarsh, 1997; Baine, 2001; Bulleri & Chapman, 2004; Komyakova et al., 2021).

1.5. Study Site and Species

The field work and laboratory work for this thesis were conducted in Wellington, New Zealand. In-situ experiments were conducted in Te Whanganui a Tara, Wellington Harbour, and otolith analyses were undertaken at the Victoria University of Wellington Coastal Ecology Laboratory (VUCEL).

There is significant construction work occurring throughout a 4.5km stretch of Wellington Harbour's northern coastline, and more work is being conducted in other areas around the harbour margins. These projects, aimed at upgrading transport corridors for the growing human population in Wellington, are causing ecological disturbances to a large portion of coastal habitats in the area. Artificial marine habitats are being used to mitigate losses to the marine environment within the harbour (Bull, 2023). However, it is widely accepted that coastal infrastructure does not support similar species assemblages compared to natural habitats, and therefore it is important that mitigation efforts include considerations for the ecological processes that drive changes in marine communities (Perkol-Finkel et al., 2018).

There has been a historic lack of research on the use of artificial habitats in a specific, Wellington-based context. Jackson et al. (2021) is a recent paper outlining 'ecological enhancements' used along a new coastal pathway built on a rock revetment. This paper outlines the necessity of ecological design being incorporated into coastal reclamation projects, however, the paper does not provide analysis of the effect of such 'ecological enhancements' and monitoring of these enhancements is yet to happen.

This thesis focuses on a range of species commonly found on rocky reef habitats in Te Whanganui a Tara – Wellington Harbour, and more specifically those that colonise artificial structures. This includes a range of fish and invertebrate species; some of the most common species in this research are spotty wrasse, *Notolabrus celidotus*, banded wrasse, *Notolabrus fucicola*, common triplefin, *Forsterygion lapillum*, variable triplefin, *Forsterygion varium*, eleven-armed starfish, *Coscinasterias muricata*, New Zealand common cushion star, *Patiriella regularis*, and cats eye snail, *Lunella smaragda*. A section of this thesis focuses on the growth rates of *F. lapillum*. This species was chosen as a focal species in the study due to their small home-ranges (Mensink & Shima, 2015), and the ability to analyse the otoliths of specimens to find daily growth of individuals living on artificial reefs.

Figure 1.1. Adult common triplefin (*Forsterygion lapillum*) showing typical colouration on an artificial habitat unit from Chapter 3.

1.6. Aims and Thesis Structure

This thesis aims to evaluate the potential for artificial marine habitats to be used as tools for the mitigation of ecological degradation and the restoration of temperate rocky reefs, and evaluate the effect of methods used to enhance the habitat creation potential of artificial reefs.

In Chapter Two, I conduct a Before-After-Control-Impact-Paired Series (BACIPS) design to study the establishment of subtidal communities on two artificial islands. These artificial islands are large-scale artificial habitats, and were implemented by a construction project as a form of ecological mitigation. I addressed the questions:

1) Does the addition of three-dimensional structure increase the densities of fish and invertebrate species across trophic groups on an artificial marine habitat?
2) Does the addition of three-dimensional structure on an artificial marine habitat shape community assemblages?
3) How does size structure of fish and invertebrate communities vary between an artificial habitat with additional three-dimensional structure and an artificial habitat without additional structure?

In Chapter Three, I evaluate the settlement dynamics and community assemblages of 24 artificial reef units under varying treatments. I constructed and deployed these reef units under particular treatments, and used them to study recruitment at a smaller scale than that of the artificial islands in the previous chapter. Creating these artificial reef units allowed me to have more control and manipulation over the treatments I wanted to investigate. I examined the questions:

1) Does the presence of supplemental structure and the location of an artificial marine habitat increase the abundance of fish and invertebrate species?
2) Does the placement of an artificial reef and the presence/absence of additional structure shape community composition?
3) Does the placement and design of artificial reefs influence the growth of a common species occupying them?

In Chapter Four, I present a synthesis of my two 'data chapters' and a general discussion of the findings within them, as well as a final conclusion to this thesis.

2. ENHANCING THE RECRUITMENT OF MARINE COMMUNITIES TO AN ARTIFICIAL HABITAT THROUGH THE ADDITION OF THREE-DIMENSIONAL STRUCTURAL COMPLEXITY

2.1. Introduction

Artificial reefs are man-made, submerged structures that are placed in aquatic environments to serve as additional habitat, often to enhance populations of marine organisms (Jensen, 2002; Layman & Allgeier, 2020; Vivier et al., 2021). The colonisation of new artificial structures by marine organisms is done via a process known as "recruitment". In the context of benthic ecology, recruitment typically refers to the number of individuals that successfully transition from a pelagic larval stage to a benthic juvenile stage (Caley et al., 1996). In contrast, the term is often used in a fisheries context to describe entry of individuals to a specific (e.g., fishable) size class (Plagányi et al., 2019). Here, I use this term to refer to individuals of any size that may colonise new habitat. This colonisation may occur via successful settlement of larval stages (e.g., Carr, 1989, 1991; Swearer & Shima, 2010), or via migration of older individuals from adjacent pre-existing habitats (e.g., Wilson et al., 2001; Osenberg et al., 2002). Regardless of the recruitment pathway, these initial colonisation processes are fundamentally important for the population dynamics and size structure that ultimately shapes the community of organisms on new artificial structures (Hackradt et al., 2011; Schroeter et al., 2015).

The abundance of juveniles and adults on a reef is regulated by a range of processes that dictate the survival of individuals throughout different phases of recruitment (Steele, 1997). The physical characteristics of shallow reef environments are thought to play a significant role in the high level of spatial variation seen in their biological structure and community dynamics (Schroeter et al., 2015). Light, temperature, nutrient availability, depth, and water movement are some of the most influential and commonly recognised factors (Schroeter et al., 2015). Temperate rocky reefs account for a large portion of the shallow marine environment globally, and support diverse communities of reef fish (Carr, 1994). Complexity of a marine habitat can be characterised by its three-dimensional structure (e.g., as provisioned by macroalgal canopies); high structural complexity may be positively correlated with species diversity (Lazarus & Belmaker, 2021), and with recruitment (Carr, 1989, 1991, 1994; Anderson, 1994; Levin, 1994). Canopy-forming macroalgae can provide vital cues for settlement of fish and invertebrates. Additionally, these algal canopies can provide important nursery habitat for juvenile fish and invertebrates, as well as foraging habitat and shelter sites for older life stages (Vega Fernández et al., 2009; Pérez-Matus & Shima, 2010; Komyakova et al., 2019; James &

Whitfield, 2023). Lastly, the relationship between understory species and canopy-forming species can also influence recruitment to temperate rocky reefs though supporting a variety of microhabitats (Carr, 1989; Hackradt et al., 2011).

The expectation of artificial reefs is that they will provision increased shelter and food availability, and by providing new areas for the recruitment of benthic invertebrates and fish, they can also increase species richness and biomass (Hixon & Beets, 1989; Sherman et al., 2002; Ramm et al., 2021; Vivier et al., 2021). Knowledge of recruitment dynamics and processes that drive this can help us to understand the potential consequences of artificial habitat, and may be used to inform strategies that maximise their performance. Sherman et al. (2002) tested the effect of floating attractants (additional vertical structure) on juvenile fish recruitment when they are added to artificial reefs. They found that there were no differences between the recruitment of fishes onto most of their treatments, except one, and concluded that recruitment and aggregation of diverse fish assemblages are not increased by using floating attractants (Sherman et al., 2002). However, Gorham and Alevizon (1989) recorded significantly higher numbers of juvenile fishes recruiting to artificial reefs with supplemental floating structures (i.e., "streamers") compared to those without. Their streamers consisted of multiple small ~1m lengths of polypropylene rope, unravelled, in comparison to the Sherman et al. (2002) which used long ~10m single stranded streamers, therefore providing increased refuge. This study mimics structure more typical of understory macroalgae and investigates the effect of this type of structure on recruitment of fish. However, few studies have investigated the effect of additional vertical structure that mimics large, canopy-forming macroalgae on artificial habitats.

Artificial marine habitats are often low in number and sit within a unique ecological context (Strelcheck et al., 2005). Therefore, assessing their dynamics (and the effectiveness of interventions intended to optimise their performance) can be challenging. Traditional hypothesis-testing frameworks rely on replication, random assignment of treatments, and appropriate controls (Stewart-Oaten & Bence, 2001). Before-After-Control-Impact Paired Series (BACIPS) study designs offer a useful alternative in this context. In a BACIPS study, the impact and control sites are concurrently sampled both before and after the intervention at the impact site(s) (Stewart-Oaten et al., 1986; Bence et al., 1996; Thiault et al., 2017). For every sample, i, in period , P, the difference in the sampled variable, N, is determined between the *Impact* and *Control* sites:

$$\Delta_{P,i} = N_{\mathrm{Impact},P,i} - N_{\mathrm{Control},P,i}$$

The effect of the treatment in BACIPS designs are estimated as the mean difference between the control and impact sites after the treatment minus the mean difference between the control and impacts sites before the treatment (Stewart-Oaten et al., 1986; Bence et al., 1996; Conner et al., 2015). This design can partition spatial and temporal variability to discern a pattern that may be attributable to a certain intervention, and is therefore a useful tool in evaluating human-induced or natural variations of ecological characteristics (Stewart-Oaten et al., 1986; Bence et al., 1996; Conner et al., 2015).

In this study, I investigated communities of common rocky reef species on two artificial islands in Wellington Harbour. I evaluated the potential effects of supplemental three-dimensional structure on recruitment processes. Because replication was not possible, I used a BACIPS design to evaluate these effects over nine months. More specifically, I conducted subtidal community surveys of fish and invertebrates occupying each island (with the aid of SCUBA) in a time series before and after my manipulation of three-dimensional structure on one of the islands. I used BACIPS analysis to address the following questions;

(i) Does the addition of three-dimensional structure increase the densities of fish and invertebrate species across trophic groups on an artificial marine habitat?

(ii) Does the addition of three-dimensional structure on an artificial marine habitat shape community assemblages?

(iii) How does size structure of fish and invertebrate communities vary between an artificial habitat with additional three-dimensional structure and an artificial habitat without additional structure?

2.2. Methods

2.2.1. Study Site and Species

I surveyed subtidal rocky reef habitats on two artificial island sites within Wellington Harbour, New Zealand. I quantified the density and size structure of common rocky reef fish and invertebrate species (Table A1). The artificial islands were constructed from 13,000 tonnes of large rocks to create roosting habitat for avifauna (as part of the wildlife protection plan for the Te Ara Tupua shared pathway project; Waka Kotahi New Zealand Transport Agency, 2024) between August and October 2023. They are 40m horizontal distance from shore, lie approximately 500m apart, and are located at the northern end of Te Whanganui-a-Tara, Wellington Harbour, along State Highway 2 (41°13’55.2”S, 174°50’27.6”E; Fig. 2.1).

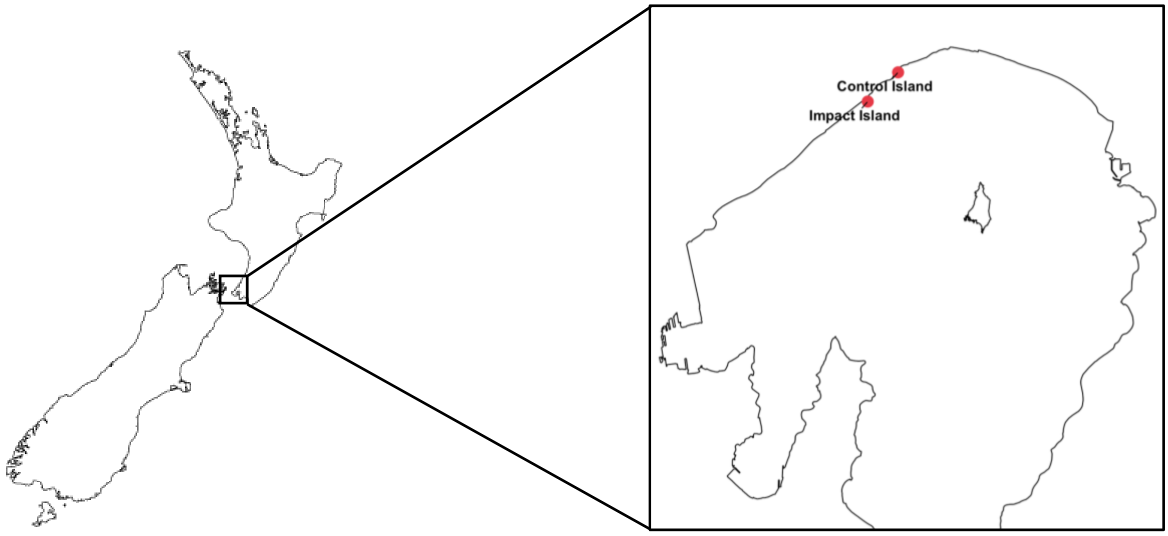

Figure 2.1. Map of New Zealand on the left, and zoomed in section displaying Wellington Harbour on the right. Location of study sites shown. Both islands indicated by red dots in the north of Wellington Harbour, control site (northernmost island) labelled 'Control Island', and impact site (southernmost island) labelled as 'Impact Island'.

2.2.2. Manipulating the Study Site

I created additional 3-dimensional vertical structure on the southern island, while the northern island did not get manipulated for this study. This study was designed as a Before-After-Control-Impact Paired Series (BACIPS) study (Green, 1979), in which I implemented a subtidal manipulation to one of the offshore island habitats while leaving the other habitat to develop on its own. I used a BACIPS approach due to the nature of the study site. There were only two artificial bird roosting islands built, and therefore there was no option for replication using these islands as a study site. Therefore, using a BACIPS approach to the study was the most effective way to gain an idea of the effect of additional vertical structure on the settlement of marine organisms to an artificial habitat. BACIPS studies can isolate intervention effects, control for natural variation, and can incorporate temporal dynamics through the repeated sampling over time. All of this increases the statistical power of the analysis, allowing for a clearer understanding of the effect of the intervention on the study sites. I randomly selected, using a random number generator, the more southern of the two islands to be manipulated. I constructed eight standard monitoring units for the recruitment of fishes (herein 'SMURF's, *sensu* Ammann (2004) – Fig. 2.2) attached to a rope with a concrete paver weight and a small buoy to manipulate the southernmost island. I used SMURFs to simulate the vertical structure that adult macroalgae would normally provide on natural, macroalgae dominated rocky reefs, and to facilitate additional opportunities for recruitment of both fishes and invertebrates. I placed the SMURFs around the circumference of the southern island relatively equal distances apart, making sure the concrete weight sat on the seabed, and the SMURF was attached approximately 3-4m above this (1-2m under the surface). The eight SMURFs on the southernmost island comprise the 'impact' – in this context the 'impact' is a putative enhancement as compared to a deleterious environmental impact. The un-modified northern island comprises the 'control'.

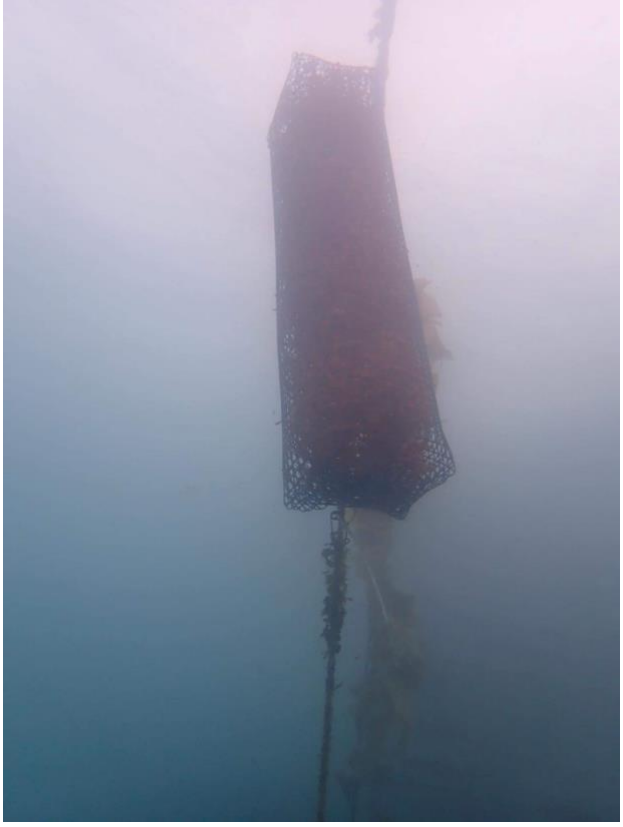

Figure 2.2. An example of one SMURF unit – this unit was used in the experiment for Chapter 3, however the same setup of structure was used in this experiment.

2.2.3. *Subtidal Community Surveys*

To monitor recruitment and faunal community changes over time, across the 'before' and 'after' period, I conducted underwater visual surveys using SCUBA on both the 'control' and 'impact' artificial islands. The 'before' period comprises the two surveys conducted before the intervention was implemented on 12th March 2024, while the 'after' period includes the five surveys conducted after this date. I surveyed each island (or treatment) at the same, or similar, time periods to understand the effect of the additional vertical structures on recruitment to artificial habitats. I conducted two types of surveys at each island, a mobile fish survey and a benthic fish and invertebrate survey.

In the mobile fish surveys, I laid a 25m transect around the circumference of approximately half of an island following the ~4m isobath, about 1m above the base of the island. I waited two minutes at the end of the transect to reduce the effect of diver disturbance on the surveys (Dickens et al., 2011). I then swam the transect at a slow pace and identified the species of fish present within 1m width of the transect (2m total width), and within a 2m ceiling – creating a total area surveyed of 100m^3 per transect. I recorded the abundance of each species and estimated the size class of each individual included in the surveys. This process was then repeated for a total of two transects, effectively surveying the entire 4m isobath, covering 200m^3 per survey, at each island. These transects are not treated as replicates for analysis purposes.

To conduct benthic fish and invertebrate surveys, I placed a 50x50cm quadrat along the transect line four times for each transect. I positioned the quadrats at 5m, 10m, 15m, and 20m on the transect every time, and attempted to lay them as flat as possible; I used this systematic approach to sampling to minimise bias within the surveys. Within each quadrat I identified any smaller fish species not identified in the transect surveys, as well as any invertebrate species present – including anything identifiable from a few millimetres in size. The abundance of each species identified, and the size class of each individual, was recorded. This was then repeated along the second transect for a total of eight quadrats at each island. I surveyed a total area of 2m^2 per island per survey; I assumed this area accurately represented the habitat being surveyed given the size of species included in the survey, and the total area of the islands.

I completed seven surveys of each reef between February and October; (1) 1st February, (2) 12th March, (3) 18th and 29th April, (4) 15th May, (5) 8th July, (6) 5th August, and (7) 18th October. I conducted two pre-manipulation surveys, before the addition of SMURFs on the southernmost island, and five post-manipulation surveys to track the trajectory of settlement to these artificial habitats.

2.2.4. Statistical Analyses

2.2.4.1. Does the addition of three-dimensional structure increase the densities of fish and invertebrate species across trophic groups on an artificial marine habitat?

To understand the effect of supplemental structure on the densities (standardised to 1m^3 areas) of marine communities on an artificial habitat I calculated the mean density of each species surveyed at each site over each survey date. I conducted a linear model using the 'lm' function as part of the 'stats' package in Base R (R Core Team, 2024) to test for the effect of site (control and impact) and period (before and after intervention), as well as their interaction effect, on the densities of marine species. Species were characterised into trophic groups based on their diet and feeding habits, and therefore the role they play in an ecosystem (Table 2.1). In this model, mean densities were analysed with site, period, and trophic level as fixed effects. I then calculated the delta densities (impact density – control density) at each survey date and conducted a linear model using the 'lm' function of the 'stats' package in base R (R Core Team, 2024) testing the density difference between the impact and control sites by the fixed effects of period (before and after the intervention) and trophic level.

The assumption of normality was violated for both models when tested using the 'shapiro.test' function in the 'stats' package of base R (R Core Team, 2024), however this assumption was still violated after log-transformation, and therefore I continued with the tests above given other assumptions were met. I tested equal variance with the 'leveneTest' function in the 'car' package (Fox & Weisberg, 2019).

2.2.4.2. Does the addition of three-dimensional structure on an artificial marine habitat shape community assemblages?

To investigate the effect of additional structure on the community composition of an artificial habitat I created a community data matrix and calculated the species richness, species evenness, and Shannon-Weiner diversity (Shannon & Weaver, 1948) of each site at each survey date. These indices fit assumptions of normality and equal variance – tested with 'shapiro.test' of the 'stats' package in base R, and the 'leveneTest' function in the 'car' package (Fox & Weisberg, 2019; R Core Team, 2024). I tested the differences in these diversity indices across site (control and impact) and period (before and after) using linear mixed-effects models with the 'lm' function of the 'stats' package in base R (R Core Team, 2024). Site, period, and the interaction between these factors were tested as the fixed effects in this model.

I then conducted a principal coordinates analysis (PCoA) to understand the trends in the community structures of both control and impact sites over time. I created a community data matrix using the Bray-Curtis dissimilarity to quantify the distance between the species composition of the two sites across periods (Bray & Curtis, 1957). I used PERMANOVA testing – 'adonis2' as part of the 'vegan' package (Oksanen et al., 2025) – to understand the effect of the factors site and period on the community composition of each island throughout the surveys. I then continued with conducting pairwise PERMANOVA tests for each factor (site and period) as well as their interaction with the 'pairwise.perm.manova' function in the 'RVAideMemoire' package (Herve, 2025).

2.2.4.3. How does size structure of fish and invertebrate communities vary between an artificial habitat with additional three-dimensional structure and an artificial habitat without additional structure?

To investigate the effect of supplemental structure on the size structure of marine communities on an artificial reef I found the three most abundant species in the community surveys conducted (*Notolabrus celidotus, Lunella smaragda,* and *Forsterygion lapillum*) and performed analyses on the distributions of their respective size structures. I analysed the effect of site and period on the distribution of size structures for each of the three species using the 'ks.test' function in the 'stats' package of base R (R Core Team, 2024). To understand the effect of the interaction between the site and period factors on size class distributions I performed aligned rank transform ANOVAs using the 'art' function of the 'ARTool' package (Wobbrock et al., 2011) due to the violation of normality in the data of all three species, tested using a 'shapiro.test' in the 'stat's package of base R (R Core Team, 2024). I used 'LeveneTest' of the 'car' package to check the assumption of equal variances, which was met for all three species (Fox & Weisberg, 2019).

All analyses were conducted in RStudio (Version 2024.12.0+467) with R 4.4.2 (R Core Team, 2024) software, and graphing was done using the 'ggplot2' package (Wickham, 2011).

2.3. Results

2.3.1. Does the addition of three-dimensional structure increase the densities of fish and invertebrate species across trophic groups on an artificial marine habitat?

There was no significant effect of site ($t_{(0)} = 0.040$, $p = 0.968$) or period ($t_{(50)} = 0.204$, $p = 0.839$) on the mean densities of species on the artificial habitats in this study. There was additionally no significant difference found between the mean densities of each trophic group ($-1.2 < t_{(50)} < 1.4, p > 0.05$). Notably, the impact of the BACIPS study – the interaction between site and period – was not significant ($t_{(50)} = -0.171$, $p = 0.865$). However, the one significant interaction found was the effect of site on filter feeders. There were significantly higher mean densities filter feeders on the impact island ($t_{(50)} = 2.248, p = 0.029$; Fig. 2.3).

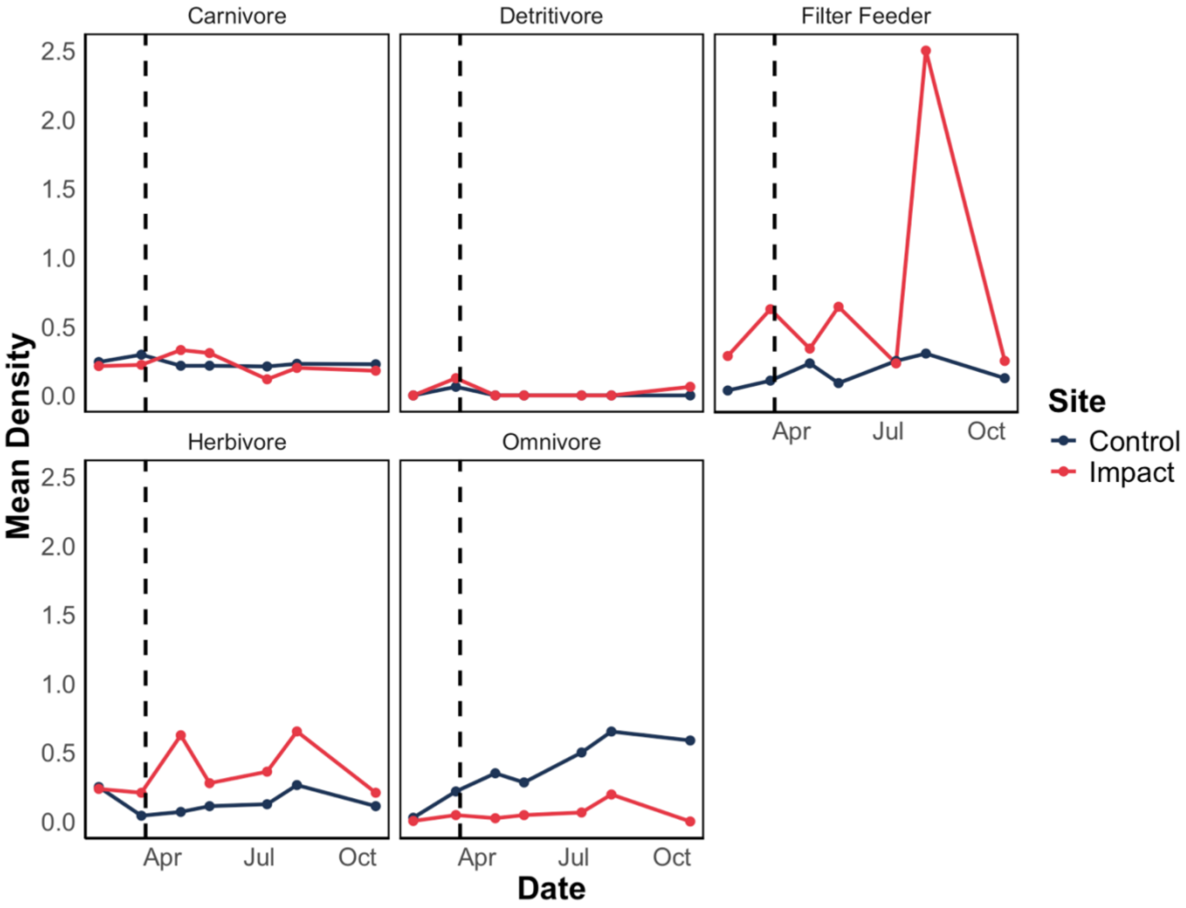

Figure 2.3. Mean density (individuals per 1m^3) of each trophic group (carnivore, detritivore, filter feeder, herbivore, and omnivore) at the control site (navy blue) and impact site (red) over the survey period (February 2024 – October 2024). The intervention date is indicated by the vertical dashed line.

The effect of period on delta densities was not statistically significant ($t_{(25)} = 0.183$, $p = 0.856$), suggesting an overall lack of effect that the supplemental structure had on densities of trophic levels. In addition, there was no significant interaction between period and any trophic level ($-0.85 < t_{(25)} < 1.15$, $p > 0.05$; Fig 2.4), indicating the intervention had little effect on the densities of species within each trophic level in the study.

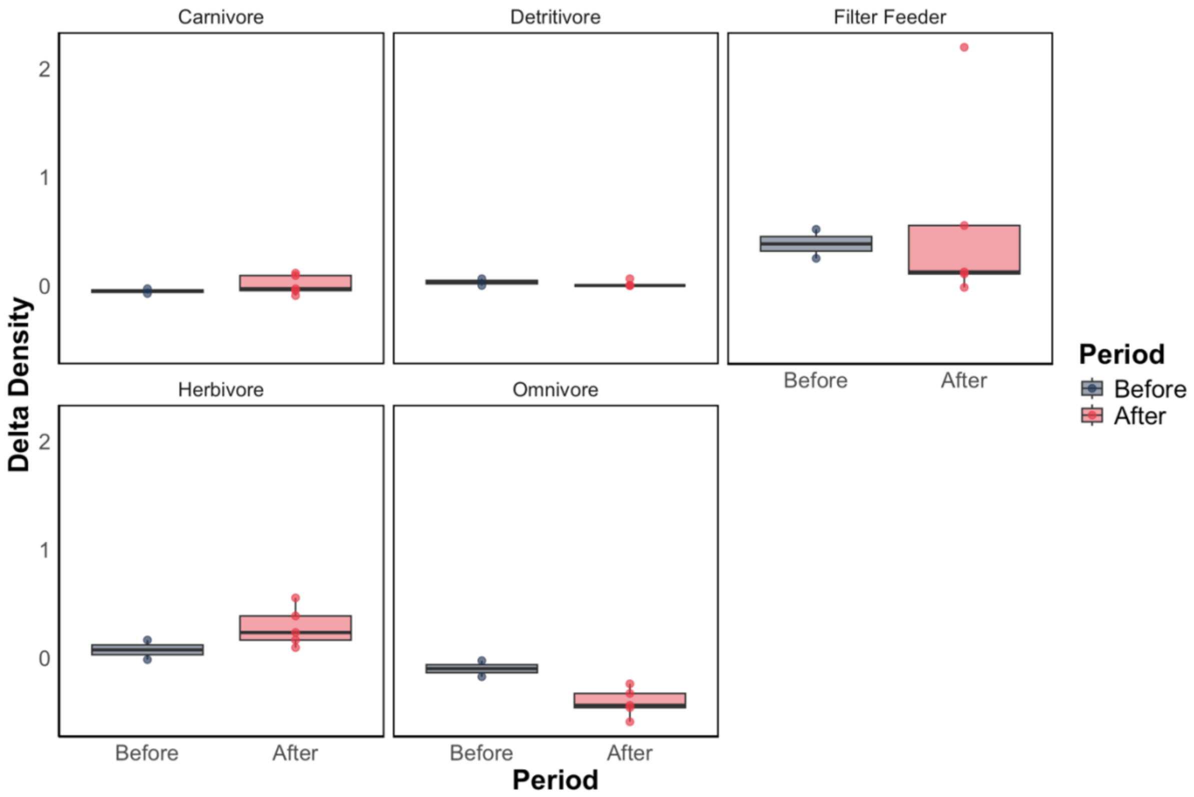

Figure 2.4. Boxplot showing mean delta densities in the before and after periods (mean impact density – mean control density), faceted by trophic group. Boxplots display the median, interquartile range, and overall distribution of delta densities.

2.3.2. Does the addition of three-dimensional structure on an artificial marine habitat shape community assemblages?

There was no significant effect of site ($t_{(10)} = 0$, $p = 1$), period ($t_{(10)} = 0.303$, $p = 0.768$), or the interaction between the two ($t_{(10)} = 0.803$, $p = 0.440$) on species richness in this study (Fig. 2.5). The species evenness of the communities studied were also not significantly influenced by period ($t_{(10)} = 1.348$, $p = 0.208$) or the site x period interaction ($t_{(10)} = 0$, $p = 1$), however, the site factor was significant ($t_{(10)} = 2.344$, $p = 0.041$), suggesting the impact site had slightly higher evenness than the control (Fig. 2.5). In terms of Shannon-Weiner diversity, there was a significant difference between control and impact sites ($t_{(10)} = 2.425$, $p = 0.358$), but no significant difference between the before and after periods ($t_{(10)} = 1.597$, $p = 0.141$). There was also no significant interaction between site and period that affected the Shannon-Weiner diversity of the communities ($t_{(10)} = -1.569$, $p = 0.148$; Fig. 2.5).

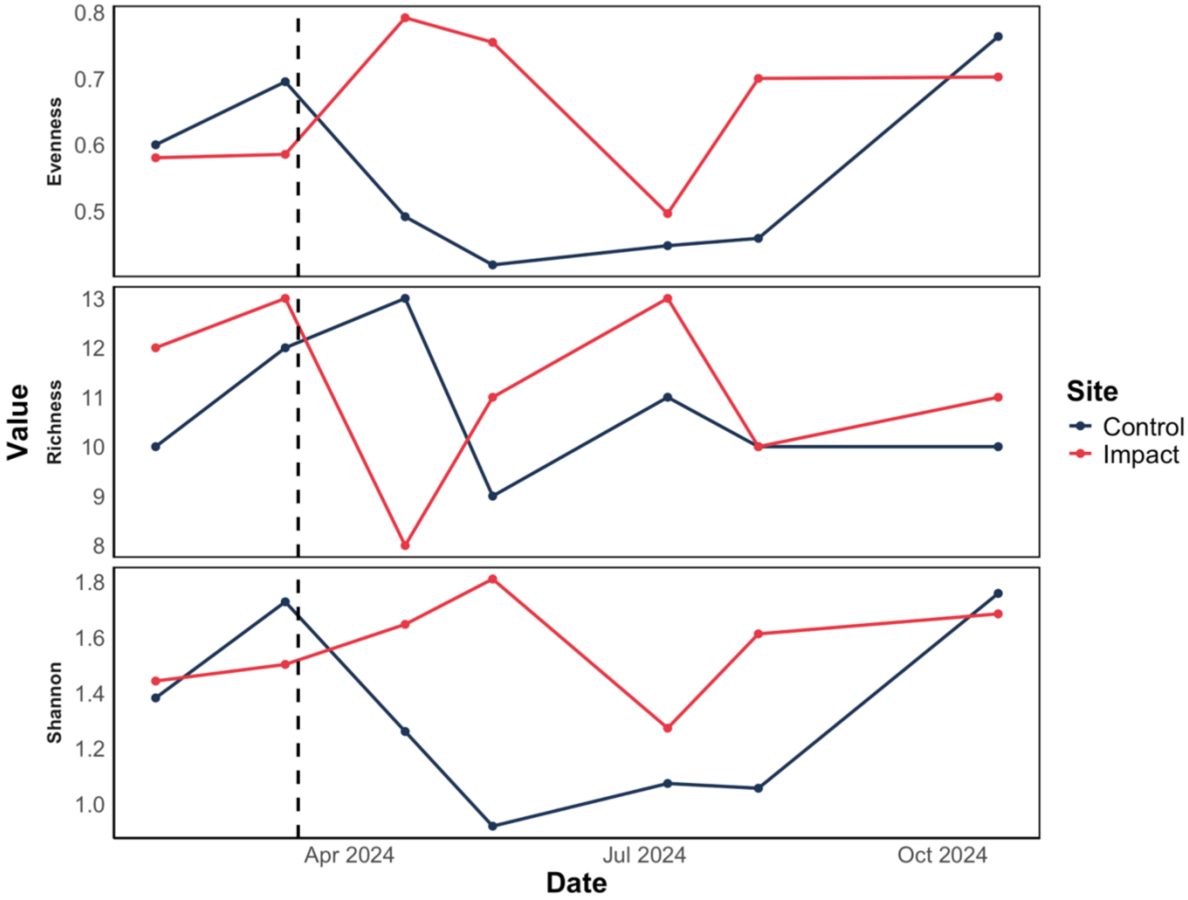

Figure 2.5. Species diversity measures (richness, evenness, Shannon-Weiner diversity) of each site (control – navy blue, and impact – red) over time (intervention date signified by vertical dashed line).

The PERMANOVA conducted on the PCoA data suggests that either site, period, or their interaction contributes to differences in the community structures in this study ($F_{(3, 13)} = 2.010$, $p = 0.036$). Post-hoc pairwise PERMANOVA tests show that neither period ($p = 0.68$), nor the interaction between site and period ($p > 0.05$ for all combinations) were significantly influencing the community structures, revealing the lack of effect the additional structure had on community assembly at the impact site. The pairwise PERMANOVA testing the effect of site indicated significant differences between the communities on control and impact sites ($p = 0.051$), which can also be seen on the PCoA plot (Fig. 2.6). This result suggests that differences in communities are primarily driven by site rather than period or the interaction between these factors.

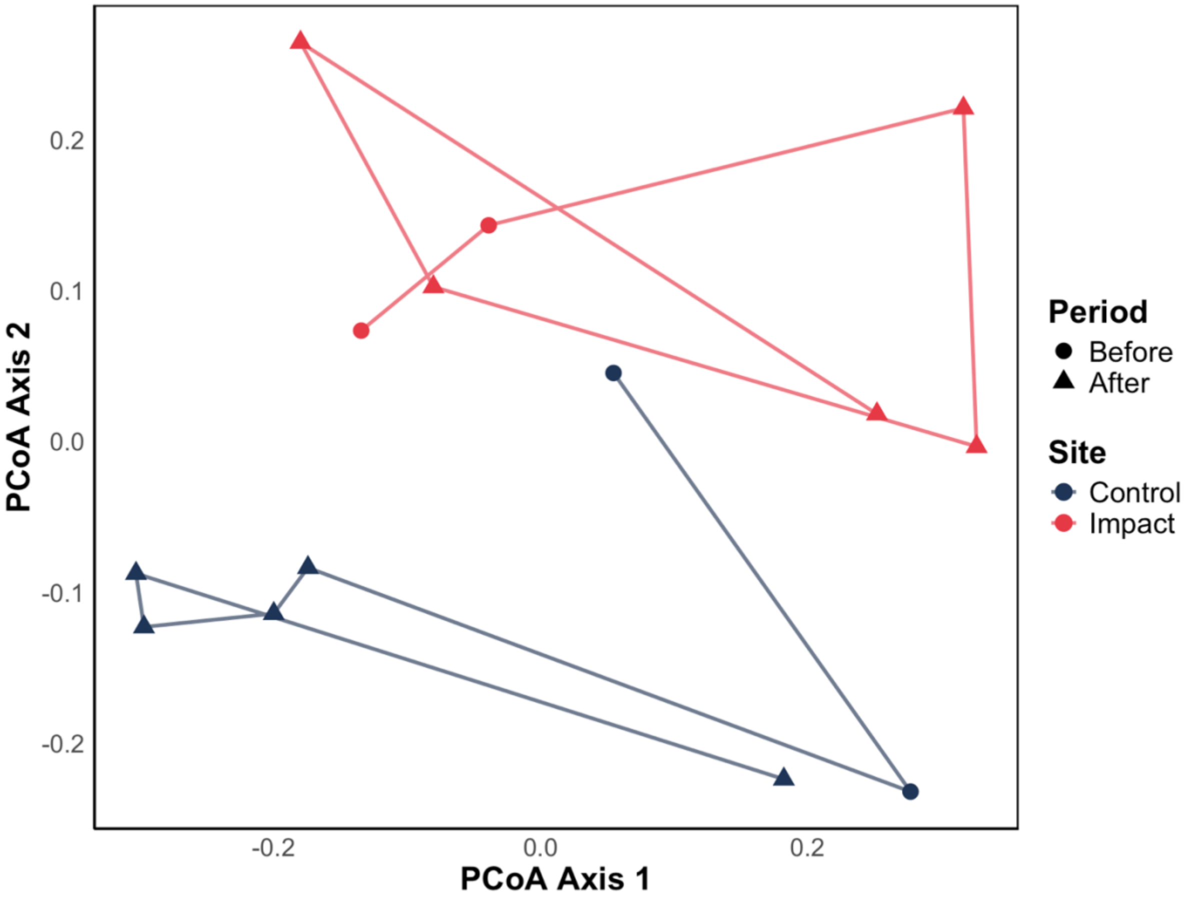

Figure 2.6. Principal Coordinates plot displaying the communities of each site across time, measured by Bray-Curtis dissimilarity. Points of the two sites (control – navy blue, and impact – red) are connected in order of time – two circular points (indicating the 'before' period), and five triangular points (indicating the 'after' period).

2.3.3. How does size structure of fish and invertebrate communities vary between an artificial habitat with additional three-dimensional structure and an artificial habitat without additional structure?

There were no clear differences in the size class distributions of the spotty wrasse (*Notolabrus celidotus*) communities when testing the effect of site (D = 0.143, p = 0.660), period (D = 0.183, p = 0.444), or the interaction between these two factors ($F_{(1,80)}$ = 1.535, p = 0.219; Fig 2.7). This indicates that the intervention of supplemental structure at the impact site had no discernible effect on the size structure of the *N. celidotus* community.

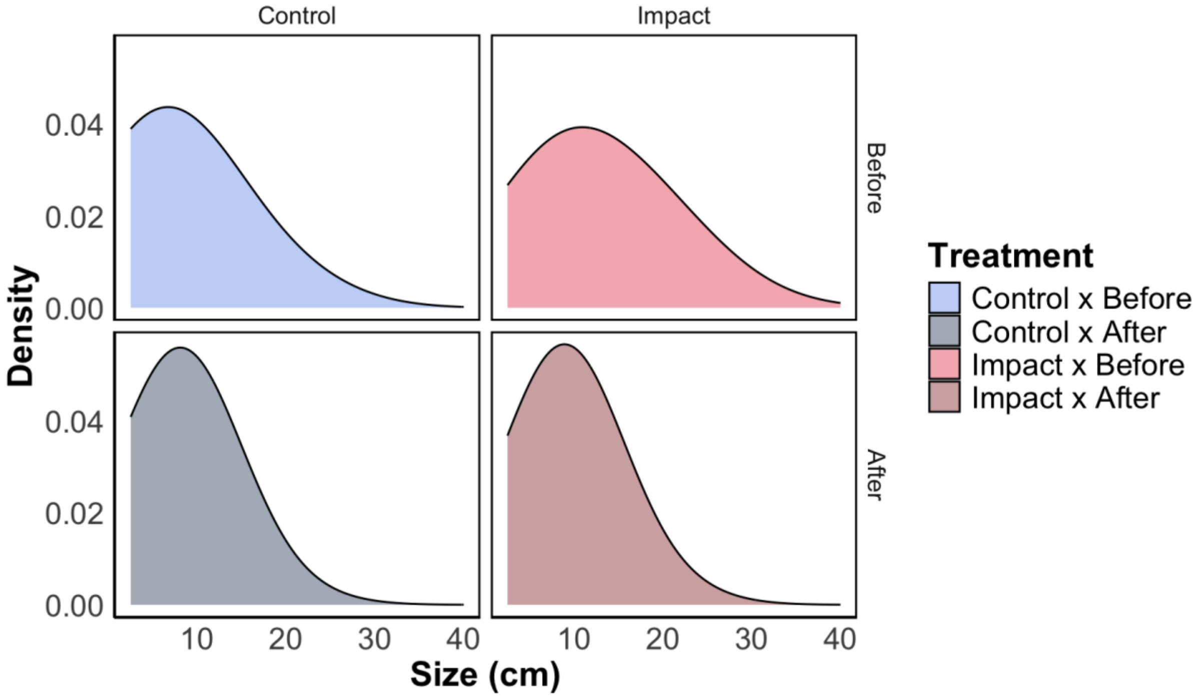

Figure 2.7. Smoothed kernel density plots displaying the estimated probability density function of *N. celidotus* size distributions between a) sites (control in grey, impact in red), and b) period (before in red, after in grey).

The size class distributions of cat's eye snail (*Lunella smaragda*) communities showed no significant differences due to the effect of site ($D = 0.119$, $p = 0.501$), indicating that the size class distributions of this species were not significantly different between the control and impact site. The effect of period (before and after) was also not significant on the size class distributions of *L. smaragda* ($D = 0.058$, $p = 0.970$). The interaction between site and period was also non-significant ($F_{(1,80)} = 0.316$, $p = 0.575$; Fig 2.8).

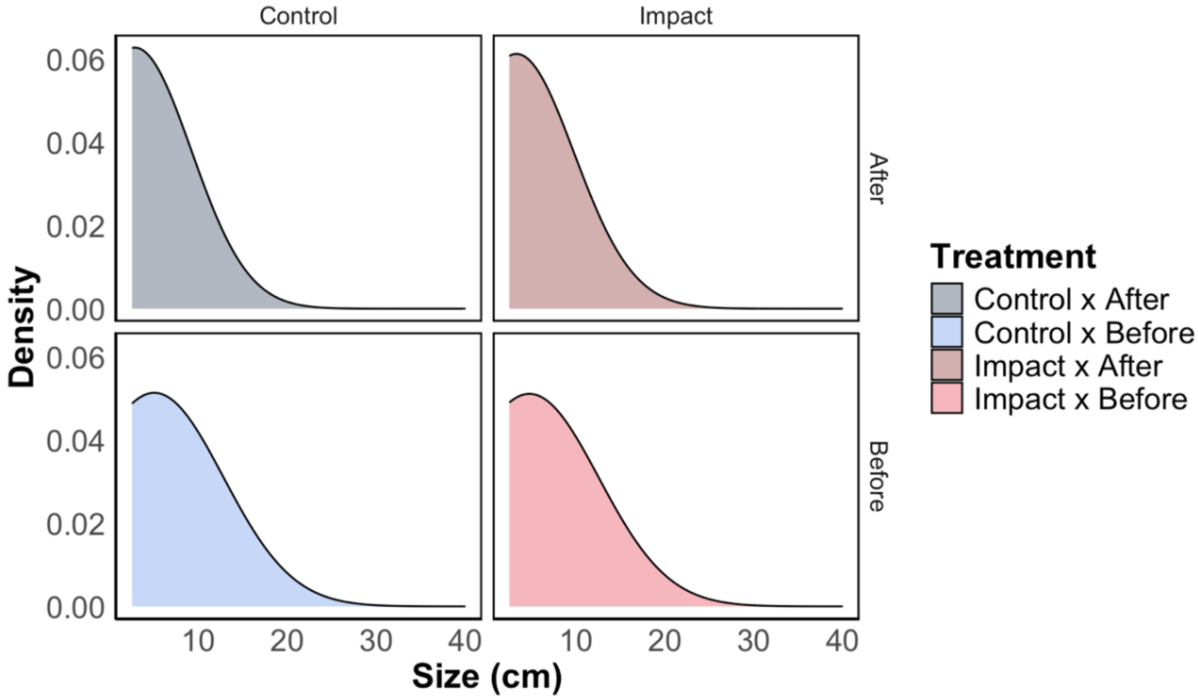

Figure 2.8. Smoothed kernel density plots displaying the estimated probability density function of *L. smaragda* size distributions between treatments – Control x Before in light blue, Control x After in dark blue, Impact x Before in light red, Impact x After in dark red.

Common triplefin (*F. lapillum*) size class distributions were not significantly affected by the factor of site (D = 0.048, p = 0.997), or period (D = 0.117, p = 0.687). Additionally, the interaction effect of site x period did not cause significant differences in these size class distributions ($F_{(1,80)}$ = 2.774, p = 0.100; Fig 2.9).

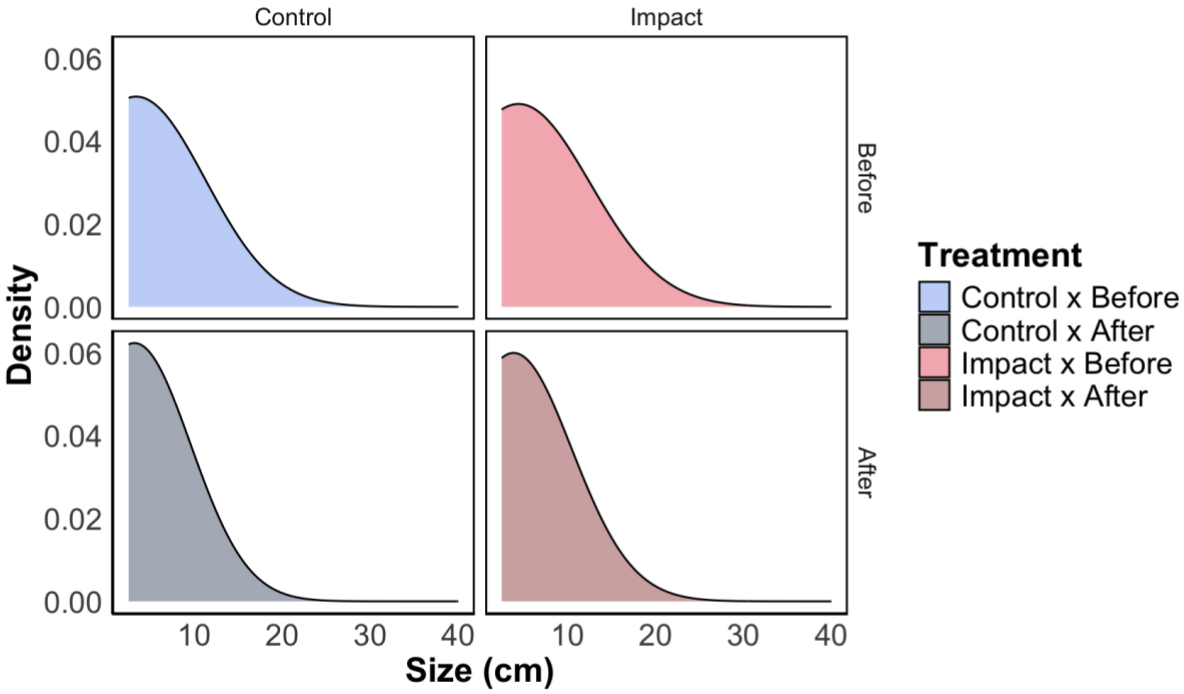

Figure 2.9. Smoothed kernel density plots displaying the estimated probability density function of *F. lapillum* size distributions between treatments – Control x Before in light blue, Control x After in dark blue, Impact x Before in light red, Impact x After in dark red.

2.4. Discussion

In this study, I investigated the relationship between additional vertical structure on artificial marine habitat and the species that recruit to them in a temperate environment. The study highlights the lack of significant effect that additional three-dimensional structure had on the overall densities, community assemblages, and size class structures of both fish and invertebrate species on an artificial marine habitat in Te Whanganui a Tara, Wellington Harbour. This finding is in accordance with similar studies such as Sherman et al. (2002) which found no effect of floating attractants on artificial reefs on the recruitment of fishes. However, it is contradictory to the findings of some studies including Gorham and Alevizon (1989) which found that higher densities of juvenile fish recruited to artificial reefs with floating attractants on them compared to those without.

Temperate reefs are being increasingly exposed to anthropogenic impacts, which can potentially lead to declines in species diversity, ecosystem productivity, and the overall biomass of these habitats (Parsons et al., 2016). Habitat structural complexity is highly important to marine ecological communities, and high species abundance and diversity are often linked to more complex habitats (Trebilco et al., 2015; Lazarus & Belmaker, 2021). Complex habitats support these diverse assemblages through the provision of niches and environmental resources, leading to reduced predation and competition, as well as creating suitable sites for reproduction (Pérez-Matus & Shima, 2010; Trebilco et al., 2015; Komyakova & Swearer, 2019; Komyakova et al., 2019).

2.4.1. Does the implementation of additional vertical structure increase the densities of fish and invertebrate species across trophic groups on artificial marine habitats?

In this study, I did not identify any link between the habitat with additional complexity and increased densities of any specific trophic group. In addition, there was no significant effect of period on the difference in densities between impact and control sites (delta densities) for any trophic level.

Parsons et al. (2016) found that fish abundance was generally influenced most significantly by the complexity of the habitat, with increased reef complexity leading to more abundant assemblages of fish. This is in line with similar studies which have determined that abundance of fish is often linked to the complexity of the studied habitat (Carr, 1989; Tupper & Boutilier, 1997; Trebilco et al., 2015; Bishop et al., 2022). Studies have also shown the correlation between macroalgae presence and the abundance of invertebrates within a temperate reef (Bégin et al., 2004; Bustamante et al., 2014).

The lack of observable differences between control and impact sites, as well as between before and after periods, in my study suggests that the structural enhancement had no overall influence on the densities of any trophic group. This result could be due to a range of further environmental factors that could influence the densities of marine communities. Many studies have highlighted the importance of canopy cover for the abundance of fish on temperate reefs, however there have been numerous studies that also emphasise the importance of both understory algae species and stipe density of canopy-forming species as factors of complexity (Carr, 1989; Hackradt et al., 2011; Trebilco et al., 2015). These studies underline the relationship between canopy-forming species and understory species, and how they influence the abundance of different species depending on their spatial arrangement because of their ability to create microhabitats. I did not quantify the coverage of understory macroalgae in this study and therefore the influence of this factor on fish and invertebrate densities on the artificial islands is unknown. Trebilco et al. (2015) identified closed canopy cover as a strong indicator for biomass, showing that overall fish biomass increased by 75% in the presence of closed kelp canopies, as opposed to open-canopy reefs. The SMURFs used in my study, while they provided additional vertical structure, did not provide closed canopy cover. This may have limited the ability of these structures to enhance settlement, and therefore affected the densities of fish aggregations. It is possible that the spatial scales of the extra structure I implemented at the south bird island did not match the scale of the base habitat, and thus did not provide the space needed in order to enhance settlement. Morton and Shima (2013) observed that there was higher settlement of triplefins to a 'clumped' habitat treatment (comprising three SMURFs attached to moorings 1m apart), as compared to their 'dispersed' (three SMURFs with moorings 5m apart) and 'solitary' (one SMURF) treatments. They speculated that the more continuous structure associated with this treatment may have provided stronger cues for settlement. In another example, James and Whitfield (2023) found that the coverage of macroalgal canopy plays an important role in the recruitment of wrasses, emperor fish, and rabbitfishes, which comprise larger, more mobile species than the common triplefin, and cover multiple trophic groups (carnivores, omnivores, and herbivores). These two studies show the importance of dense cover for the recruitment of multiple species, and therefore possibly highlight a possible improvement to my study. Given my SMURFs were set out more similarly to the 'solitary' treatment of Morton and Shima (2013), the settlement cues may have been too weak to enhance the densities of marine organisms across trophic groups at the impact site. A more dense treatment, with increased numbers and clumps of SMURFs could have a more enhancing effect on settler densities.

2.4.2. Does additional three-dimensional structure on an artificial marine habitat cause different community assemblages to form than on an artificial habitat without additional three-dimensional structure?

Species richness was not found to be different according to site, period, or the interaction between these factors. Additionally, species evenness and Shannon-Weiner diversity were only found to be different between sites, with the site x period interaction being non-significant for both of these indices. The principal coordinates analysis showed significant differentiation between communities at the control and impact sites, however neither period nor the site x period interaction were found to drive the changes in these communities. Overall highlighting the distinct lack of effect the additional three-dimensional structure had in driving changes in the ecological communities of the habitats in this study.

Several studies have reported that increasing complexity in a temperate marine habitat has positive effects on the species richness and diversity of that habitat (Charbonnel et al., 2002; Trebilco et al., 2015; Parsons et al., 2016; Lazarus & Belmaker, 2021). Large stands of macroalgae constitute substantial, complex physical structure in these environments, and the characteristics of such algae exhibit spatial and temporal variation (Anderson, 1994; Willis & Anderson, 2003). This variation can contribute to the dynamics of temperate reef fishes; for example, the percentage cover of *Macrocystis pyrifera*, giant kelp, has been found to determine the densities of several juvenile fish species (Anderson, 1994). They do this by providing habitat for rich and diverse communities of invertebrates, and therefore food sources and nurseries for diverse communities of both juvenile and adult fish species (Hüne et al., 2021).

The absence of an observable difference in the species diversity and community composition of each island across time periods could be the result of environmental variables not accounted for in the study. Sedimentation is a widespread process on most rocky shores near human populations, and can deeply influence the composition and dynamics of the assemblages in these systems (Airoldi, 2003). There is a high level of disturbance occurring ~40m away from both bird island habitats. Construction efforts, aiming to improve a transport corridor and protect reclaimed land from sea-level rise, have been releasing high influxes of sediment throughout the study period (personal observation) that may be affecting the community dynamics of the habitats. The high sediment load at the study sites, along with other factors such as the composition and density of the additional vertical structures, as well as proximity to natural reefs may have influenced the results of this study.

2.4.3. *How do size class structures of fish and invertebrates differ between an artificial habitat with additional three-dimensional structure and an artificial habitat without additional structure?*

Spotty wrasse (*N. celidotus*) size distributions did not differ by site, period, or their interaction in this study. Similarly the size structure of cat's eye snail (*L. smaragda*) communities were not significantly different between site or period, and the interaction between these factors also had no significant effect. Finally, the size distribution of common triplefin (*F. lapillum*) showed no evidence of a difference due to site, period, or the interaction between site and period. My findings suggest that the introduction of supplemental structure had no discernible effect on the size structure distributions of these species on an artificial habitat.

Fish and invertebrates are often attracted to shelters proportional to their body size (Luckhurst & Luckhurst, 1978; Eggleston & Lipcius, 1992; Parsons et al., 2016), therefore it is feasible that the structural composition of the islands themselves, even in the absence of additional vertical structure, provide enough of a refuge spectrum to shelter a wide community of fish and invertebrates. Furthermore, the breeding season of common rocky reef species in the Wellington region may differ from the survey period, and could have had effects on the results of this study. If the breeding season of a species fell within the survey period (February – October), then there could have been less chance of detecting settlement of that species to the reefs due to temporal factors. For example, the breeding season for common triplefin, *F. lapillum*, is typically from September to December in the Wellington region (Mensink et al., 2014). Larvae typically hatch three weeks after the eggs are laid, and the pelagic larval development phase generally lasts ~65 days (Kohn & Clements, 2011; Mensink et al., 2014), meaning the settlement of individuals belonging to this species should have been accurately accounted for in my study. However, other organisms have varying breeding seasons and length of development phases, potentially causing the full settlement patterns to be missed and size structure of communities surveyed to be incomplete. Finally, the proximity to natural reefs can influence the abundances and size spectra of fish and invertebrates on an artificial habitat. Artificial reefs placed in close proximity to natural reef substrates can have higher abundances of organisms compared to more isolated reefs (Parsons et al., 2016), given the relatively isolated nature of the artificial islands at the very northern end of Wellington Harbour, this may have affected the settlement potential of organisms to the habitats, and therefore affected the size structure of the communities.

2.4.4. Evaluating the Importance of the Study

Artificial reefs are being used more frequently as mitigation strategies for the loss of rocky reef habitats globally. This trend is also occurring in Wellington. The Te Ara Tupua projects, and others like it, are using artificial habitats to mitigate the loss of rocky reef habitats as a results of building the walking and cycling pathway along SH2 (Waka Kotahi New Zealand Transport Agency, 2024). It is therefore imperative that we understand the dynamics of these habitats, and if there is anything we can do to enhance them and create a more diverse, functioning community living on them. This study provides evidence that using solitary vertical structures on an artificial reef habitat may provide little to no enhancement to the settlement dynamics and community assembly on those reefs, and therefore it is more economical and ecologically wise to focus on other potential enhancement strategies. Alternatively, further research may be done in this area to understand if different compositions of vertical structure that create more canopy-coverage, or provide stronger settlement cues for fish and invertebrates, can be used to the advantage of ecological communities on artificial marine habitats.

2.4.5. Limitations of the Study

This study was constrained by the survey period. As a Master's research project, there is a maximum of one year, more commonly about six months, available to undertake field work aspects, and therefore limited time to survey for potential changes in community structure at both artificial islands. If this study were to be continued, it is possible that stronger results may be found with additional 'before' and 'after' surveys. The survey period also was not based on the seasonality of the ecological processes involved in settlement, therefore it may have missed the settlement season of some species. However, most of the species included reproduce in spring-summer (Table A1), and therefore would be settling around the end of summer or start of autumn (when I started conducting surveys) depending on pelagic larval duration.

This research has limited statistical power as an unreplicated study. Given the nature of the artificial habitats there was no option to replicate it. The BACIPS approach to the study allowed for conclusions to be drawn from the data, however a replicated study design would have provided more power to the findings. Additionally, there was one survey (survey 3) where I was not able to conduct surveys of both islands on the same day due to weather conditions, and therefore these data are not as paired as I would have liked them to be for a BACIPS design. Given they were conducted within two weeks of each other, I still considered them 'paired' for the necessary analyses.

Surveys in this study were often in low visibility/high disturbance environments due to the proximity of construction work to the habitats studied throughout the research period. This may have affected the accuracy of the underwater visual censuses, or altered the patterns of settlement to the habitats as compared to a scenario in which this disturbance was not present. Similarly, weather was often a limiting factor in completing the surveys – conducting underwater visual censuses across time, you cannot always guarantee the conditions will be the same between different survey points.

2.4.6. Conclusion

In this study, I found that additional vertical structure on an artificial marine habitat had no significant impact on the densities, species diversity, or size structures of the ecological communities living on that habitat. These findings may be a result of multiple factors such as the composition of the floating attractants, the spatial scale of the intervention, the proximity to natural reefs, as well as other biological factors. While my results seem to provide evidence against the use of additional three-dimensional structure to enhance the communities on artificial reefs at spatial scales similar to those in my study, it provides a starting point for future research if used in conjunction with other studies. The importance of this research is highlighted in the prevalence of artificial marine habitats as mitigation and restoration strategies for lost or degraded rocky reef habitats, and the necessity to understand how we can best use these to enhance local marine communities for improved biodiversity outcomes.

3. COMMUNITY COMPOSITION AND GROWTH OF RECRUITS ON ARTIFICIAL MARINE HABITATS

3.1. Introduction

Artificial reefs are becoming an increasingly common feature of coastal environments (Jensen, 2002; Layman & Allgeier, 2020). They contribute to a useful ecosystem management strategy if they can enhance natural habitats, and provided their beneficial effects are not outweighed by additional deleterious effects (Komyakova et al., 2019). Understanding factors that influence the performance of these reefs, and their ability to provide viable habitat, is therefore important for achieving management goals.

Marine reef organisms typically develop in pelagic habitats and then settle to benthic habitats, including artificial structures, through a process called "recruitment". Recruitment can be defined broadly as the addition of new individuals to a population – both from natural settlement of juveniles, and from migration of older individuals (Caley et al., 1996). Understanding the factors and processes that contribute to variation in recruitment has long been a key objective of marine ecologists (Roughgarden et al., 1988; Caley et al., 1996; Ammann, 2004). Spatial patterns in recruitment are often driven by habitat selection, with larvae often recruiting preferentially to areas that can maximise their growth, survival, and/or reproduction (Komyakova & Swearer, 2019). Spatial and temporal variation in recruitment can shape the structure and dynamics of marine populations (Ammann, 2004), and studies of this variability can facilitate prediction of the ecological structure of populations that may occupy new artificial habitats.

Post-settlement juveniles of many temperate reef species rely on macroalgal habitats, and variability in recruitment can be influenced heavily by the identity and spatial variation of these habitats (Jones, 1984a; Levin, 1993; Tupper & Boutilier, 1997). Canopy-forming macroalgae presence is a common cue for settlement to temperate reefs, therefore affecting the recruitment dynamics of those reefs (Vega Fernández et al., 2009; Pérez-Matus & Shima, 2010). These macroalgal species often provide structural complexity (three-dimensional profile) that is associated with increased abundance and diversity of marine organisms (Carr, 1989; Lazarus & Belmaker, 2021). Previous studies have investigated the effect of floating attractants (added vertical structures) on recruitment to artificial habitats (Gorham & Alevizon, 1989; Sherman et al., 2002), however few have tried to mimic canopy-forming macroalgae with these structures. Ammann (2004) tested the ability of a standard monitoring unit for the recruitment of fishes (SMURF) to accurately quantify rates of juvenile recruitment for a range of species. Species that typically settle to the surface canopy formed by macroalgae were found to settle so surface-deployed SMURFs, thus suggesting their utility as a means to potentially enhance local recruitment.

Previous studies have suggested that location of an artificial structure influences the species richness and densities of communities that recruit to them (Bohnsack & Sutherland, 1985; Komyakova et al., 2019). The general prediction is that artificial reefs closer to recruitment sources such as natural reefs and spawning grounds of target species should have higher colonisation rates than those further from recruitment sources (Strelcheck et al., 2005). This prediction originates from the theory of island biogeography (MacArthur & Wilson, 1967) and states that it is only true under the assumption that the reefs being compared are of similar size. In general, however, the effect of proximity to natural reef sources on recruitment to artificial reefs has been less studied than factors such as substrate and reef design. It is important to understand these effects because of the increase in use of artificial reefs as an environmental mitigation technique.

An "ecological trap" is formed when an animal preferentially settles to lower quality habitat that causes reductions in fitness outcomes (Hale & Swearer, 2016, 2017; Komyakova et al., 2021; Swearer et al., 2021). Marine ecologists have highlighted the importance of designing artificial marine habitats from an ecosystem ecology perspective (Layman & Allgeier, 2020; Carral et al., 2022). Specifically, this would include assessing the ability of artificial reefs to provide quality habitat, and produce their own biomass over time, supporting healthy marine communities. Investigating fitness measures such as growth and condition is therefore important in evaluating the success of artificial habitats and determining their ability to produce biomass without becoming ecological traps (Komyakova et al., 2021). Otoliths – calcium carbonate structures in the heads of bony fish – can be used as indicators of fish age and growth rates due to the deposition of growth increments over 24-hour periods (Campana & Neilson, 1985). These growth increments are influenced by environmental variables (Campana & Neilson, 1985), and can thus provide information on the quality of habitat that a fish is occupying.

In this study, I evaluate the efficacy of artificial reef design from an ecosystem perspective to support communities of rocky reef communities. I constructed a set of 24 artificial reef units in Te Whanganui a Tara, Wellington Harbour. I used these reefs to evaluate the effect of reef placement (proximity to a natural reef) and reef design (supplemental three-dimensional structure) on the recruitment dynamics and growth rates of focal organisms within these communities. I conducted subtidal community surveys of fish and invertebrates on all 24 artificial reefs (with the aid of SCUBA) six times over a seven-month period. At the end of the study period, I sampled fish that had recruited to my reefs, and used their otoliths to estimate recent growth rates. I address the following questions:

(i) Does the presence of supplemental structure and the location of an artificial marine habitat increase the abundance of fish and invertebrate species?

(ii) Does the placement of an artificial reef and the presence/absence of additional structure shape community composition?

(iii) Does the placement and design of artificial reefs influence the growth of a common species occupying them?

3.2. Methods

3.2.1. Study Site and Species

I constructed and sampled a set of artificial reefs at two focal sites, Kau Point (41°17’20.4”S 174°50’05.3”E) and Karaka Bay (41°18’30.9”S 174°50’01.0”E), on the Miramar Peninsula in Wellington, New Zealand (Fig. 3.1). These sites both consist of a natural, macroalgae-dominated rocky reef habitat that is distributed from the shoreline to approximately the 5-7m depth contour, and less structurally complex, sand-dominated substrate from the 6-8m depth. At Kau Point, the deeper sandy area is predominantly bare, with scattered patches of *Carpophyllum flexuosum* and *Undaria pinnatifida*, while Karaka Bay includes the presence of some small tubeworm communities as well as the sandy seafloor. For the purposes of this study, I am considering these areas as similar in terms of structure because they are dominated by sand and are significantly less structurally complex than the natural reefs they are adjacent to. The two sites are located on the same peninsula ~2.5km apart, and are orientated in the same direction (facing east) within Wellington Harbour. I surveyed the communities that colonised these reefs, including a range of benthic invertebrates and fish species commonly found within Wellington Harbour (Table 2.1).

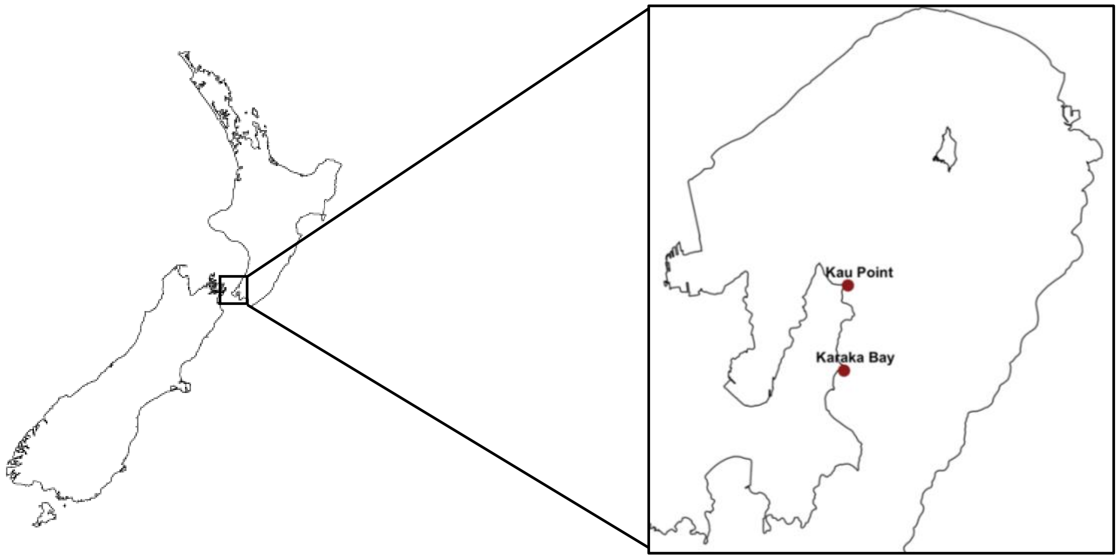

Figure 3.1. Map of New Zealand on the left, and zoomed in section displaying Wellington Harbour on the right. Location of study sites indicated by red dots on the eastern coast of the Miramar Peninsula in Wellington Harbour. Sites labelled as 'Kau Point' and 'Karaka Bay'.

I also collected samples of common triplefin (*Forsterygion lapillum*) to estimate the growth of organisms recruiting to my artificial reefs (described in more detail below). The common triplefin is a small-bodied reef fish that is commonly found on shallow rocky reef habitats throughout New Zealand (Hardy, 1989; Hickey & Clements, 2003; Feary & Clements, 2006). Juveniles and adults of this species feed on small benthic organisms and are preyed upon by larger reef-associated fish species (A. C. Smith, 2009). Adult *F. lapillum* are strongly site-attached and tend to have very small home ranges (Shima et al., 2012; Mensink & Shima, 2014), meaning their growth and fitness is directly related to their home range and the quality of habitat it provides. This makes *F. lapillum* an ideal study species to aid our understanding of marine organisms growth rates on artificial habitats.

3.2.2. Artificial Habitat Assembly and Experimental Setup

To conduct this study, I used 120 Firth Concrete™ grass pavers to assemble 24 artificial reef units. I chose to use these pavers as they are generally made from natural materials such as sand, quartz, and calcium carbonate. The pavers also had five large holes, which allowed for swim-throughs and crevices, these are important for both rocky reef fish and invertebrates for protection from competition and predation (Sherman et al., 2002). Additionally, the pavers were rough in texture, which has been shown to facilitate settlement by invertebrates and algae in previous studies (Köhler et al., 1999). Each reef unit consisted of five stacked pavers;

successive layers were rotated 45 degrees to create additional complexity; cumulative size of each reef was approximately 40x40x40cm (Fig. 3.2).

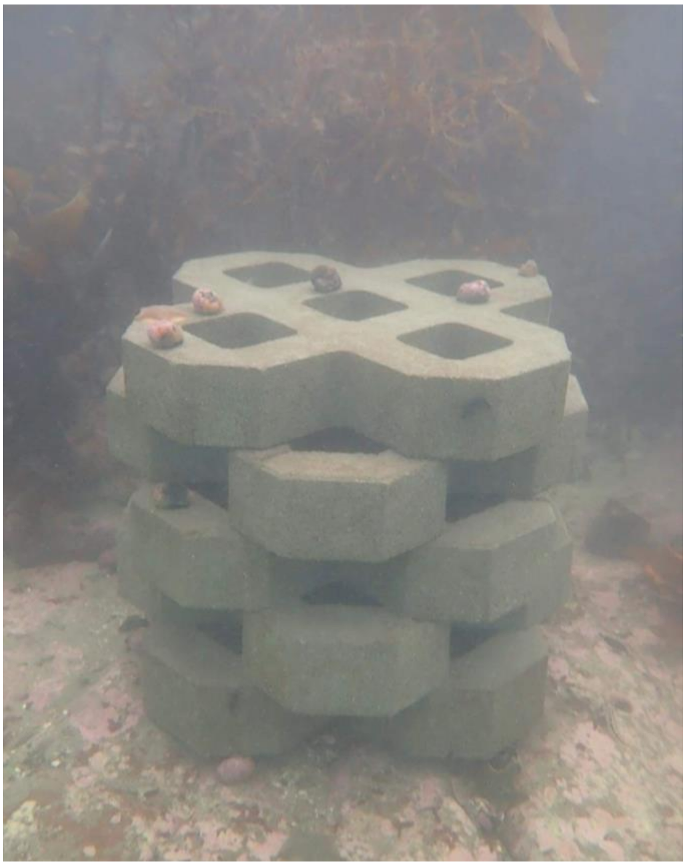

Figure 3.2. Final set up of an artificial reef 'unit' in this study. This reef unit is located on the reef edge with no additional structure added.

I deployed 12 reef units at each of two sites. Within each site, I placed half of the reef units along the natural reef edge (within ~1m), and half approximately 10-20m away on the predominantly sand substrate. I then randomly selected half of the reef units at each site and added additional three-dimensional structure to them, making sure this additional structure was evenly spread between reef substrate and bare substrate units. This experimental design allowed me to test the effects of multiple variables, proximity to natural rocky reef (substrate) and presence of additional three-dimensional structure, and their interaction effect on the settlement of marine organisms to an artificial habitat over seven months.

3.2.3. Subtidal Community Surveys

I conducted SCUBA surveys in order to understand the settlement patterns of marine organisms to my artificial reef units. I surveyed fish and invertebrate communities on each reef at each location six times over the span of a seven month period (April 2024 – October 2024). I used different methods to quantify larger mobile fishes, and smaller, more cryptic fishes and invertebrates. I conducted surveys two weeks after initial deployment of artificial reefs, and thereafter at 4-6 week intervals for the next seven months.

To survey larger mobile fish species I followed a similar method to that in a study by Komyakova et al. (2019). I recorded all mobile fish species within ~1m of the reef unit. I conducted each survey from a distance of ~2m from the focal reef, and limited my duration of observation to three minutes. I identified the species, abundance, and size class – estimated total lengths categorised into bins (0-2.5cm, 2.5-5cm, 5-10cm, 10-20cm, 20-30cm, and 30+cm) – of every fish in the survey parameters.

To survey smaller cryptic fishes and invertebrates, I systematically searched all exterior surfaces and visible holes/crevices of each artificial reef unit for a total of two minutes. During these surveys I identified organisms to species level, and recorded their size class – in the same categories as the mobile fish surveys. These data also enabled estimates of local abundance of each species surveyed.

3.2.4. Specimen Collection

I collected specimens of *F. lapillum* using SCUBA methods. I completed collections using hand nets, and all specimens were collected within a four week period from 23rd October – 29th November, 2025. I aimed to collect specimens all of similar a size (~40mm in length), and assumed that this meant each specimen collected was at the same stage of life (between six months to one year of age). I collected 16 specimens from the reef units located at Kau Point – 10 from the habitats located on bare substrate, and 6 from the habitats along the reef edge, as well as 16 from the artificial reef units at Karaka Bay – 10 from the reef edge habitats, and 6 from the bare substrate habitats. Specimens were collected from a mix of reef units with and without SMURFs attached. I attempted to collect at least two *F. lapillum* that me the criteria for collection on each reef when I conducted the collection dives. Fish had to be strongly associated with the reef unit – either directly on/in, or less than 10cm from the base of the reef unit – to be considered as ‘occupying’ a habitat. The reef unit that each fish was collected from was recorded and included in statistical analysis as a random effect.

3.2.5. Otolith Extraction and Preparation

I extracted the sagittal otoliths (n = 2) from each fish (n = 32) and removed any visible tissue. Otoliths were separated and cleaned with DI water twice before drying. One otolith from each pair was selected at random and prepared for increment analysis. I mounted each otolith to a glass microscope slide using thermoplastic adhesive (Crystalbond) resin. Otoliths were mounted with the proximal surface facing down and were pushed flat against the glass slide. I ground this side down until the daily growth increments began to resolve using a 9mm lapping film. I then reheated the thermoplastic adhesive and repositioned the otolith so that the distal surface faced the glass slide, and ground the other side down using a 9mm lapping film until a flat sagittal section was formed. I then used a 3mm lapping film to further polish the otolith section for a more clear resolution. I photographed each otolith, using a Leica DMC4500 digital microscope camera mounted to a Leica DM2500 LED compound microscope, at 40X magnification to resolve the growth increments on the sagittal plane of the prepared otolith (Fig. 3.3). Of the total 32 otoliths processed, 23 facilitated estimates of ‘recent’ growth, and nine were rendered unreadable during the preparation procedure.

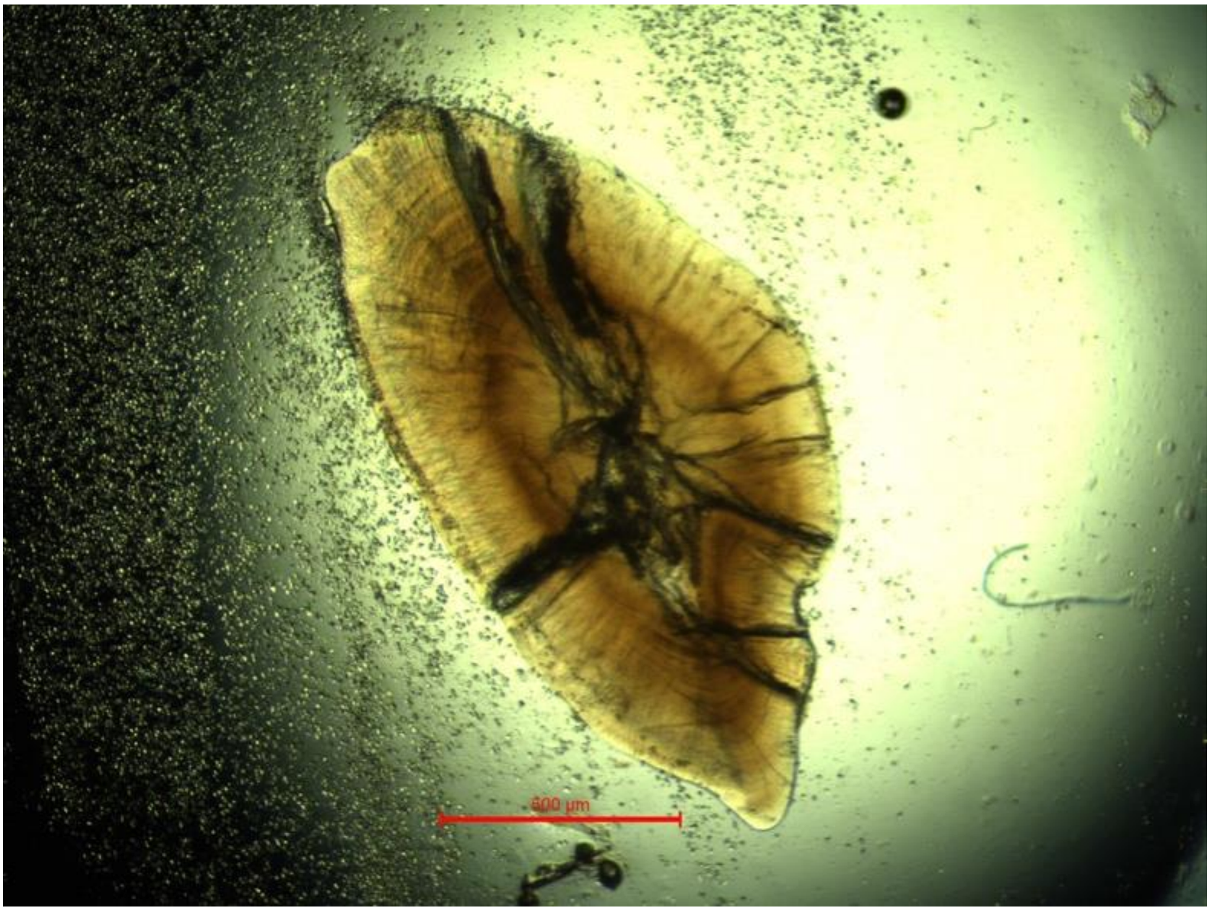

Figure 3.3. Ground otolith showing the exposed sagittal plane at 10X magnification. Scale bar (in red) is 500µm.

3.2.6. Otolith Increment Analysis

I analysed the microstructure of the imaged otoliths using the Otolith M application in Image Pro Premier (version 9.2). I measured the distance between successive daily growth increments to find the mean daily growth of each otolith over the most recent 19 days of growth for each fish (Fig. 3.4). This metric allowed me to test the growth of each fish from when it was occupying one my reef units.

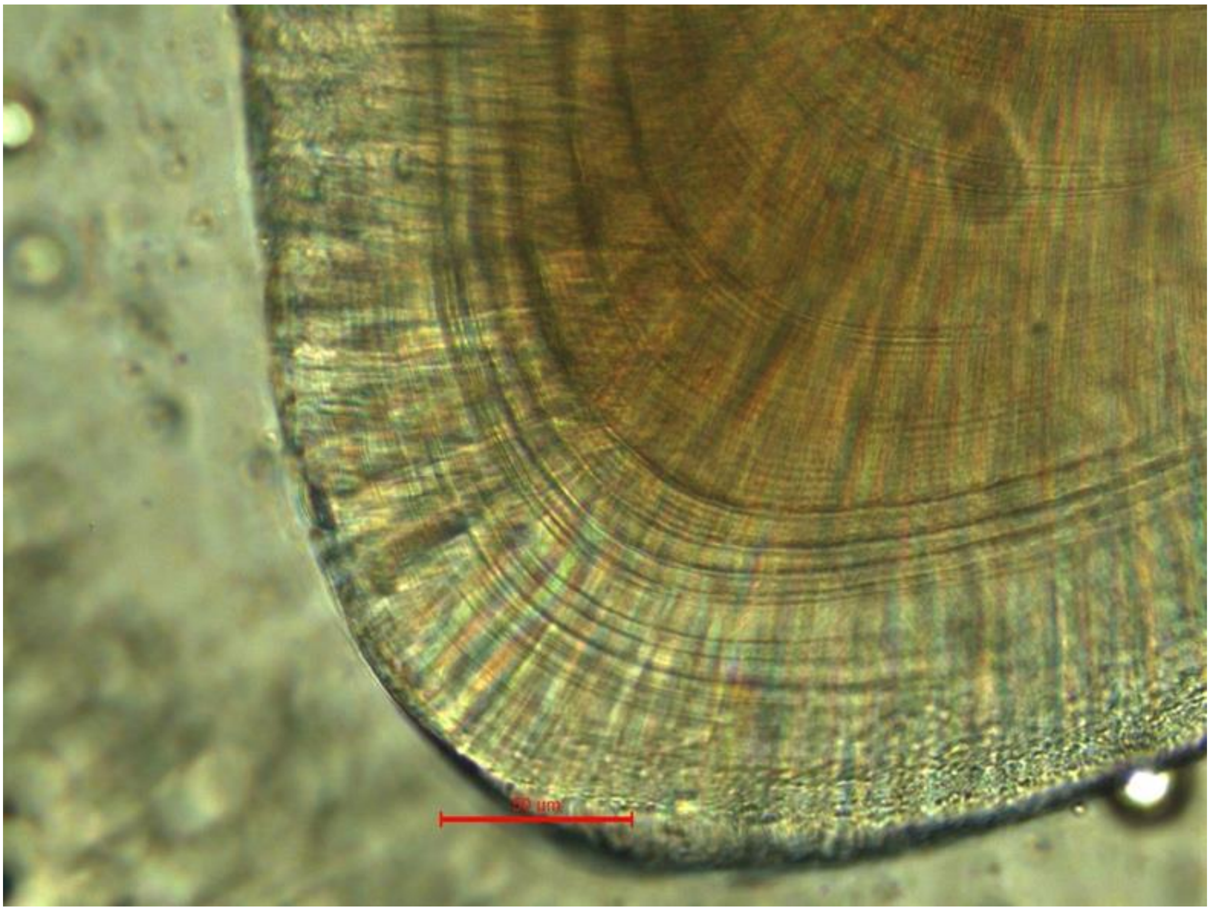

Figure 3.4. Otolith at 40X magnification showing exposed growth increments at the edge of the otolith. Scale bar (in red) is 50µm.

3.2.7. Statistical Analyses

3.2.7.1. Does the presence of supplemental structure and the location of an artificial marine habitat increase the abundance of fish and invertebrate species?

To investigate the trends in species abundances on artificial reefs under different substrate x structure treatments throughout the first six months of deployment I performed generalised linear models on mean abundance data of each species surveyed. I used the ‘glm’ function of the base R ‘stats’ package (R Core Team, 2024) following a poisson model. I used this model despite the overdispersion of the data detected by checking the overdispersion ratio on residual deviance and degrees of freedom. I continued with the poisson generalised linear model because the alternative models – negative binomial regression, quasipoisson, and zero-inflated models – did not fix the issue of overdispersion.

3.2.7.2. Does the placement of an artificial reef and the presence/absence of additional structure shape community composition?

I calculated the three diversity indices – species richness, species evenness, and Shannon-Wiener diversity index (Shannon & Weaver, 1948) – for each site and survey number, and included SMURF presence and substrate information in the dataframe. I then tested the normality and homogeneity of variance assumptions using ‘shapiro.test’ in base R and ‘leveneTest’ function as part of the ‘car’ package (Fox & Weisberg, 2019; R Core Team, 2024).

Testing these metrics by the factors in my study allowed me to understand whether the factors of structure, reef proximity, or time (survey) had significant effects in shaping the biodiversity, and therefore community composition of the reef units I surveyed. I tested the effects of supplemental structure, reef proximity, and survey number on the diversity indices calculated by fitting generalised linear mixed models to each metric using the ‘lmer’ function within the ‘lme4’ package (Bates et al., 2015). I used SMURF, substrate, and survey (as an ordered variable) as fixed effects, and site as the random effect in these analyses. I tested the assumption of normality using the ‘shapiro.test’ function and the assumption of homoscedasticity with the ‘qqnorm’ and ‘qqline’ functions of the base R ‘stats’ package (R Core Team, 2024).

I created a matrix of community data using the Bray-Curtis measure of dissimilarity – the ‘vegdist’ function in the ‘vegan’ package (Bray & Curtis, 1957; Oksanen et al., 2025), and constructed a principal coordinates analysis of this data with the ‘cmdscale’ function of base R (R Core Team, 2024). I tested the distribution of communities with different habitat characteristics (SMURF x Substrate x Survey) with a PERMANOVA using the ‘adonis2’ function in the ‘vegan’ package (Oksanen et al., 2025). I then conducted one-factor PERMANOVAs with the ‘adonis2’ function (Oksanen et al., 2025) for each factor separately (SMURF, Substrate, and Survey). These analyses allowed be to understand how different the community compositions of reef units were between different treatments, and whether they became more similar or different over time.

To investigate the effect of supplemental structure and proximity to a natural reef source to size classes distributions of key fish and invertebrate species I performed Kolmogorov-Smirnov distribution tests using the ‘ks.test’ function as part of the base R package (R Core Team, 2024). I compared size distributions of each species (spotty wrasse, variable triplefin, kina, cat’s eye snail, and top-shells) by treatment combinations of structure and reef proximity. I did not include time as a factor in these analyses, therefore they tested the means of all data by treatment.

3.2.7.3. Does the placement and design of artificial reefs influence the growth and fitness of a common species occupying them?

I tested the difference in mean increment width of otoliths analysed using a generalised linear mixed-effects model. In the model I compared mean increment between units with and without additional structure (SMURF) as well as by proximity to the reef (substrate), and the interaction between SMURF x substrate using the 'lmer' function in the 'lme4' package (Bates et al., 2015). Reef unit was included in the model as a random effect to account for potential repeated measures. I tested normality of the data using the 'shapiro.test' function of the 'stats' package in base R and homogeneity of variance using 'leveneTest' of the 'car' package (Fox & Weisberg, 2019; R Core Team, 2024).

All statistical analyses were conducted in RStudio (Version 2024.12.0+467) using R 4.4.2 (R Core Team, 2024). All graphs were created using the 'ggplot2' package (Wickham, 2011).

3.3. Results

3.3.1. Does the presence of supplemental structure and the location of an artificial marine habitat increase the abundance of fish and invertebrate species?

I tested the mean abundance of each species surveyed by subsrate, structure, and across time (categorical survey number). The models showed a significant effect of at least one factor on the recruitment of 12 out of the total 41 species studied (all results reported in Appendix A – see Table A2), and all other species were found to have no significant trends for any factors or interactions ($p > 0.05$). I have chosen five of these to report as they displayed interesting trends with the factors tested, and they consist of a range of species across trophic groups and across both invertebrates and fish.

The most abundant species overall was the spotty wrasse (*Notolabrus celidotus*). The interaction between substrate and structure reduces the mean abundances of spotty wrasse ($z_{(136)} = -3.325$, $p = 0.001$), suggesting when SMURFs are present on units located on reef substrate, abundance of spotties drops relative to the expected effects of the factors alone. The three-way interaction (SMURF x Substrate x Survey) suggests that the effect of structure and substrate changes throughout time ($z_{(136)} = 3.443$, $p = 0.001$; Fig. 3.5). The presence of additional structure significantly increased the abundance of *N. celidotus* ($z_{(136)} = 2.120$, $p = 0.034$), and reef units in close proximity to the natural reef also had increased abundances of spotty wrasse ($z_{(136)} = 3.178$, $p = 0.001$).

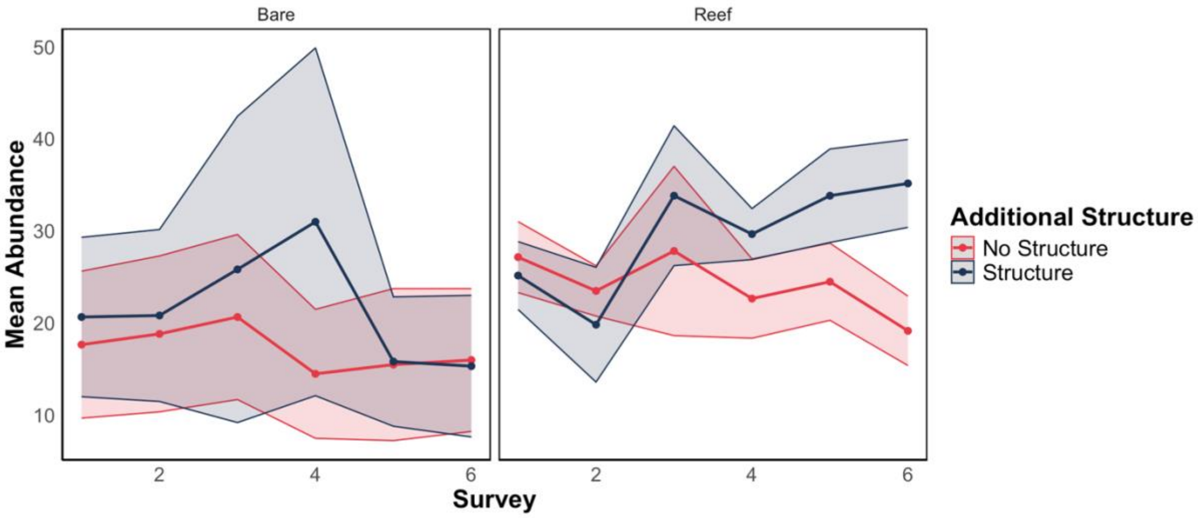

Figure 3.5. Mean abundance of *N. celidotus* by substrate (bare and reef) and additional structure (no structure indicated in red, additional structure indicated in blue). Ribbons represent standard error.

The interaction between structure and survey number was marginally significant for abundances of variable triplefins ($z_{(136)} = 1.710$, $p = 0.087$), suggesting that the presence of additional structure may tend to increase abundances of *F. varium* over time (Fig. 3.6). Abundances of variable triplefins were higher at reef sites overall compared to bare substrate ($z_{(136)} = 2.357$, $p = 0.018$), and the effect of structure was not significant on abundances ($z_{(136)} = -0.921$, $p = 0.357$).

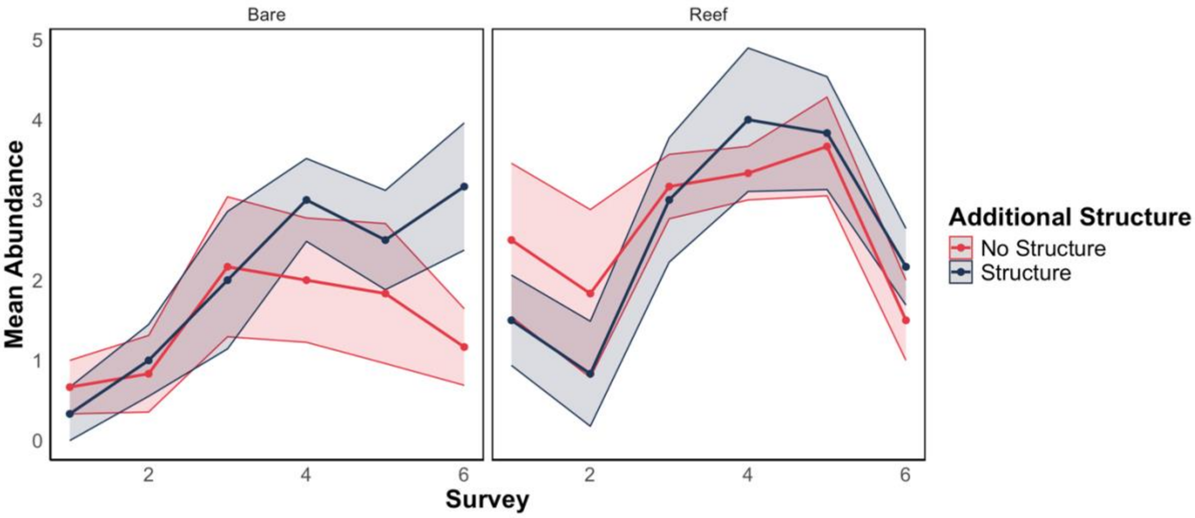

Figure 3.6. Mean abundance of *F. varium* by substrate (bare and reef) and additional structure (no structure indicated in red, additional structure indicated in blue). Ribbons represent standard error.

The abundance of *E. chloroticus* increased over time ($z_{(136)} = 2.245$, $p = 0.025$), and interaction effects with survey number show that the influence of additional structure ($z_{(136)} = 3.130$, $p = 0.002$) and substrate ($z_{(136)} = 3.737$, $p < 0.001$) change over time (Fig. 3.7). *E. chloroticus* were found to be more abundant at reef units where additional structure was not present ($z_{(136)} = -5.829$, $p < 0.001$), and at reef units on bare substrate compared to those on natural reef substrate ($z_{(136)} = -7.329$, $p < 0.001$).

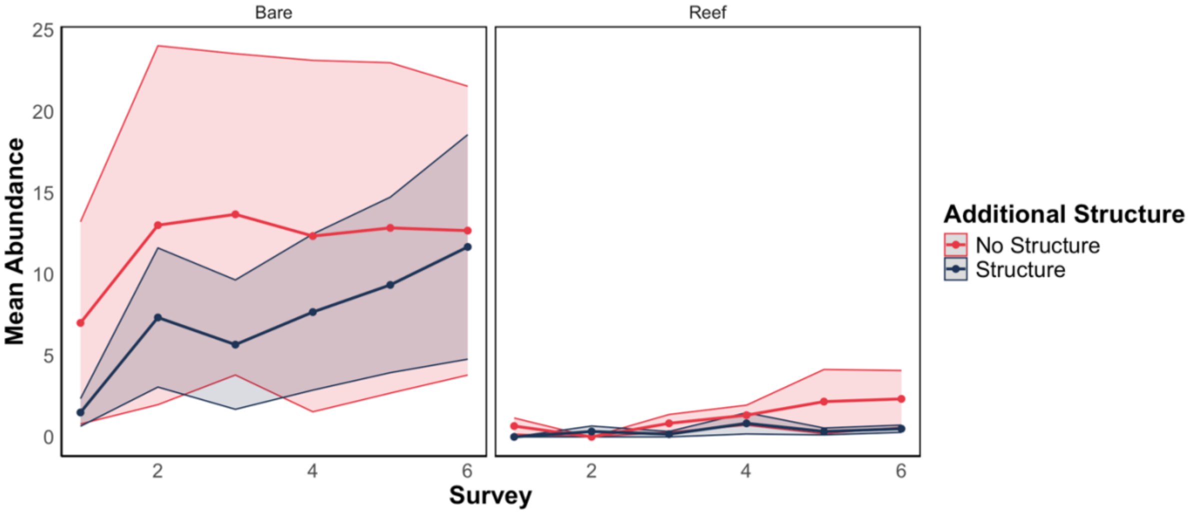

Figure 3.7. Mean abundance of *E. chloroticus* by substrate (bare and reef) and additional structure (no structure indicated in red, additional structure indicated in blue). Ribbons represent standard error.

Mean abundances of *L. smaragda* were positively affected by the presence of additional structure the longer the reef unit was in place (Fig. 3.8), indicated by the interaction between structure and survey ($z_{(136)} = 2.414$, $p = 0.016$). The mean abundance of cat's eye snails was higher on reef units that lacked additional structure ($z_{(136)} = -3.035$, $p = 0.002$), and substrate seemed to have little effect on these abundances ($z_{(136)} = 0.395$, $p = 0.693$). Abundances of *L. smaragda* tended to decrease slightly over time ($z_{(136)} = -2.505$, $p = 0.012$).

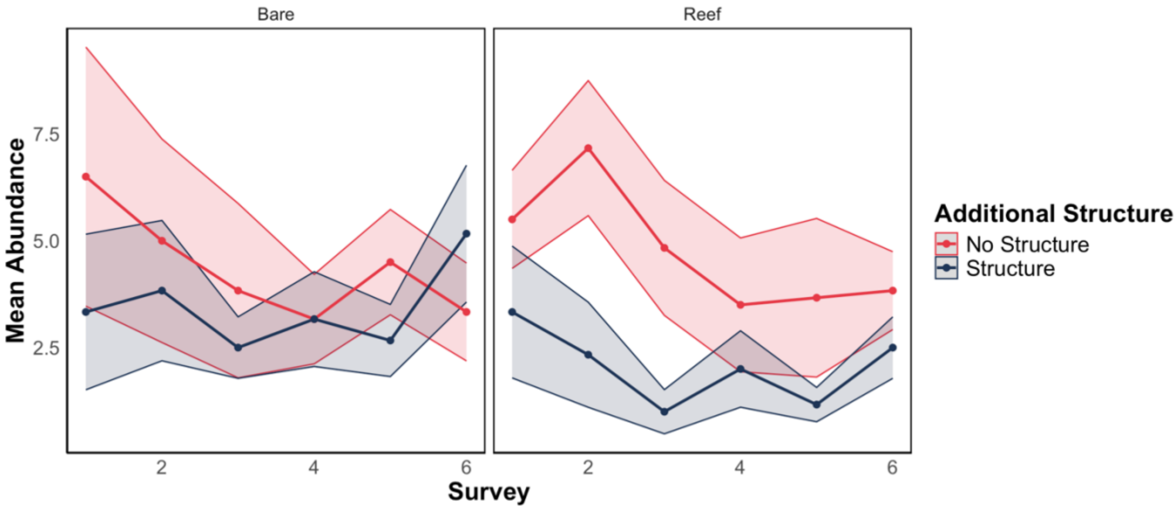

Figure 3.8. Mean abundance of *L. smaragda* by substrate (bare and reef) and additional structure (no structure indicated in red, additional structure indicated in blue). Ribbons represent standard error.

The effect of additional structure on the mean abundances of *Trochidae spp.* was dependent on the substrate that the reef units were on ($z_{(136)} = 2.180$, $p = 0.029$). Both substrate and structure had significant interaction effects on *Trochidae spp.* abundances – substrate x survey ($z_{(136)} = 3.133$, $p = 0.002$), and structure x survey ($z_{(136)} = 2.031$, $p = 0.042$). Additionally, the combined three-way interaction effect of substrate, structure, and survey is important in shaping the abundances of top-shells on artificial habitats ($z_{(136)} = -1.975$, $p = 0.048$). Mean abundances of top-shells tend to increase more on artificial habitats with additional structure as time went on (Fig. 3.9). Mean abundances of top-shells (*Trochidae spp.*) were higher overall on reef units without additional structure ($z_{(136)} = -2.108$, $p = 0.035$), and were not significantly different between reef and bare substrate sites ($z_{(136)} = -1.404$, $p = 0.160$).

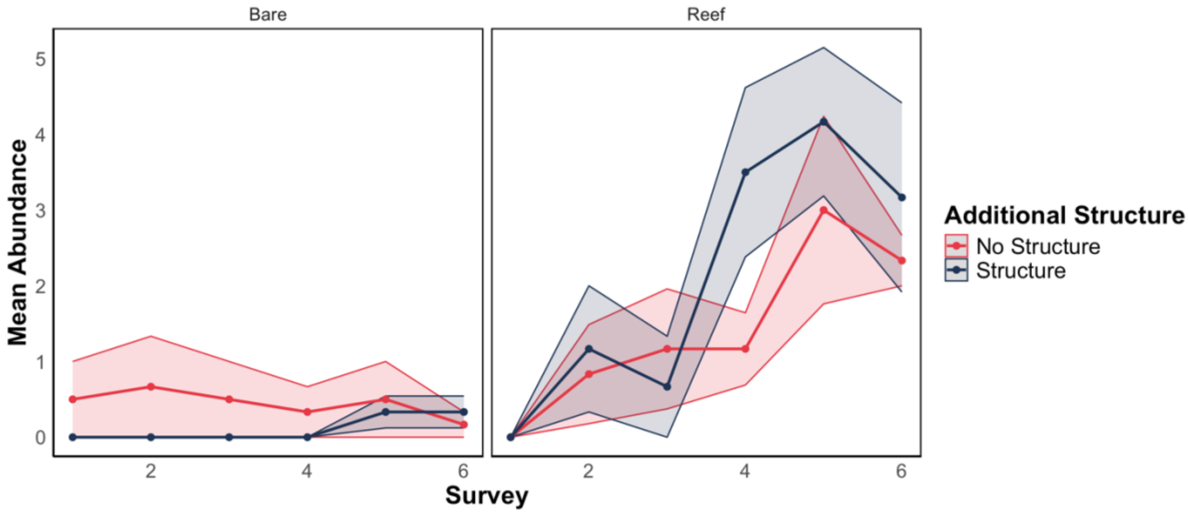

Figure 3.9. Mean abundance of *Trochidae spp.* by substrate (bare and reef) and additional structure (no structure indicated in red, additional structure indicated in blue). Ribbons represent standard error.

3.3.2. Does the placement of an artificial reef and the presence/absence of additional structure shape community composition?

I tested the diversity indices that I calculated (evenness, richness, Shannon-Weiner diversity) using generalised linear mixed-effects models. Species evenness was not significantly affected by additional structure ($t_{(23)} = 0.871$, $p = 0.393$), or the substrate that the reef unit was situated on ($t_{(23)} = 0.087$, $p = 0.931$). Evenness was also not significantly affected by any two-way, or three-way interactions between factors ($p > 0.05$; Fig. 3.10). The species richness of the reef units deployed did not significantly differ by structure ($t_{(23)} = 0.234$, $p = 0.817$) or substrate factors ($t_{(23)} = 0.469$, $p = 0.644$). Additionally, there was no significant influence of any two-way or three-way interactions between the factors of substrate, structure, and survey on species richness ($p > 0.05$; Fig. 3.10). Similarly, the GLMM I conducted found that neither additional structure ($t_{(23)} = 1.027$, $p = 0.315$), nor the substrate the reef units were located on ($t_{(23)} = 0.400$, $p = 0.693$) had a significant effect on Shannon-Weiner diversity. There were no significant interaction effects (either two-way or three-way) on Shannon-Weiner diversity of the artificial habitats ($p > 0.05$).

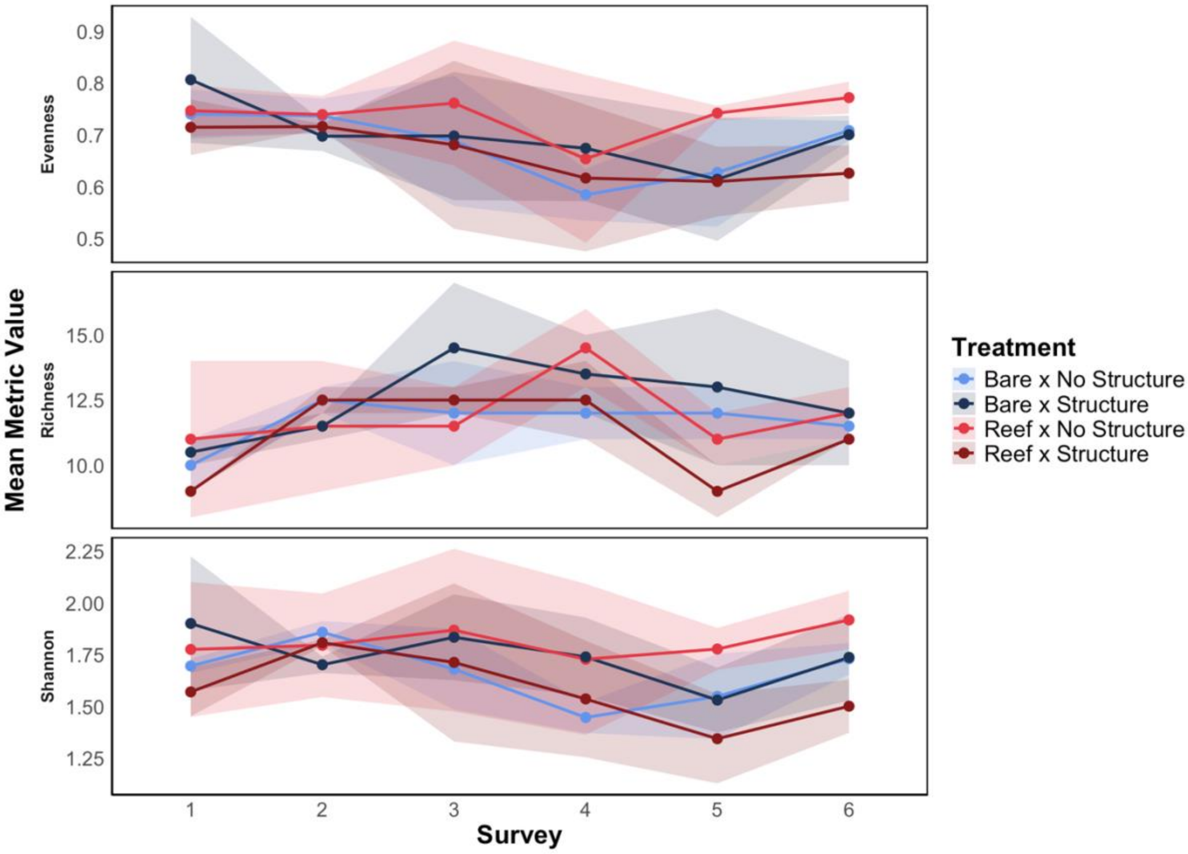

Figure 3.10. Diversity measures (Richness, Evenness, and Shannon diversity) on artificial reef treatments – bare x no structure (light blue), bare x structure (dark blue), reef x no structure (light red), and reef x structure (dark red) – across time. Shading indicates the standard error associate with each metric and treatment combination.

To further understand if additional structure or the proximity to a natural reef effects the communities that form on artificial reefs, I conducted a principal coordinates analysis on the community data. The overall PERMANOVA testing the effect of supplemental structure, reef proximity, and survey number showed that there was no difference in communities based on these factors together ($F_{(23,47)} = 0.815$, $p = 0.805$). The effect of supplemental structure was not significant on the community composition ($F_{(1,47)} = 0.625$, $p = 0.598$), and survey number was also not significant ($F_{(5,47)} = 1.260$, $p = 0.225$) according to the one factor PERMANOVAs I conducted. However, I found substrate (reef proximity) to be a significant factor in the composition of artificial reef communities ($F_{(1,47)} = 12.726$, $p = 0.001$; Fig. 3.11). Due to the lack of differences in diversity indices previously reported, it can be inferred that the difference in community composition between reef and bare sites (by PCoA) is being caused by alternative factors.

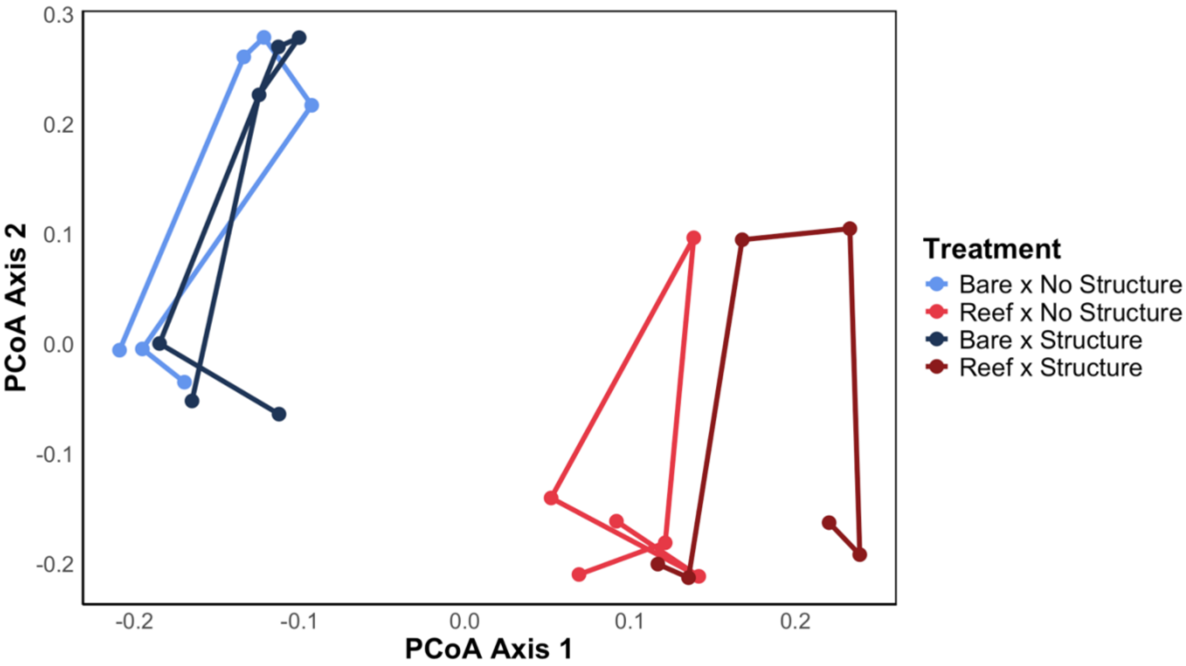

Figure 3.11. Principal coordinates analysis (PCoA) of community composition based on Bray-Curtis dissimilarity. Each point represents a survey mean for that treatment (combination of substrate x structure). Colours indicate the treatment – bare x no structure in light blue, bare x structure in dark blue, reef x no structure in light red, and reef x structure in dark red.

I tested the influence of different treatments on the size structure of the five key species that I focused on in the abundance analyses. This was to understand if more juveniles or adults were recruiting to each different treatment, and therefore understand how the treatments were influencing another factor of community composition. The size structure of spotty wrasse (*N. celidotus*) was significantly different between artificial habitat units on reef substrate compared to those on bare, with the median size class being slightly higher on bare substrates and a higher abundance of larger sized individuals ($p < 0.001$; Fig. 3.12). The presence of additional structure had no substantial impact on the size structure of *N. celidotus* communities on artificial habitats ($p = 0.928$).

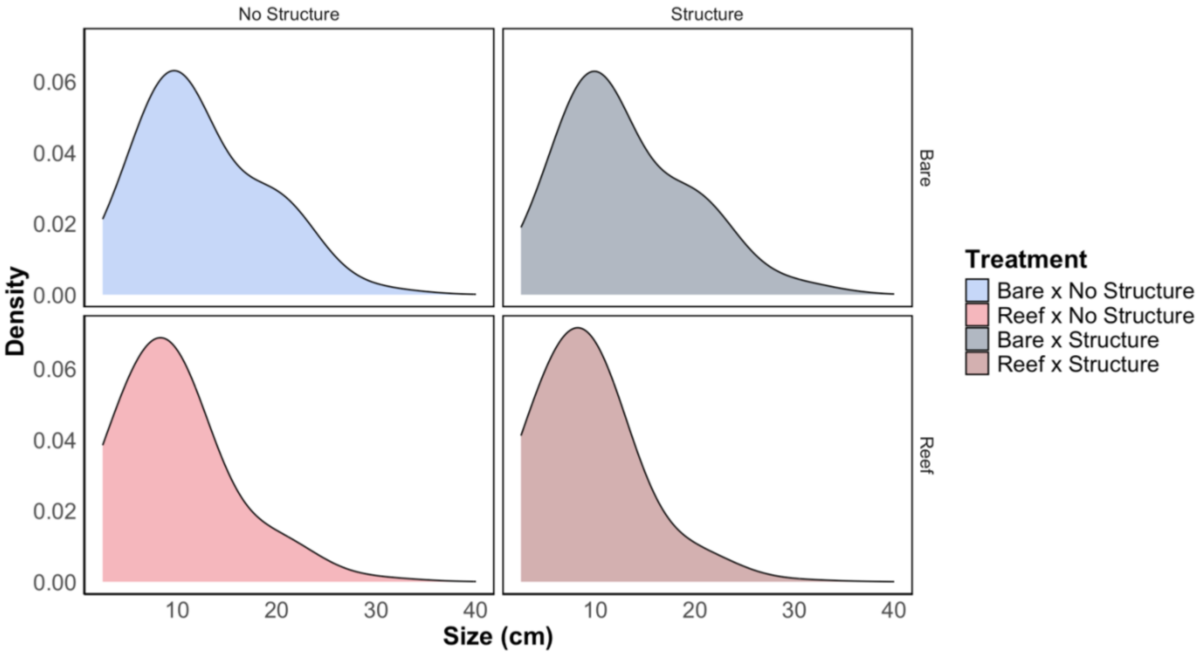

Figure 3.12. Smoothed kernel density plots showing the estimated probability density function of *N. celidotus* by artificial reef treatment (Structure x SMURF combination) – bare x no structure (light blue), bare x structure (dark blue), reef x no structure (light red), reef x structure (dark red).

Forsterygion varium (variable triplefin) size class structures on artificial habitats were not significantly different between bare and reef substrates (p = 0.161), or between those with additional structure and those without (p = 1; Fig. 3.13).

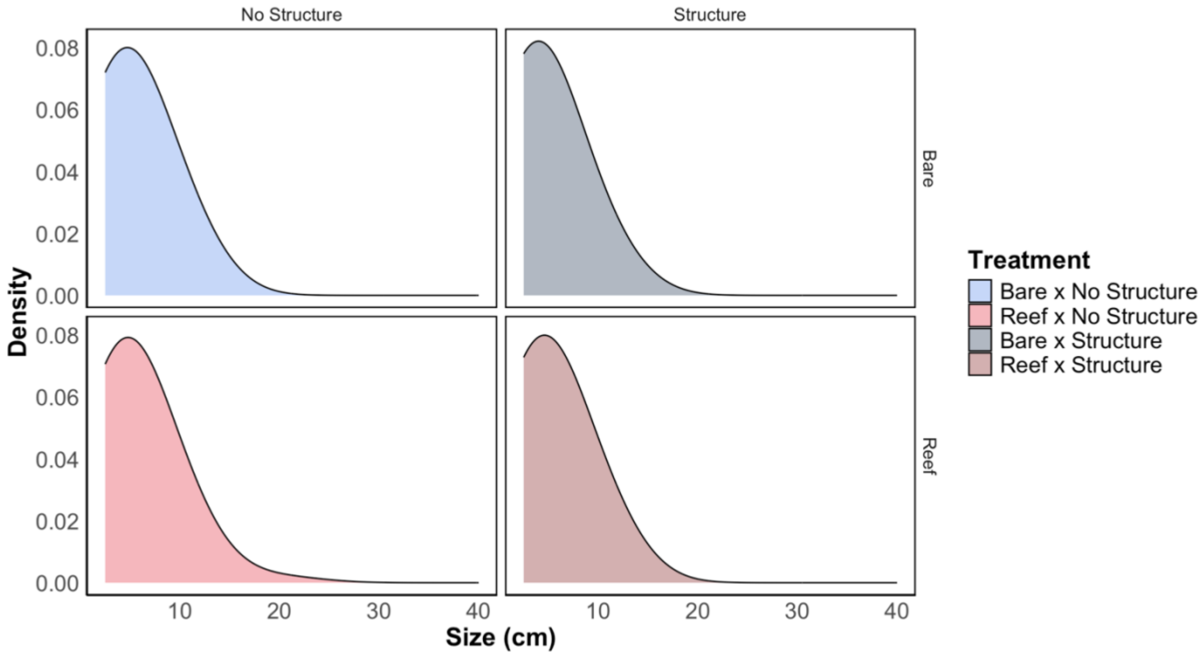

Figure 3.13. Smoothed kernel density plots showing the estimated probability density function of *F. varium* by artificial reef treatment (Structure x SMURF combination) – bare x no structure (light blue), bare x structure (dark blue), reef x no structure (light red), reef x structure (dark red).

The size structure distributions of kina (*Evechinus chloroticus*) did not differ between artificial reef units that had additional structure and those that did not ($p = 1$). However, they were significantly influenced by the proximity to a natural reef source ($p = 0.004$). Reef units on bare substrate tended to have higher abundances of larger individuals (Fig. 3.14).

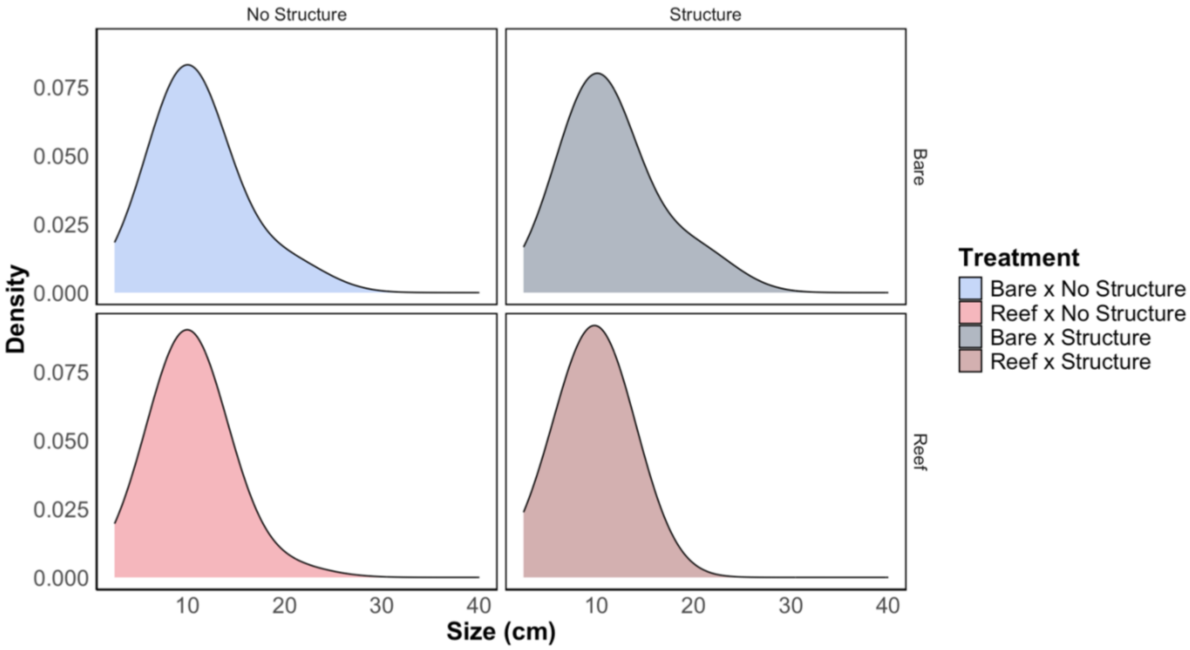

Figure 3.14. Smoothed kernel density plots showing the estimated probability density function of *E. chloroticus* by artificial reef treatment (Structure x SMURF combination) – bare x no structure (light blue), bare x structure (dark blue), reef x no structure (light red), reef x structure (dark red).

Cat's eye snail (*Lunella smaragda*) size class distributions were not significantly affected by either structure (p = 0.847) or substrate (p = 0.999) factors, meaning distributions of size structures were almost identical between all treatments (Fig. 3.15).

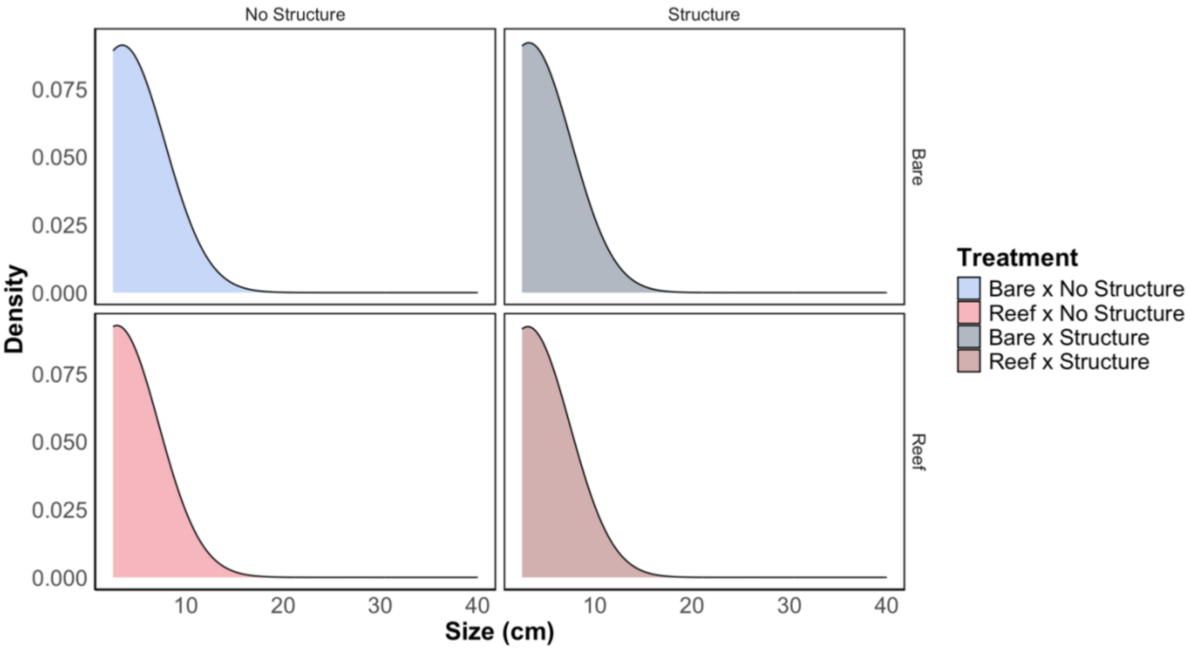

Figure 3.15. Smoothed kernel density plots showing the estimated probability density function of *L. smaragda* by artificial reef treatment (Structure x SMURF combination) – bare x no structure (light blue), bare x structure (dark blue), reef x no structure (light red), reef x structure (dark red).

Substrate did not have a significant effect on the size class distributions of *Trochidae spp.* (p = 0.368). The presence of additional structure also did not have a significant effect on the size class distributions of top-shells (p = 1; Fig. 3.16).

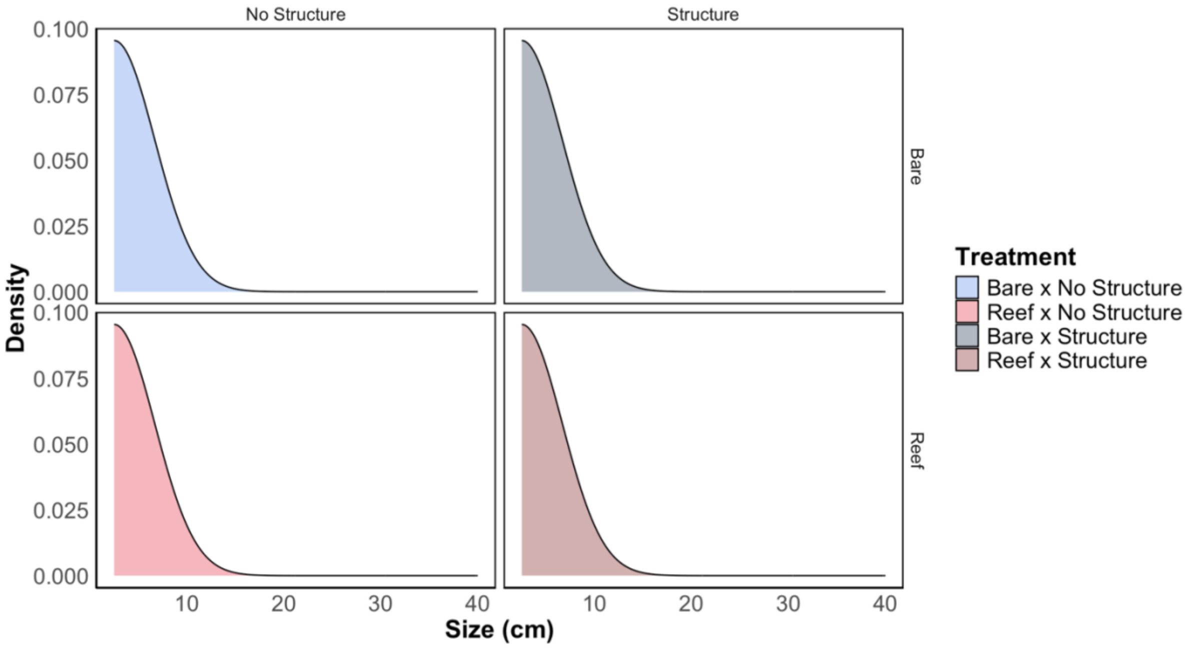

Figure 3.16. Smoothed kernel density plots showing the estimated probability density function of *Trochidae spp.* by artificial reef treatment (Structure x SMURF combination) – bare x no structure (light blue), bare x structure (dark blue), reef x no structure (light red), reef x structure (dark red).

3.3.3. Does the placement and design of artificial reefs influence the growth and fitness of a common species occupying them?

The generalised linear mixed-effects model suggests that daily growth (mean otolith increment width over the most recent 19 days of life) of *F. lapillum* was not significantly different between artificial reefs with or without supplemental structure ($t_{(23)} = 0.793$, $p = 0.436$). Mean increment also did not differ significantly depending on the proximity to natural reefs ($t_{(23)} = 0.205$, $p = 0.840$). There was additionally no significant interaction effect (SMURF x substrate) on mean increment width ($t_{(23)} = -1.061$, $p = 0.300$). These results demonstrate the lack of effects that SMURF presence (structure) and substrate had on the mean daily otolith growth of the *F. lapillum* specimens from the artificial habitats deployed (Fig. 3.17). Assumptions of normality ($W = 0.931$, $p = 0.115$) and equal variance ($F_{(3,19)} = 0.135$, $p = 0.938$) were met for these analyses.

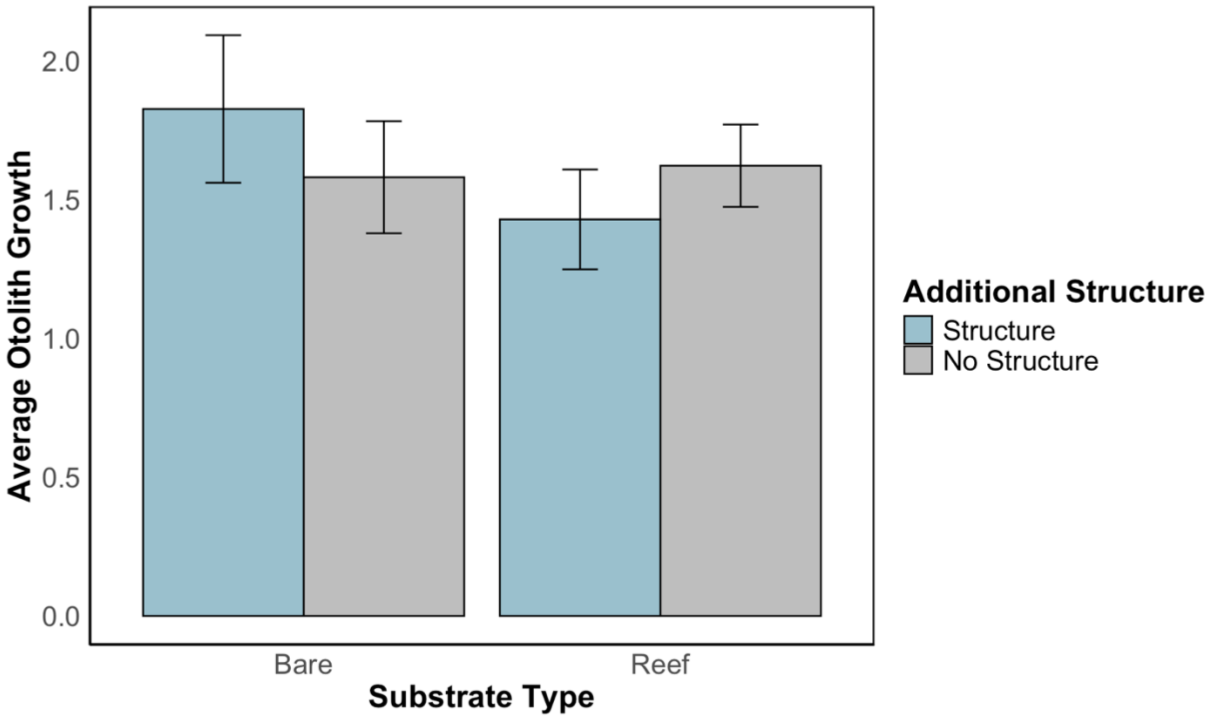

Figure 3.17. Mean daily otolith increment growth (over the most recent 19 days) by substrate and presence/absence of additional structure. Additional structure signified in blue and absence of additional structure in grey. Error bars indicate standard error.

Table 3.1. Sample sizes of otoliths analysed from reef units displayed by substrate and SMURF factors tested.

Substrate	**Additional Structure**	**N**
Reef	Yes	7
Reef	No	6
Bare	Yes	6
Bare	No	4

3.4. Discussion

Many studies have purported the importance of habitat structure on the recruitment of fish and invertebrates, with highly diverse communities being associated with more complex habitats (Carr, 1989; Tupper & Boutilier, 1997; Lazarus & Belmaker, 2021). The proximity of an artificial reef to a nearby natural reef can also influence the species diversity, abundance, and size structures (Strelcheck et al., 2005; Schroeter et al., 2015). Understanding these effects in the context of local artificial reefs can have a profound effect on the importance of these factors for conservation efforts that include the use of artificial marine habitats.

In this study, I endeavoured to understand the relationship between supplemental structure and proximity to a natural reef source on the recruitment and growth of marine fishes and invertebrates to artificial reefs. Analysing the effects of two factors across seven months of reef development provides a more complex understanding of recruitment dynamics to artificial reefs, and the growth analysis conducted provides evidence for the ability of artificial reefs to provide viable habitat for a common rocky reef species, *F. lapillum*. Recruitment to artificial habitats was significantly affected by supplemental structure and proximity to a natural reef, however responses to these factors were species-specific; this highlights the need for clear management goals when implementing these structures as a restoration strategy. Diversity indices were not significantly influenced by the main effects tested, and did not change significantly across time in this study, however PCoA analysis confirmed significant variation in community composition between reef and bare treatments. While the similarity of diversity indices initially sounds positive for the implementation of artificial reefs to support biodiversity, the differentiation between ‘reef’ and ‘bare’ units underpins the importance of understanding that the placement of these habitats will directly influence the communities that they will attract. Additionally, both structural complexity and reef proximity had varying effects on the size distributions of focal species in the study. This emphasizes the species-specific nature of recruitment onto these habitats, and the difference in their ability to facilitate healthy populations of varying species based on the factors tested. Finally, the growth of *F. lapillum* did not differ between treatments in the otolith increment analysis conducted. This finding may point to the ability of artificial reefs to provide viable habitats for common rocky reef species, however it is important to take other factors into account when interpreting this result, and complete further research in this area.

3.4.1. Does the presence of supplemental structure and the location of an artificial marine habitat increase the abundance of fish and invertebrate species?

Additional structure and/or the substrate that a reef unit is placed on were important factors for 12 out of the 41 species surveyed in terms of recruitment and abundance on the reef. Different responses were exhibited by the five key species that I focused on, depending on the species. These species represent multiple trophic groups (carnivores and herbivores) and a range of classes (Actinopterygii, Gastropoda, and Echinoidea) with varying relationships to macroalgae. Spotty wrasse (*N. celidotus*) tended to have significantly higher abundances at reef sites compared to bare sites, and on reef units with additional structure compared to those without. However, when these two factors interacted, there were slightly less *N. celidotus* than would be expected from the effect of the two factors separately. Variable triplefin (*F. varium*) were found to be more abundant on reef sites. The factor of additional structure had no significant effect on *F. varium* abundances, however when interacting with the time (survey) factor, reef units with additional structure tended to increase abundances more than those without over time. Kina (*E. chloroticus*) were the only focal species to have higher abundances on bare sites compared to reef sites, and they also tended to be in higher abundances on reef units with no additional structure. Interestingly, both gastropod species included in the focal analyses had similar reactions to the treatments tested. *L. smaragda* (cat's eye snail) and *Trochidae spp.* (top-shells) were both more abundant on reef units with no supplemental structure present, and neither had significant differences in abundance between reef and bare sites. Despite having a negative correlation with additional structure, it seems the longer a reef unit is in place, the more effect that additional structure will have. Abundances of both gastropod species tended to increase with additional structure over time, as seen in the structure x survey interaction effects.

In a study by Komyakova and Swearer (2019), natural reefs received the highest recruitment compared to artificial reefs overall across three focal fish species, however the habitat choices of the focal species differed slightly. They found that *Vincentia conspersa* recruited in higher numbers to an artificial reef treatment as compared to the natural reef, however state that previous research has demonstrated that *V. conspersa* has no distinct habitat preferences. Previous studies *Trachinops caudimaculatus* was also found to have a strong affinity for conspecifics, and were found to recruit to treatments where populations of *T. caudimaculatus* were already present (Komyakova & Swearer, 2019). This is likely why *N. celidotus* had higher abundances on reef units in close proximity to the natural reef in my study, coupled with the affinity for many temperate reef fish to recruit to areas with high canopy coverage of macroalgal stands (Carr, 1991, 1994). The relationship between predator and prey may explain the contrasting recruitment patterns between spotty wrasse and kina in my study, with kina tending to recruit in significantly higher numbers on artificial reefs that were on bare substrate, away from the natural reef. Urchins (kina) are a key prey species for spotty wrasse, and therefore would likely be in limited numbers on reefs where high abundances of spotty wrasse are present (Denny, 2005).

The lack of effect that additional structural complexity had on the smaller-bodied focal species, variable triplefin, cat's eye snails, and top-shells, could be explained by the attraction of fish and invertebrates to shelters that are in proportion to their body size (Luckhurst & Luckhurst, 1978; Parsons et al., 2016). The reef units themselves had a high level of structural complexity in their base design, and therefore may have already possessed the shelter necessary for small fish and invertebrates to recruit to, leaving the large additional structures to have little to no influence on these species' abundances.

3.4.2. Does the proximity to a natural reef and the presence/absence of additional structure cause different communities to assemble on artificial reefs?

Neither reef proximity, nor supplemental structure had a significant effect on the species richness, species evenness, and Shannon-Weiner diversity of the artificial reef communities studied. This result is seemingly in opposition to many other studies which have highlighted the importance on complex structure on the recruitment of diverse communities (Carr, 1989, 1994; Vega Fernández et al., 2009; Bustamante et al., 2014). It is possible that the divergence between treatments has not been observed due to the short study period. Becker et al. (2022) revisited an artificial reef deployed 10 years previous and found that over that time both abundance of key species and overall diversity had increased significantly. While they also found that the community on that artificial reef did not resemble those of nearby natural reefs, the artificial reef achieved its objectives over the 10 year time period.

Despite little difference found in diversity metrics between treatments, the PCoA analysis conducted shows that communities assembling on the reef units placed in close proximity to a natural reef represent distinct communities compare to those on bare substrate reef units. The presence of additional structure, however, was not likely responsible for any differences in community composition. Given this is a study over the first few months of community development on artificial reefs, it is expected that reef units with different treatments should exhibit distinct communities; Komyakova et al. (2019) found that dissimilarities in community composition between artificial reef treatments over time declined over time. This was not found in my study as time (survey number) was not a significant factor in shaping the communities on the artificial reef units. This result could be due to the short study period of around six months; it is possible that if the study were to have been conducted over a longer time frame, it would have been possible to see the convergence of community composition between treatments. Communities associated with artificial reefs can become stable after time periods between a few months to several years, and in general it takes between one and three years to stabilise (Becker et al., 2018; Wu et al., 2019).

Reef proximity was a significant factor shaping the size structure distributions of key species on the artificial reef units studied. Although it is important to recognise that if I had analysed these variables by each survey (time) instead of testing the means across all surveys, I may have obtained different results. The results show that both *N. celidotus* and *E. chloroticus* had significant differences in size distributions between the near-reef units and the bare substrate units, with higher mean sizes and larger individuals being found more frequently on the bare substrate units. In a study by Trebilco et al. (2015), greater canopy cover was associated with higher fish biomass overall, however increased structural complexity accounted for an increase in the proportion of the smallest fishes. Anderson (1994) similarly found close associations between juvenile kelp perch densities and *Macrocystis pyrifera* canopy compared to larger, adult fish, in line with assumptions that juvenile fish will occupy more structurally complex habitats in a balance of foraging potential and predation risk. Additionally Hylkema et al. (2020) observed that all of the artificial reef plots in their study attracted high densities of 0-5cm fish compared to other size classes, similar to my study, and additionally found that fish larger than 25cm were scarce in their surveys. My findings are in line with the findings of Anderson (1994) and Trebilco et al. (2015) given the increased nearby canopy cover of the natural reef compared to the bare substrate habitats. However, it potentially suggests that the SMURF modules attached to certain reef units to create supplemental vertical structure did not provide the necessary cover for juvenile recruitment. This is demonstrated by the lack of significant effect that supplemental structure had on the size distributions of any focal species. For example, Ammann (2004) reported that recruits in their study varied by deployment methods of the SMURFs. Species that are typically associated with canopy and surface-water recruited more to SMURFs deployed at the surface, whereas mid-water SMURFs recruited less species in terms of abundance and diversity. If I deployed the SMURFs used in this study at the surface, there may have been a greater effect of this on recruitment to the artificial reef units. It is also known that juveniles tend to use macroalgal structures – canopies, stipes, and varying branch morphology – to avoid predation (James & Whitfield, 2023), and therefore the proximity of the 'near-reef' structures to the natural reef may have provided more opportunity for predator evasion.

Variable triplefin, cat's eye snail, and top-shells size distributions were not significantly influenced by the presence of supplemental structure or the proximity of a reef unit to the natural reef. There were no differences in size distributions found between treatments for any of these species. This may be due to the small body size of these species relative to the survey's size class categories. *F. varium* grow to a maximum length of about 10cm (Ruck, 1980), meaning they will not be found in size classes larger than the 5-10cm size class in my survey, for example. Therefore restricting the level of distribution we can observe in this species through this study. Similarly, for smaller gastropod species such as *L. smaragda* and *Trochidae spp.* it can be hard to discern whether the treatments had any effect on their size structures due to their very small body size that would not have been captured in detail in my survey design.

3.4.3. Does the placement and design of artificial reefs influence the growth and fitness of a common species occupying them?

The common triplefin, *F. lapillum*, is known to be a heavily site-attached species with juveniles generally occupying home ranges of less than 0.1m^2, and adults rarely moving more than a few metres from their home ranges on rocky-cobble substrates (Shima et al., 2012; Mensink & Shima, 2015). Home range size may vary with habitat type, conspecific density, or food availability, but tend to remain very small and thus the characteristics of settlement sites may shape variation in growth and condition patterns for this species (Mensink & Shima, 2015). It is important to understand the effect of habitat characteristics on species growth and fitness to understand whether artificial reefs can provide viable alternative habitats, or simply become ecological traps, when they are implemented as conservation strategies (Hale & Swearer, 2016; Komyakova et al., 2021).

I found no significant effect of either proximity to a natural reef, the presence of supplemental three-dimensional habitat, or the interaction between these factors on the growth of *F. lapillum* specimens in this research. These findings tend to suggest that the characteristics of an artificial reef habitat have little effect on the growth of *F. lapillum* individuals living on that reef. This may be a species specific response as the common triplefin is a widespread species found abundantly at most shallow-depth reefs throughout New Zealand (Wellenreuther et al., 2007; Francis, 2016), and thus could be understood to be a relatively hardy species that is able to thrive in many environments. Alternatively, it could provide evidence that artificial reefs, in most circumstances, provide viable habitat for *F. lapillum* individuals to recruit to, and therefore could be important in supporting healthy communities of the species in terms of conservation or restoration of rocky reef habitats.

3.4.4. Limitations of the Study

The construction of the artificial reef units used in this study was completed between February-April 2024, with the first surveys being conducted in April 2024. Many species have seasonal recruitment, and temporal variation in abundance, therefore this study may have missed the recruitment season for certain species. Despite this, the project ran over several seasons in order to provide the clearest picture of recruitment and community composition at the study sites. Surveys were often conducted in differing conditions due to the project running through several seasons. This may have affected the underwater visual censuses if, for example, visibility was lower due to weather or wave action. Weather also became a limiting factor in undertaking the surveys, and therefore the surveys were not always conducted at equal time points throughout the study.

This project had half of the artificial reef units placed on the natural reef edge, therefore testing the effect of a natural reef on the community composition on artificial reefs, however surveys of a natural reef could have been conducted for a more complete comparison between artificial and natural reefs.

The specimens used in the growth (otolith) analysis were collected over a span of four dives, and four weeks due to personnel and weather constraints. Therefore each fish was collected at a slightly different time, potentially causing subtle differences in growth patterns to be analysed. However, the fish were all collected in the same season, therefore I assume growth patterns would have been relatively similar between fish throughout the period of collection.

3.4.5. Conclusion

In this study, the effect of treatments was variable on the abundance of focal species observed. Most species had higher abundances on artificial reef units in close proximity to the natural reef, however *E. chloroticus* was found to be in higher abundances on bare sites. Focal species also had varying responses to additional structure, with some species recruiting in higher numbers to units with additional structure, and some found in higher abundances on those without. Time was found to be a key influence in how multiple species associated with additional structure, with the responses in abundance caused by structure changing across surveys. The species diversity (richness, evenness, and Shannon-Weiner diversity) of the artificial reef units were not heavily affected by either reef proximity or the presence of supplemental structure. However, PCoA analysis demonstrated that community compositions were significantly different between substrate types, and that convergence of community composition between treatments had not been observed over the period of this study. I observed that size class distributions of two focal species on artificial marine habitats are influenced by the proximity of an artificial reef to a natural reef, but are not significantly influenced by the presence of additional structure. Although, neither proximity to natural reef, nor additional structure seemed to have an effect on the size distributions of smaller focal species. The range of results observed in this study give an idea of the complexity of recruitment dynamics on artificial habitats. The results could be a consequence of numerous factors acting upon each other, including a combination of treatment factors, as well as natural ecological processes such as seasonal variation and trophic interactions between marine organisms. Additionally, there was no difference found between otolith growth, and therefore the growth of *F. lapillum* individuals, between treatments in terms of mean increment width or total recent growth. This finding could present evidence for the ability of artificial reefs to provide viable habitat for marine communities to recruit to and occupy. However it would be both necessary and informative to study the effects of artificial reefs on the growth patterns of an increased range of species. This would endeavour to provide an overall picture of the growth and fitness potential on these habitats, as compared to the natural habitats they aim to mimic.

4. GENERAL DISCUSSION

4.1. Overview

Artificial reefs are becoming increasingly common in coastal environments, fast becoming a popular tool for restoring biodiversity, and protecting the health of faunal marine communities (Sherman et al., 2002; Vivier et al., 2021). The process of recruitment is integral for the formation of diverse biological communities on artificial marine habitats. For marine reef organisms with complex life histories, settlement cues, such as the presence of canopy-forming macroalgae, conspecific presence, shelter and food availability, are crucial in guiding these organisms towards the benthic habitats they typically colonise (Levin, 1994; Vega Fernández et al., 2009; Komyakova et al., 2019). In this thesis, I aimed to assess the potential for artificial marine habitats to be used as ecological mitigation and restoration tools. I evaluated the capacity of habitat modification and placement to enhance the ability of artificial reefs to support and/or restore temperate rocky reef ecosystems. I concentrated on the effects of additional vertical structure and the proximity of an artificial reef to a natural reef source on 1) the recruitment and abundance of focal fish and invertebrate species to artificial reefs, 2) the overall community composition and diversity of artificial reefs, and 3) the growth of one focal species on artificial reefs. I addressed these aims using two in-field experiments that manipulated artificial marine habitats to create multiple different treatments. I combined the community analysis conducted in these experiments with laboratory analysis of otolith growth on *Forsterygion lapillum* (common triplefin) to gain insight into the effect of artificial reefs on the growth of organisms that recruit to them. My results have demonstrated that the effects of artificial reefs are both species- and spatial scale-specific, with different species exhibiting varying responses across both treatments and experiments. The knowledge gained in this thesis can help to form an increased understanding of artificial reef dynamics and – in conjunction with previous literature – help to inform the potential enhancement of these habitats in efforts to restore and/or protect rocky reef habitats.

4.2. Recruitment

The majority of marine reef organisms will undergo pelagic larval development before settling to benthic habitats that they will occupy for the remainder of their lives (Fontes et al., 2009; Shima & Swearer, 2010; Bae et al., 2022). Recruitment is influenced by a range of biotic and abiotic factors including food availability, predator presence, conspecific presence, and structural complexity (Carr, 1989; Levin, 1993, 1994; Fontes et al., 2009, 2011). The combination of these factors, as well as many others, has the ability to shape marine communities by dictating the rate of recruitment for reef organisms.

The influence of structural complexity on the recruitment of marine reef organisms has been studied extensively over the past few decades. Notably, the effect of macroalgal stands and canopy cover on the recruitment of juvenile fish has been the topic of numerous studies. The canopy-forming properties of large macroalgal species increases the amount of available habitat, and therefore create shelter, nurseries, and an abundant food source for a range of fish (Carr, 1989, 1991, 1994; Levin, 1993, 1994; Anderson, 1994; Vega Fernández et al., 2009; Trebilco et al., 2015; James & Whitfield, 2023). In addition to this, Carr (1989), Hackradt et al. (2011), and Trebilco et al. (2015) have emphasised the importance of understory cover in the recruitment of fishes, as well as the interaction between canopy and understory species. These studies typically focus on common fish species such as kelp bass, rockfish, and multiple wrasse species in temperate environments. The link between recruitment and artificial reef success has been studied in order to improve the outcomes of artificial reef implementation in ecological mitigation/restoration strategies. This includes many studies on the effect of hard-substrate topography, and rugosity on recruitment to artificial reefs (Hixon & Beets, 1989; Tupper & Boutilier, 1997; Charbonnel et al., 2002; Komyakova & Swearer, 2019; Komyakova et al., 2019). However, when researching recruitment on artificial marine habitats, additional vertical complexity has rarely been studied as a factor influencing recruitment. The results of my studies indicate the potential species- and spatial scale-specific responses of marine recruitment to artificial reefs. The study in Chapter 2 did not reveal any increase in recruitment across trophic groupings (carnivores, omnivores, herbivores, filter feeders, and detritivores) at the 'impact' site, which would be the expected result of increased vertical structure. Although, previous studies have suggested that the percentage of canopy cover is integral to providing shelter and habitat for reef fishes to inhabit (Trebilco et al., 2015; James & Whitfield, 2023). While the 'impact' I implemented in Chapter 2 did increase the vertical complexity of the habitat, it likely did not provide the necessary canopy cover to have a meaningful impact on the recruitment of fish and invertebrates. In contrast to this, additional vertical structure had a significant effect on several focal species in my Chapter 3 study, yet not all of these species exhibited the same response. *N. celidotus* was found in higher abundances on reef units with additional structure, however *E. chloroticus*, *L. smaragda*, and *Trochidae spp.* were more frequently recruiting to reef units without supplemental structure. Additionally, *F. varium* recruitment did not show significant variation between the treatments. These results suggest that the effects of a habitat enhancement can be species-specific based on the life history traits of the study species. The increase in abundance of *N. celidotus* aligns with the results of previous studies on this species, and other similar reef fish species, which found links between canopy cover/vertical structure and increased recruitment (Jones, 1988; Carr, 1989, 1994; Taylor, 1998; Hackradt et al., 2011; Trebilco et al., 2015). Small-bodied invertebrates are also known to be attracted to shelters proportional to their body size (Luckhurst & Luckhurst, 1978; Parsons et al., 2016). Since the base structure of my artificial reef units included complexity in swim throughs and cavities, there may have been sufficient shelter for these species to recruit to the reef units without the need for additional structure. Interestingly, if a reef unit had additional vertical structure attached, the effect of that structure would become more positive over time on the abundances of gastropods *L. smaragda* and *Trochidae spp* despite those species being found in higher abundances on units with no additional structure. This is possibly due more complex recruitment patterns of these species that rely on factors other than the structural complexity of a habitat. For example, Watanabe (1984) found that species in the same family as those in my study (*Trochidae*) differentially recruited to habitats of different depths. In my study, the reef units nearby to a natural reef source would have facilitated early settlement through the significant presence of macroalgae in close vicinity to them. Whereas, bare substrate reef units would not have allowed for this to happen, as the units were between 5-8m in depth. The presence of SMURFs on these bare substrate reef units, however, may have begun to facilitate settlement. I may have only detected this effect in later surveys due to the sparse nature of their implementation, and therefore the time it would have taken time for populations to begin settling to these habitats.

N. celidotus and *F. varium* were found to be more abundant on reef units in close proximity to a natural reef, whereas *E. chloroticus* were found in higher abundances on bare substrate reef units. Neither *L. smaragda*, nor *Trochidae spp.* had a significant relationship with natural reef proximity (substrate). The influence of macroalgal coverage on the recruitment of reef fish (Carr, 1989, 1991, 1994; Anderson, 1994; James & Whitfield, 2023) is likely responsible for the increased recruitment rates of *N. celidotus* on near-reef habitats. This finding is also consistent with a study by Komyakova and Swearer (2019) in which recruitment rates of three reef fish species was significantly higher at natural reef sites as compared to artificial reef sites. The study by Komyakova and Swearer (2019), as well as others such as Osenberg et al. (2002), also found that it is common for reef fish to have density-dependent recruitment based on the presence of conspecifics (Komyakova & Swearer, 2019). Reefs that already supported populations of *T. caudimaculatus* experienced higher recruitment rates of the species over subsequent surveys compared to other sites. In addition, Jones (1984) identified that juvenile *N. celidotus* tended to aggregate into loose schools for foraging. This could have influenced the higher recruitment levels of *N. celidotus* on reef units that were in close proximity to the natural reef. *E. chloroticus* recruitment can be explained by the high abundances of *N. celidotus* on reef units in close proximity to the natural reef. *N. celidotus* are a prominent predator of *E. chloroticus* (Denny, 2005), and reef environments are typically linked with higher abundances of these (and other) predators. Therefore, the contrast in the recruitment patterns of spotty wrasse and kina can be explained by this relationship; kina may tend to preferentially settle away from reef environments (on bare substrate) to lower predation risk. In addition, *E. chloroticus* has previously been found to preferentially settle to habitats where shell is the predominant substrate (Glockner-Fagetti & Phillips, 2020), and have not been recorded to have a preference for recruitment to macroalgal-dominated habitats despite their diet and feeding behaviour.

4.3. Community Composition

High levels of structural complexity in temperate marine habitats increases the diversity of the communities that inhabit them (Charbonnel et al., 2002; Lazarus & Belmaker, 2021). Macroalgal stands provide variation in structural complexity across spatial and temporal scales, contributing to the dynamics of invertebrate and fish communities, and therefore are important in forming healthy diverse coastal marine ecosystems (Anderson, 1994; Willis & Anderson, 2003; Hüne et al., 2021). I found no significant interactions between site and period factors on species richness, Shannon-Weiner diversity, and species evenness in my Chapter 2 study. Additionally, in Chapter 3, I observed no discernible difference in the same diversity metrics based on structure, substrate, and survey factors. These results represent the absence of effect that both additional structure and proximity to natural reef sources had on the communities on artificial habitats across both studies, and points towards the influence of alternative factors in the shaping of these communities. The results conflict with several pieces of previous research that link additional structure, as well as reef proximity, with increasingly diverse communities (Vega Fernández et al., 2009; Bustamante et al., 2014; Parsons et al., 2016). However, it is likely that more time studying these communities would have provided a clearer picture of the factors driving diversity in these studies. Artificial reef communities typically become stable after one to three years in place, and given my field observations covered only the first six to seven months of community assembly, a longer study may have gleaned different results (Becker et al., 2018; Wu et al., 2019).

Community composition – interpreted by PCoA analyses in both studies – was not heavily influenced by site or period in Chapter 2, or by structure or survey in Chapter 3. Demonstrating how little the composition of ecological communities was affected by the presence of additional structure in both pieces of research. In Chapter 2 there was considerable disturbance, and therefore high levels of sedimentation, occurring around the study sites. This may have been a contributing factor in determining the communities on the islands given the significant influence sedimentation can have on community dynamics (Airoldi, 2003). Artificial reef units on bare substrate had distinct communities when compared to those on units near the natural reef edge in Chapter 3, which is consistent with the theory of island biogeography (MacArthur & Wilson, 1967), as well as further research in this area. In general, the placement of artificial reefs is thought to influence the communities that recruit to them (Bohnsack & Sutherland, 1985; Komyakova et al., 2019), and it is predicted that artificial reefs in close proximity to recruitment sources (e.g., natural reefs) will have higher colonisation rates (Strelcheck et al., 2005). Community composition did not seem to converge within the study period of Chapter 3, however in more time, there is the potential that this could occur as found by Komyakova et al. (2019).

In Chapter 2, the size distributions of three focal species did not differ by treatments. It is possible that attributes of the benthic structure in the study had an effect on this statistic. Fish and invertebrates tend to colonise shelters that are proportional to the body size of the individual (Luckhurst & Luckhurst, 1978; Eggleston & Lipcius, 1992), therefore the islands (given they are constructed with large boulders) may have provided the necessary spectrum of refugia for a range of species before additional structure was added. In Chapter 3, size distributions of several focal species were influenced by both substrate and structure variables, but each species had varying responses to these. Both *N. celidotus* and *E. chloroticus* had higher abundances of larger individuals, as well as larger mean sizes of individuals on the bare substrate reef units. This finding was consistent with previous studies in which reef substrates (macroalgal habitats) tended to support higher abundanes of juveniles and smaller individuals. The larger individuals have the ability to leave the protection of the macroalgae without as much risk of predation, and therefore can be found in higher abundances off the reef. The lack of effect that additional structure had on the size distributions of these species could be attributed to the method of SMURF deployment used in the study. Different species will recruit to SMURFs deployed at varying heights, with surface-deployed SMURFs attracting increased recruitment compared to mid-water SMURFs. I deployed my SMURF units in the midwater in an attempt to capture both surface-dwelling and more benthic species recruitment, which may have affected the recruitment of certain species, and therefore size distributions of those species.

The consistent difference in effects between the two studies seems to suggest the importance of spatial scales in the implementation of artificial marine habitats. Chapter 2 focused on two large artificial islands, and the additional structure placed on one of the islands had no observable effect on the communities that colonised them. However, additional structure and proximity to natural reefs had significant effects on a myriad of metrics studied in Chapter 3. Acknowledging the small size of the artificial reef units in Chapter 3 relative to the artificial islands in Chapter 2, we can infer that the variables tested had more significant effects on the communities in Chapter 3 due to matching the spatial scale of both the reefs and the organisms being studied. There is potential that the 'intervention' of additional structure on the islands in Chapter 2 was not large enough to cause meaningful differences to the communities surveyed.

4.4. Growth

Numerous recent studies have emphasized the potential for artificial reefs to become "ecological traps", where organisms preferentially settle to habitat that is of a lower quality, which then reduces their growth and fitness potential (Hale & Swearer, 2016, 2017; Komyakova et al., 2021; Swearer et al., 2021). Where artificial reefs are implemented as conservation strategies, it is integral to understand their effect on the growth of species that colonise them in order to determine whether they can provide viable habitats for marine communities (Hale & Swearer, 2016; Komyakova et al., 2021). The lack of significant effect that either substrate or proximity to natural reef had on the growth of common triplefin (*F. lapillum*) living on artificial reefs could reflect the potential for the creation of viable habitat for a small, highly site-attached species. The similarity in growth patterns between individuals that were occupying artificial reefs under different treatments may indicate that any additional hard-substrate habitat will provide space for an increased population of *F. lapillum* to recruit to, and therefore support healthy populations of this species. Alternatively, these results may simply confirm the hardy nature of the common triplefin as a widespread, abundant species in most shallow reef environments throughout New Zealand (Wellenreuther et al., 2007; Francis, 2016). Therefore further growth studies on an increased range of species that occupy artificial reefs is necessary to gain a more complete understanding of whether they can provide a valid option for restoration to support diverse, healthy marine communities.

4.5. Limitations

I acknowledge the limitations of this study, and the affect this has on the interpretation of the results. As this was a Master's research project, the studies were constrained by the time period available to implement and conduct the necessary field and laboratory analyses for both Chapter 2 and Chapter 3. Variable weather, as well as variable personnel availability meant that some of the surveys were not conducted at exactly the same intervals each time, and some even had to be split over multiple days, creating slightly unpaired data in Chapter 2. I analysed the data as if it was a paired series due to the type of analysis that was necessary to conduct, and therefore this should be taken in to account when interpreting the results. In addition to the limited time available to ascertain changes in communities recruiting to artificial habitats, the short time-frame may have caused the recruitment of some species to be missed in the surveys. Marine reef species have varying reproductive seasons, and the start of my research did not account for this factor. However, most species included in both studies reproduce over spring-summer, and then the larvae undergo pelagic larval development for several weeks to months, meaning most of them would be recruiting at a similar time to when my research commenced. Yet, it is still something to take into account when interpreting the results of both data chapters.

I also acknowledge that Chapter 2 was an unreplicated study following a BACIPS design, and therefore had limited statistical power when analysing the results, potentially leading to the lack of effects found in the study. It was unreplicated due to the nature of the artificial habitats that I studied as there was no possibility of more than two islands being available to research.

Chapter 3 attempted to compare between artificial reef units placed on bare substrate with those placed in close vicinity to the natural reef. However, for stronger conclusions to be drawn from this study, it would have been ideal to also collect data from the natural reef itself. Therefore allowing comparisons between two artificial reef treatments and a natural reef treatment. Additionally, I collected the specimens for the growth analyses in this chapter over a span of four weeks and multiple different dives. Ideally, these specimens would have been collected on the same day, and an equal amount of specimens would have been collected per treatment for a more reliable result.

4.6. Conclusion

To conclude, this thesis shows that supplemental vertical structure, as well as proximity to natural reef can have significant, yet variable effects on marine communities inhabiting artificial reefs. The responses to these factors are likely to be species-specific, as well as particular to the spatial scale of the artificial reef structures themselves. My thesis covers a wide range of species due to the survey design, and allows for more of an ecosystem perspective on recruitment, community composition, and growth of marine reef organisms on artificial habitats. Commonly, studies will focus on one (to a few) main species, and will often concentrate on either fish or invertebrates separately. In my research, the inclusion of a range of benthic fish and invertebrates, as well as the testing of multiple factors influencing recruitment patterns, allows for more of an ecosystem perspective on communities that colonise artificial habitats in the first six months of deployment. It highlights the importance of understanding the factors that affect recruitment for a wide range of species before implementing ecological restoration or environmental mitigation strategies that include the use of artificial marine habitats. Overall, my research has contributed to an increased understanding artificial reefs and their ability to support healthy and diverse marine ecosystems, particularly in temperate environments.

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APPENDIX A

Table A1. List of the common and scientific names of fish identified in the community surveys of Chapter 2 and Chapter 3 (Andrew, 1988; Miller, 1996; Mills et al., 2014; Francis, 2016; McMillan & Struthers, 2019; Willan et al., 2020; Beentjes, 2021; Kelly & Herr, 2022; Page et al., 2022; Froese & Pauly, 2024; WoRMS Editorial Board, 2025).

Common Name (Code)	**Scientific Name**	**Trophic Level**	**Seasonal Reproduction**	**Relationship to Macroalgae**
Spotty wrasse (STY)	*Notolabrus celidotus*	Carnivore	Spring-Summer	Indirect (forages near algae)
Banded wrasse (BPF)	*Notolabrus fucicola*	Carnivore	Spring-Summer	Indirect (forages near algae)
Blue cod (BCO)	*Parapercis colias*	Carnivore	Winter-Summer	No direct relationship
Silver sweep (SWE)	*Scorpis lineolata*	Omnivore	Spring-Summer	Indirect (feeds on algae-dwelling plankton)
Tarakihi (TAR)	*Nemadactylus macropterus*	Omnivore	Winter-Spring	No direct relationship
Blue moki (MOK)	*Latridopsis ciliaris*	Omnivore	Spring-Summer	Indirect (forages near algae)
Butterfish (BUT)	*Odax pullus*	Herbivore	Spring-Summer	Direct (feeds on macroalgae)
Yellow-eye mullet (YEM)	*Aldrichetta forsteri*	Omnivore	Spring-Summer	Indirect (forages in areas with algae)
Oblique-swimming triplefin (OST)	*Forsterygion maryannae*	Carnivore	Spring	Indirect (inhabits algae-covered surfaces)
Common triplefin (CTR)	*Forsterygion lapillum*	Carnivore	Spring-Summer	Indirect (inhabits algae-covered surfaces)
Variable triplefin (VTR)	*Forsterygion varium*	Carnivore	Spring	Indirect (inhabits algae-covered surfaces)
Mottled triplefin (MTR)	*Forsterygion malcolmi*	Carnivore	Spring-Summer	Indirect (inhabits algae-covered surfaces)
Cat's eye snail (CAT)	*Lunella smaragda*	Herbivore	Summer	Direct (feeds on macroalgae)

Tuatua (TUA)	*Paphies subtriangulata*	Filter feeder	Spring-Summer	No direct relationship
Black sea hare (BSH)	*Aplysia vaccaria*	Herbivore	Summer	Direct (feeds on macroalgae)
Tiara top shell (TTS)	*Coelotrochus tiaratus*	Herbivore	Spring-Summer	Direct (feeds on macroalgae)
Scarlet tubeworm (STU	*Galeolaria hystrix*	Filter feeder	Year-round	No direct relationship
Kina/sea urchin (KIN)	*Evechinus chloroticus*	Herbivore	Spring-Summer	Direct (feeds on macroalgae)
Saddle sea squirt (SSS)	*Cnemidocarpa bicornuta*	Filter feeder	Year-round	No direct relationship
New Zealand common cushion star (CST)	*Patiriella regularis*	Omnivore	Spring-Summer	Indirect (lives near macroalgae)
Turret shell (TSH)	*Maoricolpus roseus*	Detritivore	Year-round	No direct relationship
Ribbon worm (RBW)	*Noteonemertes novaeealandiae*	Carnivore	Unknown	No direct relationship
Eleven-armed sea star (EAS)	*Coscinasterias calamaria*	Carnivore	Spring-Summer	No direct relationship
Orange sponge (CRI)	*Crella incrustans*	Filter feeder	Year-round	No direct relationship
Cook's turban (COO)	*Cookia sulcata*	Herbivore	Spring	Direct (feeds on macroalgae)
New Zealand hermit crab (PNO)	*Pagurus novazealandiae*	Omnivore	Spring-Summer	Indirect (uses algae-covered shells)
Seven-armed sea star (SAS)	*Astrostole scabra*	Carnivore	Spring-Summer	No direct relationship
Duck's bill limpet (DBL)	*Scutus breviculus*	Herbivore	Spring-Summer	Direct (feeds on macroalgae)
Pāua/abalone (PAU)	*Haliotis iris*	Herbivore	Autumn-Winter	Direct (feeds on macroalgae)
Decorator crab (NOT)	*Notomithrax sp.*	Omnivore	Spring	Indirect (uses macroalgae for camouflage)
Common sea cucumber (SMO)	*Stichopus mollis*	Detritivore	Year-round	No direct relationship
Vase sea squirt (INT)	*Ciona intestinalis*	Filter feeder	Year-round	No direct relationship
Top shells (TRO)	*Trochidae sp.*	Herbivore	Spring-Summer	Direct (feeds on macroalgae)
Big-belly seahorse (HIP)	*Hippocampus abdominalis*	Carnivore	Spring-Summer	Indirect (lives near macroalgae)

Red rock crab (RRC)	*Giunusia chabrus*	Omnivore	Spring	Indirect (forages in algae-covered areas)
Purple shore crab (PSC)	*Hemigrapsus nudus*	Omnivore	Spring	Indirect (forages in algae-covered areas)
Dorid nudibranch (GAU)	*Atagema carinata*	Carnivore	Spring-Summer	Indirect (feeds on sponges near algae)
Colonial tunicate (ABE)	*Aplidium benhami*	Filter feeder	Year-round	No direct relationship
Sea perch (PER)	*Helicolenus percoides*	Carnivore	Spring-Summer	No direct relationship
Māori octopus (OPU)	*Macroctopus maorum*	Carnivore	Year-round	No direct relationship
Barnacle sp. (CIR)	*Cirripedia sp.*	Filter feeder	Year-round	No direct relationship
Butterfly chiton (CRY)	*Cryptoconchus porosus*	Herbivore	Spring	Direct (feeds on macroalgae)
Reef starfish (RST)	*Stichaster australis*	Carnivore	Year-round	No direct relationship

Table A2. General linear model results for abundances of each species. Species codes used can be found in Table A1. Significant terms shown in bold.

Species	Term	Estimate	Std_Error	Z_value	P_value
STY	**Structure**	**0.253**	**0.119**	**2.120**	**0.034**
	Substrate	**0.370**	**0.117**	**3.178**	**0.001**
	Survey	**-0.041**	**0.024**	**-1.729**	**0.084**
	Structure * Substrate	**-0.530**	**0.159**	**-3.325**	**0.001**
	Structure * Survey	-0.008	0.032	-0.242	0.809
	Substrate * Survey	-0.009	0.031	-0.299	0.765
	Structure * Substrate * Survey	**0.143**	**0.041**	**3.443**	**0.001**
SWE	Structure	3.003	2.373	1.266	0.206
	Substrate	0.682	3.318	0.206	0.837
	Survey	0.630	0.398	1.582	0.114

Species	Term	Estimate	Std_Error	Z_value	P_value
	Structure * Substrate	-3.003	4.385	-0.685	0.493
	Structure * Survey	-0.804	0.528	-1.522	0.128
	Substrate * Survey	-0.455	0.722	-0.630	0.528
	Structure * Substrate * Survey	0.804	1.002	0.803	0.422
BPF	Structure	-1.162	1.306	-0.890	0.373
	Substrate	**1.826**	**0.956**	**1.910**	**0.056**
	Survey	-0.115	0.242	-0.476	0.634
	Structure * Substrate	1.100	1.434	0.767	0.443
	Structure * Survey	0.417	0.321	1.296	0.195
	Substrate * Survey	-0.134	0.272	-0.492	0.622
	Structure * Substrate * Survey	-0.476	0.373	-1.276	0.202
BCO	Structure	-0.216	0.416	-0.519	0.604
	Substrate	-0.748	0.609	-1.229	0.219
	Survey	-0.099	0.073	-1.365	0.172
	Structure * Substrate	-0.489	1.165	-0.420	0.675
	Structure * Survey	-0.084	0.119	-0.707	0.480
	Substrate * Survey	-0.348	0.213	-1.634	0.102
	Structure * Substrate * Survey	-0.098	0.461	-0.213	0.831
TAR	Structure	3.417	4.409	0.775	0.438
	Substrate	-14.996	9738.696	-0.002	0.999
	Survey	0.630	0.796	0.791	0.429
	Structure * Substrate	-3.417	13772.595	0.000	1.000
	Structure * Survey	-0.630	0.897	-0.702	0.483
	Substrate * Survey	-0.630	2500.666	0.000	1.000
	Structure * Substrate * Survey	0.630	3536.476	0.000	1.000

Species	Term	Estimate	Std_Error	Z_value	P_value
BUT	Structure	0.000	37437.793	0.000	1.000
	Substrate	0.000	37437.793	0.000	1.000
	Survey	0.000	6797.515	0.000	1.000
	Structure * Substrate	21.403	45851.745	0.000	1.000
	Structure * Survey	0.000	9613.138	0.000	1.000
	Substrate * Survey	0.000	9613.138	0.000	1.000
	Structure * Substrate * Survey	-0.630	11773.641	0.000	1.000
YEM	Structure	19.925	2172.997	0.009	0.993
	Substrate	0.000	3073.081	0.000	1.000
	Survey	0.000	557.974	0.000	1.000
	Structure * Substrate	-19.925	3763.740	-0.005	0.996
	Structure * Survey	-0.057	557.974	0.000	1.000
	Substrate * Survey	0.000	789.094	0.000	1.000
	Structure * Substrate * Survey	0.057	966.439	0.000	1.000
OST	Structure	0.000	8353.501	0.000	1.000
	Substrate	16.064	5906.818	0.003	0.998
	Survey	0.000	1516.731	0.000	1.000
	Structure * Substrate	3.014	8353.501	0.000	1.000
	Structure * Survey	0.000	2144.981	0.000	1.000
	Substrate * Survey	0.175	1516.731	0.000	1.000
	Structure * Substrate * Survey	-0.349	2144.981	0.000	1.000
MOK	Structure	0.000	276629.952	0.000	1.000
	Substrate	0.000	276629.952	0.000	1.000
	Survey	0.000	50227.219	0.000	1.000
	Structure * Substrate	0.000	391213.831	0.000	1.000

Species	Term	Estimate	Std_Error	Z_value	P_value
	Structure * Survey	0.000	71032.014	0.000	1.000
	Substrate * Survey	0.000	71032.014	0.000	1.000
	Structure * Substrate * Survey	0.000	100454.438	0.000	1.000
CTR	Structure	-0.091	0.276	-0.328	0.743
	Substrate	-0.012	0.282	-0.042	0.967
	Survey	**-0.168**	**0.058**	**-2.890**	**0.004**
	Structure * Substrate	0.404	0.388	1.040	0.298
	Structure * Survey	0.093	0.078	1.199	0.230
	Substrate * Survey	0.016	0.081	0.196	0.844
	Structure * Substrate * Survey	-0.191	0.112	-1.700	0.089
MTR	Structure	0.443	0.490	0.905	0.366
	Substrate	**1.327**	**0.521**	**2.547**	**0.011**
	Survey	0.052	0.090	0.580	0.562
	Structure * Substrate	**-2.024**	**0.843**	**-2.402**	**0.016**
	Structure * Survey	-0.128	0.127	-1.009	0.313
	Substrate * Survey	**-0.681**	**0.183**	**-3.731**	**0.000**
	Structure * Substrate * Survey	**0.489**	**0.272**	**1.799**	**0.072**
CAT	**Structure**	**-0.824**	**0.271**	**-3.035**	**0.002**
	Substrate	0.092	0.234	0.395	0.693
	Survey	**-0.118**	**0.047**	**-2.505**	**0.012**
	Structure * Substrate	-0.107	0.403	-0.265	0.791
	Structure * Survey	**0.171**	**0.071**	**2.414**	**0.016**
	Substrate * Survey	-0.004	0.065	-0.065	0.948
	Structure * Substrate * Survey	-0.142	0.109	-1.304	0.192
TUA	Structure	0.000	276629.952	0.000	1.000

Species	**Term**	**Estimate**	**Std_Error**	**Z_value**	**P_value**
	Substrate	0.000	276629.952	0.000	1.000
	Survey	0.000	50227.219	0.000	1.000
	Structure * Substrate	0.000	391213.831	0.000	1.000
	Structure * Survey	0.000	71032.014	0.000	1.000
	Substrate * Survey	0.000	71032.014	0.000	1.000
	Structure * Substrate * Survey	0.000	100454.438	0.000	1.000
VTR	Structure	-0.446	0.484	-0.921	0.357
	Substrate	**0.976**	**0.414**	**2.357**	**0.018**
	Survey	0.106	0.082	1.295	0.195
	Structure * Substrate	-0.134	0.600	-0.223	0.824
	Structure * Survey	**0.190**	**0.111**	**1.710**	**0.087**
	Substrate * Survey	-0.099	0.102	-0.976	0.329
	Structure * Substrate * Survey	-0.046	0.141	-0.324	0.746
BSH	Structure	0.000	276629.952	0.000	1.000
	Substrate	0.000	276629.952	0.000	1.000
	Survey	0.000	50227.219	0.000	1.000
	Structure * Substrate	0.000	391213.831	0.000	1.000
	Structure * Survey	0.000	71032.014	0.000	1.000
	Substrate * Survey	0.000	71032.014	0.000	1.000
	Structure * Substrate * Survey	0.000	100454.438	0.000	1.000
TTS	Structure	0.000	276629.952	0.000	1.000
	Substrate	0.000	276629.952	0.000	1.000
	Survey	0.000	50227.219	0.000	1.000
	Structure * Substrate	0.000	391213.831	0.000	1.000
	Structure * Survey	0.000	71032.014	0.000	1.000

Species	**Term**	**Estimate**	**Std_Error**	**Z_value**	**P_value**
	Substrate * Survey	0.000	71032.014	0.000	1.000
	Structure * Substrate * Survey	0.000	100454.438	0.000	1.000
STU	Structure	-0.095	0.153	-0.621	0.535
	Substrate	**-1.887**	**0.283**	**-6.667**	**0.000**
	Survey	**0.104**	**0.026**	**3.915**	**0.000**
	Structure * Substrate	**2.137**	**0.323**	**6.612**	**0.000**
	Structure * Survey	**0.071**	**0.036**	**1.969**	**0.049**
	Substrate * Survey	0.071	0.066	1.081	0.280
	Structure * Substrate * Survey	**-0.246**	**0.076**	**-3.231**	**0.001**
KIN	**Structure**	**-1.207**	**0.207**	**-5.829**	**0.000**
	Substrate	**-3.631**	**0.495**	**-7.329**	**0.000**
	Survey	**0.064**	**0.028**	**2.245**	**0.025**
	Structure * Substrate	0.559	0.941	0.594	0.552
	Structure * Survey	**0.178**	**0.048**	**3.737**	**0.000**
	Substrate * Survey	**0.327**	**0.105**	**3.130**	**0.002**
	Structure * Substrate * Survey	-0.308	0.205	-1.501	0.133
SSS	Structure	0.000	37437.793	0.000	1.000
	Substrate	0.000	37437.793	0.000	1.000
	Survey	0.000	6797.515	0.000	1.000
	Structure * Substrate	19.064	45851.745	0.000	1.000
	Structure * Survey	0.000	9613.138	0.000	1.000
	Substrate * Survey	0.000	9613.138	0.000	1.000
	Structure * Substrate * Survey	0.175	11773.641	0.000	1.000
CST	Structure	-0.195	0.245	-0.797	0.425
	Substrate	**-0.493**	**0.251**	**-1.964**	**0.050**

Species	Term	Estimate	Std_Error	Z_value	P_value
	Survey	**-0.122**	**0.047**	**-2.582**	**0.010**
	Structure * Substrate	0.303	0.360	0.843	0.399
	Structure * Survey	0.047	0.067	0.691	0.490
	Substrate * Survey	**0.143**	**0.067**	**2.147**	**0.032**
	Structure * Substrate * Survey	-0.099	0.096	-1.031	0.303
TSH	Structure	0.000	276629.952	0.000	1.000
	Substrate	0.000	276629.952	0.000	1.000
	Survey	0.000	50227.219	0.000	1.000
	Structure * Substrate	0.000	391213.831	0.000	1.000
	Structure * Survey	0.000	71032.014	0.000	1.000
	Substrate * Survey	0.000	71032.014	0.000	1.000
	Structure * Substrate * Survey	0.000	100454.438	0.000	1.000
RBW	Structure	0.000	276629.952	0.000	1.000
	Substrate	0.000	276629.952	0.000	1.000
	Survey	0.000	50227.219	0.000	1.000
	Structure * Substrate	0.000	391213.831	0.000	1.000
	Structure * Survey	0.000	71032.014	0.000	1.000
	Substrate * Survey	0.000	71032.014	0.000	1.000
	Structure * Substrate * Survey	0.000	100454.438	0.000	1.000
EAS	Structure	0.887	0.668	1.329	0.184
	Substrate	1.359	0.863	1.576	0.115
	Survey	0.069	0.132	0.523	0.601
	Structure * Substrate	**-2.818**	**1.287**	**-2.190**	**0.029**
	Structure * Survey	-0.138	0.170	-0.810	0.418
	Substrate * Survey	**-0.883**	**0.355**	**-2.489**	**0.013**

Species	Term	Estimate	Std_Error	Z_value	P_value
	Structure * Substrate * Survey	**0.836**	**0.443**	**1.889**	**0.059**
CRI	Structure	0.000	276629.952	0.000	1.000
	Substrate	0.000	276629.952	0.000	1.000
	Survey	0.000	50227.219	0.000	1.000
	Structure * Substrate	0.000	391213.831	0.000	1.000
	Structure * Survey	0.000	71032.014	0.000	1.000
	Substrate * Survey	0.000	71032.014	0.000	1.000
	Structure * Substrate * Survey	0.000	100454.438	0.000	1.000
COO	Structure	-4.523	4.322	-1.046	0.295
	Substrate	-1.106	2.112	-0.524	0.601
	Survey	-0.371	0.466	-0.795	0.426
	Structure * Substrate	5.124	4.785	1.071	0.284
	Structure * Survey	1.001	0.922	1.085	0.278
	Substrate * Survey	0.371	0.624	0.595	0.552
	Structure * Substrate * Survey	-1.058	1.066	-0.992	0.321
PNO	Structure	-0.192	0.355	-0.539	0.590
	Substrate	**-1.933**	**0.642**	**-3.009**	**0.003**
	Survey	-0.033	0.060	-0.543	0.587
	Structure * Substrate	-0.356	1.157	-0.307	0.759
	Structure * Survey	-0.063	0.096	-0.656	0.512
	Substrate * Survey	0.008	0.168	0.050	0.960
	Structure * Substrate * Survey	-0.087	0.326	-0.268	0.789
SAS	Structure	1.386	2.102	0.660	0.510
	Substrate	-18.403	5906.817	-0.003	0.998
	Survey	-0.630	0.796	-0.791	0.429

Species	Term	Estimate	Std_Error	Z_value	P_value
	Structure * Substrate	18.103	5906.818	0.003	0.998
	Structure * Survey	0.000	0.890	0.000	1.000
	Substrate * Survey	0.630	1516.731	0.000	1.000
	Structure * Substrate * Survey	-0.488	1516.731	0.000	1.000
DBL	Structure	13.436	3582.666	0.004	0.997
	Substrate	17.915	3582.666	0.005	0.996
	Survey	0.000	919.944	0.000	1.000
	Structure * Substrate	-13.684	3582.667	-0.004	0.997
	Structure * Survey	0.814	919.944	0.001	0.999
	Substrate * Survey	-0.074	919.944	0.000	1.000
	Structure * Substrate * Survey	-0.595	919.944	-0.001	0.999
PAU	Structure	0.000	13772.594	0.000	1.000
	Substrate	18.450	9738.695	0.002	0.998
	Survey	0.000	2500.666	0.000	1.000
	Structure * Substrate	1.657	13772.594	0.000	1.000
	Structure * Survey	0.000	3536.476	0.000	1.000
	Substrate * Survey	0.175	2500.666	0.000	1.000
	Structure * Substrate * Survey	-0.622	3536.476	0.000	1.000
NOT	Structure	0.000	8353.501	0.000	1.000
	Substrate	15.977	5906.817	0.003	0.998
	Survey	0.000	1516.731	0.000	1.000
	Structure * Substrate	2.538	8353.501	0.000	1.000
	Structure * Survey	0.000	2144.981	0.000	1.000
	Substrate * Survey	0.447	1516.731	0.000	1.000
	Structure * Substrate * Survey	-0.244	2144.981	0.000	1.000

Species	Term	Estimate	Std_Error	Z_value	P_value
SMO	Structure	2.744	1.978	1.387	0.165
	Substrate	-0.124	2.355	-0.052	0.958
	Survey	0.175	0.426	0.410	0.682
	Structure * Substrate	-2.051	2.671	-0.768	0.443
	Structure * Survey	-0.395	0.478	-0.828	0.408
	Substrate * Survey	0.241	0.523	0.461	0.645
	Structure * Substrate * Survey	0.395	0.605	0.653	0.514
INT	Structure	3.798	2.470	1.537	0.124
	Substrate	-15.094	5906.817	-0.003	0.998
	Survey	0.630	0.460	1.370	0.171
	Structure * Substrate	-3.798	8353.501	0.000	1.000
	Structure * Survey	-0.543	0.490	-1.109	0.267
	Substrate * Survey	-0.630	1516.731	0.000	1.000
	Structure * Substrate * Survey	0.543	2144.981	0.000	1.000
OPU	Structure	6.823	4.841	1.410	0.159
	Substrate	-13.272	9738.696	-0.001	0.999
	Survey	1.087	0.836	1.299	0.194
	Structure * Substrate	-6.823	13772.595	0.000	1.000
	Structure * Survey	-1.717	1.008	-1.703	0.089
	Substrate * Survey	-1.087	2500.666	0.000	1.000
	Structure * Substrate * Survey	1.717	3536.476	0.000	1.000
TRO	**Structure**	**-7.025**	**3.332**	**-2.108**	**0.035**
	Substrate	-0.969	0.690	-1.404	0.160
	Survey	-0.152	0.150	-1.017	0.309
	Structure * Substrate	**7.375**	**3.383**	**2.180**	**0.029**

Species	Term	Estimate	Std_Error	Z_value	P_value
	Structure * Survey	**1.239**	**0.610**	**2.031**	**0.042**
	Substrate * Survey	**0.554**	**0.177**	**3.133**	**0.002**
	Structure * Substrate * Survey	**-1.228**	**0.622**	**-1.975**	**0.048**
HIP	Structure	0.000	37437.793	0.000	1.000
	Substrate	0.000	37437.793	0.000	1.000
	Survey	0.000	6797.515	0.000	1.000
	Structure * Substrate	21.403	45851.745	0.000	1.000
	Structure * Survey	0.000	9613.138	0.000	1.000
	Substrate * Survey	0.000	9613.138	0.000	1.000
	Structure * Substrate * Survey	-0.630	11773.641	0.000	1.000
RRC	Structure	0.000	22707.169	0.000	1.000
	Substrate	20.105	16056.393	0.001	0.999
	Survey	0.000	4122.901	0.000	1.000
	Structure * Substrate	-20.105	27810.489	-0.001	0.999
	Structure * Survey	0.000	5830.663	0.000	1.000
	Substrate * Survey	0.000	4122.901	0.000	1.000
	Structure * Substrate * Survey	0.000	7141.074	0.000	1.000
PSC	Structure	0.000	22707.169	0.000	1.000
	Substrate	19.412	16056.394	0.001	0.999
	Survey	0.000	4122.901	0.000	1.000
	Structure * Substrate	-19.412	27810.489	-0.001	0.999
	Structure * Survey	0.000	5830.663	0.000	1.000
	Substrate * Survey	0.000	4122.901	0.000	1.000
	Structure * Substrate * Survey	0.000	7141.074	0.000	1.000
GAU	Structure	0.000	37437.793	0.000	1.000

Species	Term	Estimate	Std_Error	Z_value	P_value
	Substrate	21.403	26472.517	0.001	0.999
	Survey	0.000	6797.515	0.000	1.000
	Structure * Substrate	-21.403	45851.745	0.000	1.000
	Structure * Survey	0.000	9613.138	0.000	1.000
	Substrate * Survey	-0.630	6797.515	0.000	1.000
	Structure * Substrate * Survey	0.630	11773.641	0.000	1.000
ABE	Structure	0.000	22707.169	0.000	1.000
	Substrate	18.071	16056.394	0.001	0.999
	Survey	0.000	4122.901	0.000	1.000
	Structure * Substrate	-100.138	29459.118	-0.003	0.997
	Structure * Survey	0.000	5830.663	0.000	1.000
	Substrate * Survey	0.488	4122.901	0.000	1.000
	Structure * Substrate * Survey	16.608	6616.693	0.003	0.998
PER	Structure	-20.403	16056.393	-0.001	0.999
	Substrate	-20.403	16056.394	-0.001	0.999
	Survey	-0.630	0.796	-0.791	0.429
	Structure * Substrate	36.398	22707.170	0.002	0.999
	Structure * Survey	0.630	4122.901	0.000	1.000
	Substrate * Survey	0.630	4122.901	0.000	1.000
	Structure * Substrate * Survey	0.000	5830.663	0.000	1.000
RST	Structure	17.162	5906.817	0.003	0.998
	Substrate	16.064	5906.818	0.003	0.998
	Survey	0.000	1516.731	0.000	1.000
	Structure * Substrate	-17.162	5906.818	-0.003	0.998
	Structure * Survey	0.175	1516.731	0.000	1.000

Species	Term	Estimate	Std_Error	Z_value	P_value
	Substrate * Survey	0.175	1516.731	0.000	1.000
	Structure * Substrate * Survey	-0.175	1516.731	0.000	1.000