Combating biodiversity decline in coastal waters with intertidal eco-engineering and Green Gravel

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science
in
Biological Science

at Massey University, Albany, New Zealand

Ella Lis

2023

General Abstract

Biodiversity generates a multitude of benefits for humanity, such as food provision, maintenance of clean air and water, climate regulation, and soil erosion prevention. Widespread human activities in the oceans continue to cause declines in species diversity and abundance, threatening ecosystem services and ecological stability. The persistence of biogenic habitats emerges as a critical countermeasure against biodiversity loss and the preservation of ecosystem health. This thesis examines the effects of engineered coastal structures for rockpool biodiversity and a kelp forest restoration technique termed Green Gravel. In Chapter Two, I analysed differences in the biodiversity of natural and artificial rockpools, including riprap and concrete structures. Riprap and concrete exhibited comparable taxa richness and functional group prevalence to natural substrates; however disturbances, particularly smothering, significantly reduced taxa richness in all habitats. Distinct taxa associations emerged in response to disturbance and habitat type with encrusting algae and grazers favouring riprap habitats with normal pool conditions, and surprisingly, artificial structures showed resistance to nonindigenous species. This chapter underscores the importance of microhabitat diversity in supporting species and ecosystem health on artificial structures, guiding eco-engineering strategies to optimize their ecological value while accommodating inevitable urbanization. In Chapter Three, I explore the efficacy of different Green Gravel methodologies for restoring collapsed *Ecklonia radiata* forests and investigate the impact of environmental conditions on gravel retention and sporophyte length. Gluing gravel to the substrate significantly improved gravel retention, and interestingly sporophyte lengths varied between attachment methods, with sporophytes on placed gravel initially being 100mm shorter than sporophytes on glued Green Gravel. Notably, these initial differences in sporophyte length between placed and glued Green Gravel disappeared by the end of the experiment indicating that placed Green Gravel experienced greater growth toward the end of the experiment. Despite having 40% lower retention than glued Green Gravel, 20% of placed Green Gravel were still present after 14-months offering significant restoration potential, especially for resource-restricted community groups. Due to the relative ease of implementation, Green Gravel offers promise as a tool for community-led active marine restoration and ameliorating some of the challenges our declining kelp forests face. Addressing these biodiversity declines requires immediate and collective endeavors to facilitate transformative changes that foster nature conservation, restoration, and sustainable resource utilization, all while striving to achieve overarching global societal objectives.

Acknowledgements

I would like to extend my sincere gratitude to everyone who has provided support and guidance during my journey through my Master's degree. It is with immense appreciation that I begin with acknowledging my supervisor, David Aguirre. Your unwavering belief in my potential, your continuous encouragement, and your insightful guidance has guided my path through university. Thank you for skippering most of our Green Gravel fieldtrips, I hope we can get you in the water soon to finally show you in person how our little kelplings are doing. I have gained a great deal from your mentorship, and I wish you all the best as you enter this new phase of parenthood with Libby, Māri, and of course Tiki.

I want to acknowledge those who assisted with data collection and fieldwork - Nina Lis, John Lis and Odette Howarth with the rockpool experiment and Hochang Yoo, Emma Betty, Dennis Van Hulten and Marara Van Buuren with the Green Gravel experiment. Your support was essential and is greatly appreciated.

A profound and special acknowledgment is due to Glenn Edney and Hamish Clueard. Your unwavering support and collaboration in the Tutukaka Kelp Regeneration project, under Te Wairua O Te Moananui, resonate deeply. The journey you've undertaken to rejuvenate Tutukaka's harbour and your willingness to pioneer the Green Gravel technique, despite its nascent stage and our ever-evolving understanding, exemplify the spirit of innovation and partnership we have made.

Of course a special shout-out for my parents, John and Wanda Lis. It is through your unwavering encouragement, guidance, and steadfast support that I've found the courage to wholeheartedly chase my dreams and pursue my passions, and for that, I am eternally grateful.

Last but definitely not least, I want to thank Beau Masters, my No.1 dive buddy, research assistant, and fiancé. Your consistent support and encouragement has been a cornerstone to all my research endeavours, and I am truly appreciative. Thank you!

I am grateful for the scholarship and funding that supported my thesis. My research was supported by a Rutherford Discovery Fellowship (MAU1904) awarded to J. D. Aguirre.

Table of Contents

Chapter One: General Introduction

1.1 Rationale for study

Biodiversity loss in our coastal seas

The Convention on Biological Diversity defines biodiversity as the variability among living organisms from all sources, encompassing diversity within species, between species, and within ecosystems (Díaz et al. 2019). In turn, biodiversity generates a multitude of benefits for humanity, including ecosystem services, economic value, scientific insights, and cultural significance (Beaumont et al. 2008, Knapp et al. 2017). These services encompass vital functions such as food provision, maintenance of clean air and water, climate regulation, and soil erosion prevention (Cardinale 2011, Cardinale et al. 2012, Díaz et al. 2019). Traditionally, studies of biodiversity have sought to quantify community composition, and determine abiotic and biotic factors that influence species coexistence with emphasis on the regulation and maintenance of diversity (Hillebrand and Matthiessen 2009). Recently, the focus has shifted towards examining the emergent properties of biodiversity and in particular its effect on ecosystem functions. Within this context, diversity emerges as a driver of ecosystem processes, and the intricate interplay between biodiversity and ecosystem productivity, stability, and functionality has yielded significant advancements in understanding (Tilman 1994, Loreau et al. 2001, Hughes et al. 2008, Hillebrand and Matthiessen 2009).

Widespread human activities in the oceans continue to cause declines in species diversity and abundance, threatening ecosystem services and ecological stability (Gibson et al. 2007, Butchart et al. 2010, Firth et al. 2016b). The primary drivers of shifts in biodiversity include changes in land and sea utilisation, direct exploitation of organisms, pollution, climate change, and the encroachment of non-native species (Kingsford et al. 2009, Smith et al. 2023). These drivers are interconnected through a complex web of direct and indirect effects, influenced by societal values and behaviors. Biodiversity loss in coastal oceans is most concentrated within intertidal and shallow coastal zones, where human activities are most intense, including urban centers, shipping lanes, and areas marked by prevalent fishing, aquaculture, and coastal development (Floerl et al. 2021). Addressing this decline requires collective endeavors to facilitate transformative changes that foster nature conservation, restoration, and sustainable resource utilization, all while striving to achieve overarching global societal objectives.

Understanding how global change impacts various ecosystems and their biodiversity is crucial for ensuring the sustainable provision of goods and services (Beaumont et al. 2008, McLeod and Leslie 2009, Bennett et al. 2016, Knapp et al. 2017, Díaz et al. 2019, Kriegisch et al. 2019), while ensuring proper ecosystem function (Firth et al. 2013a, Aguilera et al. 2014, Firth et al. 2014b). Maintaining biogenic habitats plays an important role in reducing biodiversity loss and preserving ecosystem health (Thrush et al. 2001, Morrison et al. 2014). Biogenic habitats are biodiversity hotspots (Perkol-Finkel et al. 2012, Dafforn et al. 2015, Teagle et al. 2017, Strain et al. 2018), created and maintained by living organisms, ranging from expansive structures including coral reefs, kelp forests, seagrass beds, and mangrove forests to more localized formations such as barnacles, bivalves and turf-forming algae. These habitats not only provide refuge and resources for diverse species but also facilitate a range of ecosystem functions that contribute to overall stability and productivity (Barbier et al. 2011, Bennett et al. 2016, Bulleri et al. 2018). The degradation and loss of biogenic habitats can initiate cascading effects on affiliated species and ecosystem functions, therefore, maintaining biogenic habitats is central for implementing effective conservation and management strategies to safeguard biodiversity and ecosystem services in the face of ongoing global changes (Bellwood et al. 2004, Edgar et al. 2014).

Eco-engineering of intertidal habitats

Intertidal habitats are highly productive, biodiverse habitats that provide ecosystem services including shoreline protection, water filtration, nutrient cycling and carbon sequestration. However, these habitats are increasingly susceptible to anthropogenic impacts, such as coastal development and pollution (Thomalla and Vincent 2003, Bulleri and Chapman 2004, Cuadrado et al. 2005, Zyserman et al. 2005, Scyphers et al. 2011, Temmerman et al. 2013). Coastal hardening, involving artificial reinforcement of soft, unconsolidated coastlines with hard features, primarily focuses on safeguarding urban settlements from erosion (Firth et al. 2016a) and is rapidly becoming the predominant coastal substrate worldwide (Chapman and Underwood 2011, Firth 2011, Firth et al. 2013a, Dafforn et al. 2015, Airoldi et al. 2021). Coastal infrastructure, such as groynes, sea walls, marinas, ports, and wharfs, are typically constructed in the intertidal and adjacent subtidal zone to support recreational and commercial activities (Bulleri and Chapman 2010, Chapman and Underwood 2011, Ido and Shimrit 2015, Firth et al. 2016a, Strain et al. 2018, Firth et al. 2020). Coastal urbanization and hardening alter the marine ecosystem by modifying near-shore water currents, which transport suspended organic material and chemical pollutants, introducing novel artificial surfaces into shallow-water and intertidal habitats, as well as smothering existing environments, leading to species and habitat loss and consequent reduction in overall biodiversity (Benedetti-Cecchi et al. 2001, Bulleri and Chapman 2004, Zyserman et al. 2005, Mangialajo et al. 2008, Martins et al. 2009).

In response to the challenges presented by the transformation of coastal environments, eco-engineering has emerged as a promising avenue for restoring, enhancing, and managing intertidal habitats, striking a balance between ecological resilience and human demands (Bergen et al. 2001, Firth et al. 2016a). Eco-engineering entails integrating ecological principles into infrastructure design and has demonstrated efficacy across terrestrial and marine contexts (Chapman and Underwood 2011, Francis and Lorimer 2011). In marine habitats, eco-engineering has been employed to create and restore intertidal habitats, improve artificial reefs, restore degraded ecosystems, and enhance ecosystem services such as biodiversity, water quality, and coastal protection (Browne and Chapman 2011, Firth et al. 2014b, Dafforn et al. 2015, Mayer-Pinto et al. 2017, Chapman et al. 2018, Strain et al. 2021). The field of eco-engineering is expanding, with numerous studies focusing on various eco-engineering techniques in the intertidal zone (Menge et al. 1983, Chapman and Blockley 2009, Chapman 2012, Perkol-Finkel et al. 2012, Browne and Chapman 2014, Ng et al. 2015, Mayer-Pinto et al. 2017, Strain et al. 2020, Salauddin et al. 2021). These strategies aspire to integrate marine life into constructed environments by manipulating substrate composition, surface topography, and complexity, often mirroring natural rockpools with water-retaining features (Browne and Chapman 2011, Firth et al. 2016a). Consequently, eco-engineering in intertidal habitats may provide innovative and sustainable solutions that support biodiversity in the face of human-induced modifications.

The effectiveness of an eco-engineered structure depends on its tailored design to site-specific conditions. Elements such as materials, complexity, resilience, size, and orientation significantly influence the performance of eco-engineered substrates in comparison to natural counterparts (Perkol-Finkel and Benayahu 2004). Incorporating microhabitats and adding surface complexity to infrastructure designs during the initial phases of construction will maximize the effectiveness of an eco-engineered structure in an environment (Firth et al. 2013b). Nonetheless, existing structures can be retrofitted by introducing more microhabitats to enhance indigenous biodiversity (Chapman and Blockley 2009, Dugan et al. 2011, Perkol-Finkel et al. 2012, Aguilera et al. 2014, Browne and Chapman 2014, Dafforn et al. 2015, Ng et al. 2015). This dynamic approach ensures the continued harmonization of human development and ecological sustainability.

Restoration of eco-engineering species

In contrast, ecosystem engineering species are species that modify, maintain, and/or create habitats, for other species either directly or indirectly (Jones et al. 1994). Ecosystem engineers possess the capacity to alter local environmental attributes through structural engineering, abiotic modulation, and biotic interactions, thereby influencing resource distribution and biodiversity (Jones et al. 2010, Layton et al. 2019b). Unfortunately, escalating human activities have culminated in the decline and in some cases the disappearance of many ecosystem engineering species, including mangroves, oyster and coral reefs, and kelp forests, threatening the existence of these important ecosystems (Fujita 2011, Johnson et al. 2011, Moy and Christie 2012, Krumhansl et al. 2016, Blamey and Bolton 2018, Wernberg et al. 2019b, Filbee-Dexter et al. 2020, Tait et al. 2021, Wing et al. 2022). Consequently, the loss of these ecosystems precipitates a dramatic reduction in biodiversity and ecosystem productivity (Ling et al. 2009, Scyphers et al. 2011, Filbee-Dexter and Scheibling 2014, Bennett et al. 2016, Krumhansl et al. 2016, Heron et al. 2017, Arranz et al. 2022).

Considering their pivotal roles in shaping habitats and driving ecological dynamics, restoration of threatened ecosystem engineering species is critical. The restoration of these species can be approached via active or passive strategies. Active restoration involves direct human intervention to transplant or rebuild eco-engineering species in degraded areas, while passive restoration relies on natural processes and the promotion of natural recovery through the reduction of human impacts (Walters and Holling 1990, Eger et al. 2022a). The choice between passive and active restoration depends on a careful assessment of the specific ecosystem, the extent and severity of degradation, resource availability, and restoration project objectives (Eger et al. 2022a).

Kelp forests dominate temperate and sub-polar coastlines globally, often consisting of a single species of Laminarian kelp (Wernberg et al. 2019a). Kelp are ecosystem engineers (Jones 2014), responsible for supporting incredibly diverse, structurally complex, and highly productive coastal ecosystems by providing refuge, sustenance, and nursery grounds for an extensive array of organisms (Steneck et al. 2002, Teagle et al. 2017, Layton et al. 2019b, Arranz et al. 2022). Furthermore, kelp modify local abiotic variables, such as light exposure, water currents, and sediment deposition, all of which influence the ecosystem's stability (Eckman et al. 1989, Layton et al. 2019a, Layton et al. 2019b). These kelp forests aid coastal resilience, mitigating the impact of wave energy and stabilizing seafloors, thereby curbing coastal erosion and infrastructure damage (Blamey and Bolton 2018). Additionally, kelp forests hold a vital role in marine ecosystems by sequestering carbon dioxide from the atmosphere and contributing to oxygen production through photosynthesis (Velimirov et al. 1977, Bulleri et al. 2002, Abdullah et al. 2017, Blamey and Bolton 2018, Filbee-Dexter et al. 2022). High structural complexity, particularly within the kelp holdfast, fosters remarkable diversity (Anderson et al. 2005, Bennett et al. 2016, Arranz et al. 2022). As such, the prosperity of temperate rocky reef ecosystems is often deeply interconnected with the population dynamics of a single ecosystem engineering species.

Global observations of persistent kelp loss with limited natural recovery (Martínez et al. 2018, Coleman et al. 2020, Fredriksen et al. 2020), encourage the use of active restoration for kelp forests, if feasible and appropriate, to prevent further loss and enhance population resilience (Aitken and Whitlock 2013, Fredriksen et al. 2020, Cebrian et al. 2021, Gleason et al. 2021, Eger et al. 2022b). Techniques for active restoration vary depending on the species and the specific habitat, but may include transplantation of adult individuals or juveniles, as well as the use of artificial structures to provide a substrate for the establishment of new populations (Eger et al. 2022a). Despite progress in the field of kelp restoration in recent years, several areas require further exploration. Firstly, there is a need to explore the optimal techniques for successful restoration, considering factors such as site selection, substrate suitability, and the use of different restoration methods (e.g., transplanting, artificial structures, environmental management). Knowledge of the most effective methods under varying environmental contexts will heighten the success rates of restoration endeavours. Concurrently, rigorous monitoring of restoration outcomes is essential to evaluate their effectiveness, track shifts in ecological communities, identify potential limitations, and guide future management strategies (Eger et al. 2022a).

Marine eco-engineering and restoration in Aotearoa, New Zealand.

New Zealand has a long legacy of active restoration on land, with many national and grass-roots initiatives to remove pests and reforest disturbed areas. Conversely, marine restoration is often neglected or ignored. Even if we consider New Zealand's Marine Protected Area reputation and legacy, the 0.4% of area protected in New Zealand waters pales in comparison with the area of terrestrial land under formal protection (Cieraad et al. 2015, Davies et al. 2018). There is no doubt that the level of complexity for marine restoration out-weighs efforts in terrestrial restoration (Norse and Crowder 2005, Beaumont et al. 2008, Gleason et al. 2021). On land, restoration efforts are often more accessible, familiar, and easier to understand, whereas in a marine environment there are barriers to participation (e.g. ability to swim or dive) and higher levels of risk mitigation which can add great costs to marine restoration projects (Courtenay et al. 2012). For example, current global estimates to achieve kelp restoration sit between \$100,000 - \$1.2 million NZD per hectare (Eger et al. 2022b), which is justifiable considering the tangible and intangible value of kelp forests for New Zealand, but completely unaffordable and unscalable for many small community groups in New Zealand wanting to achieve kelp restoration at a local level.

Despite these challenges, marine eco-engineering and restoration are becoming increasingly important in New Zealand due to the significant decline in the health and biodiversity of the nation's coastal ecosystems (Fisheries New Zealand 2022). When you consider that New Zealand has one of the longest coastlines in the world (Rouse et al. 2017), much of which is dominated by kelp forests, nowhere is the application of coastal eco-engineering and restoration of eco-engineering species more relevant than in New Zealand. Examples of marine restoration and coastal eco-engineering in

New Zealand are minimal and are typically funded by small-scale research projects. Large-scale restoration efforts often rely on passive strategies like marine reserves or restrictions on harvesting techniques (Babcock et al. 1999, Shears and Babcock 2002, Babcock et al. 2010, Schiel 2013, Davies et al. 2018). Active restoration of shellfish beds has received varying levels of attention in New Zealand. Cockle restoration has so far been small-scale and usually involves transplantation of adult cockles (*Austrovenus stutchburyi*) into degraded areas (Cummings et al. 2007, Marsden and Adkins 2010). While efforts to restore mussel (*Perna canaliculus)* populations are currently expanding, with multiple industry groups and research groups heavily involved in the reseeding of harbours with adult mussels, results have varied among trials (McLeod et al. 2014, Wilcox et al. 2018, Alder et al. 2021, Alder et al. 2022, Sea et al. 2022, Benjamin 2023, Revive Our Gulf 2023). Another approach to marine restoration in New Zealand involves active management of species that drive ecosystem changes, such as the urchin (*Evechinus chloroticus)*. Large scale efforts to kill urchins in order to alleviate herbivory in kelp forests has proved successful in promoting kelp recovery in some areas, although benefits from using this technique may be short-lived (Miller et al. 2022). There are currently no published studies on the restoration of kelp forests in New Zealand using seeded substrates, although multiple organisations and community groups are looking to implement restoration strategies. Research on coastal eco-engineering is rarely published in New Zealand, with publications focusing on the engineering of coastal environments to mitigate infrastructure disturbance without mentioning biological effects of engineering in these environments (Papps and Priestley 2003, 2005). This is an important area of research as coastal infrastructure in New Zealand is predicted to increase by 49-76% by 2043 (Floerl et al. 2021).

Coastal communities are deeply dependent on the health of coastal marine environments for ecosystem services such as food security, economic benefits, and cultural practices. Ocean users within these communities are often the first to detect changes and declines in the health of an ecosystem. Further, they are the most affected by changes in the local marine environment and can be critical to the successful restoration of degraded ecosystems and the maintenance of healthy ones (Eger et al. 2022a). Collaboration between researchers, restoration practitioners, and local communities when conducting restoration will ensure that restoration efforts are aligned with community values and priorities, and ensure that restoration projects have the greatest possible impact in terms of improving ecosystem health, while supporting the sustainability of local economies (Eger et al. 2022a). Additionally, further research on the effectiveness of different restoration and eco-engineering techniques employed in New Zealand is warranted to ensure successful outcomes when managing the future of our coastlines.

1.2 Overview of thesis

This thesis examines the effects of engineered coastal structures for biodiversity and the restoration of kelp forests. This thesis is comprised of a general introduction chapter (Chapter One), two empirical data chapters (Chapters Two and Three), and a general discussion chapter (Chapter Four). Chapters Two and Three are written in manuscript format as I expect to submit these for peer-review as co-authored manuscripts shortly after receiving the examiner's comments, so I use "we" (first-person plural) to acknowledge this. Nonetheless, this thesis is my own work, completed under the guidance of my supervisor.

Chapter Two analyses differences in the biodiversity of rockpools on natural and two commonly used artificial coastal structures: riprap and concrete. I hypothesised that natural pools would support a higher species richness and greater functional group prevalence compared to concrete and riprap pools, as artificial habitats generally appear to support lower biodiversity than nearby natural rocky habitats (Chapman and Bulleri 2003, Firth et al. 2013a, Firth et al. 2015). Additionally, I hypothesised that smothering and desiccating disturbance events would negatively impact biodiversity in pools, particularly in the riprap environment as substrate material is not secured and pools in this habitat have a higher risk of disturbance (Sousa 1979, Chapman 2012).

Chapter Three analyses the effectiveness of different methodologies to seed *Ecklonia radiata* on small gravel to create Green Gravel, as well as varying techniques for transplanting the Green Gravel onto the reef. Specifically, I assessed the effect of environmental conditions: depth and habitat, as well as attachment method, on gravel retention and sporophyte lengths on Green Gravel. I hypothesised that sporophytes would exhibit increased length in shallow sites with higher light available (Smith et al. 2020), yet retention of green gravel would be compromised in such areas due to heightened susceptibility to disturbance from concentrated swell conditions. . Attaching gravel using an adhesive would positively impact the retention of Green Gravel compared with gravel that were simply placed on the seafloor by minimising disruption to both the gravel and developing sporophytes, facilitating holdfast attachment to the reef. Additionally, sporophytes transplanted within the canopy would have greater length due to reduced sediment and sub-canopy flow, while Green Gravel transplanted in barrens may have a lower retention due to being more exposed from wave action (Layton et al. 2019b). This work was completed under an MPI special permit (SP-814) and with written permission from Ngāti Manuhiri and Ngāti Whatua.

This thesis was completed part-time. Data for Chapter Two was collected between July 2019 and January 2021, providing 18 months of rockpool data. Initially, I had planned to conduct another 6 months of data to analyse rockpools over a two-year experimental period. However, due to the lockdowns and restricted travel during the COVID-19 pandemic, this plan was unable to advance. Data collection for Chapter Three was collected between April 2022 and June 2023, and is expected to continue for the next 8 months monitoring the Green Gravel as they progress through reproductive maturity. I initially hoped to collect fortnightly data on the growth of sporophytes on both batches of Green Gravel however, multiple severe weather events, particularly in late 2022 and early 2023 including cyclone Gabrielle, restricted us to collecting eleven samples of batch one between April 2022 and June 2023, but only three samples of batch two between September 2022 and June 2023. Nonetheless, I feel I progressed an ambitious research plan in both areas of research and look forward to the examiner's suggestions for improvements.

1.3 Author contributions

Chapter 1:

Ella Lis (EL): Conceptualisation, investigation, and writing – original draft, review and editing.
David Aguirre (DA): Supervision and writing—review, and editing.

Chapter 2:

EL: Investigation, fieldwork, data analysis, modelling, visualisation, and writing – original draft, review, and editing.
DA: Supervision, funding, design, data analysis, and writing—review, and editing.
Louise Firth (LF): Conceptualisation – original draft, and review.

Chapter 3:

EL: Conceptualisation, investigation, fieldwork, data analysis, modelling, visualisation, and writing – original draft, review, and editing.
DA: Supervision, funding, design, data analysis, and writing—review and editing.

Chapter 4:

EL: Conceptualisation, investigation and writing – original draft, review and editing.
DA: Supervision and writing—review, and editing.

Chapter Two: Rockpools on artificial coastal defence structures support similar biodiversity as rockpools on natural substrates.

2.1 Abstract:

Rockpools represent a refuge from environmental stress during low tide, however coastal development and pollution threaten the availability of these intertidal havens for marine life. Eco-engineering is becoming popular to minimise the negative effects of coastal hardening on biodiversity while still preserving human values. Here, we compared the biodiversity of temperate rockpools on natural substrates and two commonly used artificial coastal structures, riprap and concrete in the North-East of New Zealand. Specifically, we assessed whether taxa richness and functional group prevalence were different among habitats and levels of disturbance at two replicate sites. Riprap and concrete exhibited comparable taxa richness and functional group prevalence to natural substrates, however disturbances, particularly smothering, significantly reduced taxa richness on all substrates. Meanwhile distinct taxa associations emerged in response to disturbance and habitat type. Encrusting algae and grazers were more prevalent in riprap habitats, and surprisingly, artificial structures showed resistance to nonindigenous species. This study underscores the importance of microhabitat diversity in supporting species and ecosystem health on artificial structures, guiding engineering strategies to optimize their ecological value while accommodating inevitable urbanization. Further studies should investigate the effect of seeding artificial substrates with biogenic species and look to secure permanent pools in riprap and concrete environments to increase the availability of beneficial habitats.

2.2 Introduction

On natural rocky shores in many parts of the world, rockpools, represent a refuge from physical stress and often support higher numbers of species and different communities to the surrounding rock (Chapman and Underwood 2011, Aguilera et al. 2014, Firth et al. 2014a, Evans et al. 2015, Ostalé-Valriberas et al. 2018). These rockpools (hereafter pools) function as essential habitats fostering numerous organisms, and act as feeding grounds, refuges from predators and environmental conditions, and nurseries for various species (Aguilera et al. 2014, Firth et al. 2014a, Mayer-Pinto et al. 2017). As the tide retreats, pools create an oasis for many organisms that cannot survive without water. These pools enhance microhabitat diversity, promoting spatial heterogeneity, which favours the settlement and establishment of a greater range of species (Martins et al. 2010, Perkol-Finkel et al. 2012, Burt et al. 2013, Firth et al. 2016a, Strain et al. 2018).

Escalating coastal urbanization driven by human population growth is intensifying the demand for coastal infrastructure (Small and Nicholls 2003, Martínez et al. 2007, Dafforn et al. 2015, Firth et al. 2020). Coastal urbanisation affects the marine ecosystem by modifying near-shore water currents; which transport suspended organic material and chemical pollutants, introducing novel artificial surfaces into shallow-water and intertidal habitats as well as smothering existing environments (Thomalla and Vincent 2003, Bulleri and Chapman 2004, Cuadrado et al. 2005, Zyserman et al. 2005). Consequently, this habitat alteration can reduce biodiversity, change species composition and impact overall ecosystem health (Benedetti-Cecchi et al. 2001, Mangialajo et al. 2008, Martins et al. 2009).

Artificial structures deviate from their natural counterparts in terms of material, age, orientation, shading, and complexity (Glasby and Connell 2001, Bulleri and Chapman 2004, Bellou et al. 2012, Airoldi et al. 2015, Floerl et al. 2021). Marine intertidal habitats naturally exhibit varying degrees of both biotic (e.g. mussels, barnacles, turf algae) and physical (e.g. cracks, rockpools, smooth surfaces) heterogeneity (Menge et al. 1983). Conversely, artificial coastal structures typically smother existing microhabitats like pools and the associated biodiversity they sustain (Gibson et al. 2007, Airoldi et al. 2015, Heery et al. 2017, Mayer-Pinto et al. 2018). Habitat structural complexity influences community structure by providing microhabitats and resources, modifying predation and competition dynamics (Menge et al. 1983, Kovalenko et al. 2012, Thomsen et al. 2022). However, the degree of this impact varies among species and with environmental conditions (Strain et al. 2018, Strain et al. 2020).

The majority of global artificial coastal infrastructure consists of simple structures, such as seawalls, constructed with concrete (Chapman and Bulleri 2003, Ng et al. 2015). These structures, leaching cement materials over time, elevate surface pH and favour alkali-tolerant and endolithic taxa (Ido and Shimrit 2015, Ponti et al. 2015). Artificial seawalls have a predominantly vertical orientation, resulting in a smaller intertidal zone compared to the horizontal rocky shores they often replace (Chapman and Bulleri 2003, Bulleri et al. 2005). Both orientation and slope significantly influence assemblages in intertidal and subtidal zones (Glasby 2000, Benedetti-Cecchi et al. 2001, Cacabelos et al. 2019). The lack of structural complexity on a typical seawall limits their viability as a surrogate for natural rocky shores (Chapman and Bulleri 2003, Ng et al. 2015, Firth et al. 2016a) and their presence may even impact adjacent marine habitats by increasing the strength of currents and waves reflected off the wall (Dugan et al. 2011).

Other than simple concrete seawalls, another common coastal defence strategy used globally is ‘riprap’ (Browne and Chapman 2011, Holloway and Field 2020). Riprap structures are an uninterrupted collection of large boulders loosely piled on top of one another to absorb wave action while still allowing water to drain (Griggs and Fulton-Bennett 1988). Riprap areas are complex habitats, with pools scattered between boulders and many taxa living on, between and underneath the boulders (Perkol-Finkel and Benayahu 2004, Chapman 2012, Burt et al. 2013). These environments are vulnerable to disturbance and loss as the substrate is not secured to the coast (Chapman 2012). Excessive disturbance in these habitats can remove sessile organisms from the structure, although mobile species may successfully colonise nearby stable boulders (Smoothey and Chapman 2007). The persistence of any species in a riprap environment will depend on the frequency and extent of disturbance events (Chapman 2012).

Previous research found important differences in the composition of species observed in natural and artificial marine environments worldwide (Vaselli et al. 2008, Bulleri and Chapman 2010, Tan et al. 2015, Firth et al. 2016a). For example, concrete-based artificial structures have different benthic communities than adjacent natural hard surfaces (Moschella et al. 2005, Ido and Shimrit 2015), similarly, riprap structures exhibit reduced biodiversity values (Gacia et al. 2007, Vaselli et al. 2008). However, due to the use of natural rocks during construction, with higher microscale roughness (Liversage and Chapman 2018), riprap may host epibenthic communities more akin to those in natural habitats, compared to concrete habitats (Gacia et al. 2007, Pister 2009). The differences in species assemblages among these substrates is primarily associated with microhabitat availability (Chapman and Blockley 2009, Martins et al. 2010, Browne and Chapman 2011, Klein et al. 2011, Firth et al. 2013b, Firth et al. 2014b), although competitive interactions (Iveša et al. 2010) and the arrival of invasive species (Bulleri and Airoldi 2005) also contribute. Interestingly, Evans et al. (2015) reported that artificial structures can support high species diversity and richness similar to adjacent natural rocky structures, although this effect becomes prominent only after prolonged exposure to the marine environment.

Natural assemblages of species in space-limited systems are profoundly influenced by disturbance (Sousa 1985, Pickett et al. 1999). Rockpools are discrete, patchy habitats structured by a complex set of physical and biological factors (Benedetti-Cecchi and Cinelli 1996). Excessive disturbances in such systems can fragment communities into diverse successional states; however, ecologists have long appreciated that local disturbance is an integral part of community organization (Dayton 1985). Disturbance events include smothering by sand or rocks, erosion of pools, substrate removal, desiccation, and pollution, which can vary considerably among habitat types and seasons (Taylor and Littler 1982, Kim et al. 2017). Furthermore, boulder environments are more likely to experience substrate removal disturbances than rocky ledges, as the substrate is not permanently secured to the coast (Sousa 1979, Chapman 2012).

Eco-engineering emerges as a solution to balance coastal hardening's negative ecological impact with human needs (Chapman and Underwood 2011, Firth et al. 2016a, Mayer-Pinto et al. 2017). Eco-engineers manipulate substrate composition, surface topography, and complexity to integrate marine life into built environments, often creating water-retaining features that mimic pools (Firth et al. 2016a, Strain et al. 2018). Notably, even minor alterations to seawalls, such as adding flowerpots, can enhance colonization (Browne and Chapman 2011). Implementing eco-engineered structures requires careful consideration of material, size, orientation, complexity, resilience, and environmental factors (Perkol-Finkel and Benayahu 2004). Only purpose-built artificial structures will function effectively in their environment and provide a suitable habitat for species from natural habitats (Perkol-Finkel and Benayahu 2004).

While safeguarding natural habitats is important (Gaines et al. 2010), the burgeoning human population makes some coastal modification inevitable (Chapman and Blockley 2009, Browne and Chapman 2011). A plethora of alternative techniques and materials have already been used for coastal defence and coastal infrastructure, each varying in their effectiveness to support natural biodiversity (Moschella et al. 2005, Burt et al. 2009, Chapman and Blockley 2009, Martins et al. 2010, Perkol-Finkel et al. 2012, Coombes et al. 2015, Cacabelos et al. 2016, Mayer-Pinto et al. 2017, Sedano et al. 2020). Understanding the mechanisms that influence the composition of assemblages on these novel structures will ensure they benefit human development while conserving natural biodiversity.

Here, we compared the existing biodiversity of rockpools on natural substrates and two commonly used artificial coastal structures; riprap and concrete over an 18-month experimental period. Specifically, we assessed whether taxa richness and functional group prevalence was different among habitats and levels of disturbance at two locations. We hypothesised that natural pools would support higher taxa richness and greater functional group prevalence compared to artificial pools (Chapman and Bulleri 2003, Firth et al. 2013a, Firth et al. 2015), while disturbance events would negatively impact biodiversity in pools, especially in the riprap habitat where loose boulders increase the risk of disturbance (Sousa 1979, Chapman 2012). Assessing if artificial coastal structures support similar biodiversity to natural substrates in our coastal marine environment is a key component of understanding their role in intertidal ecosystems and ensuring they will be a sufficient substitute for natural rockpools in areas where coastal hardening is required.

2.3 Methods

2.3.1 Sample site

Auckland is the most urbanised city in New Zealand (Petrella et al. 2012) and is home to one of the busiest ports in the country (Deloitte 2023). The high levels of coastal development around the coast of Auckland make it a fitting place to examine the effects of coastal development on marine communities. The two areas in Auckland considered in this study were Takapuna and Kohimarama (Figure 2.1). These represent two similarly wave-exposed coastlines, both of which are situated in the Hauraki Gulf and are relatively sheltered from oceanic conditions by Great Barrier Island and the Coromandel Peninsula.

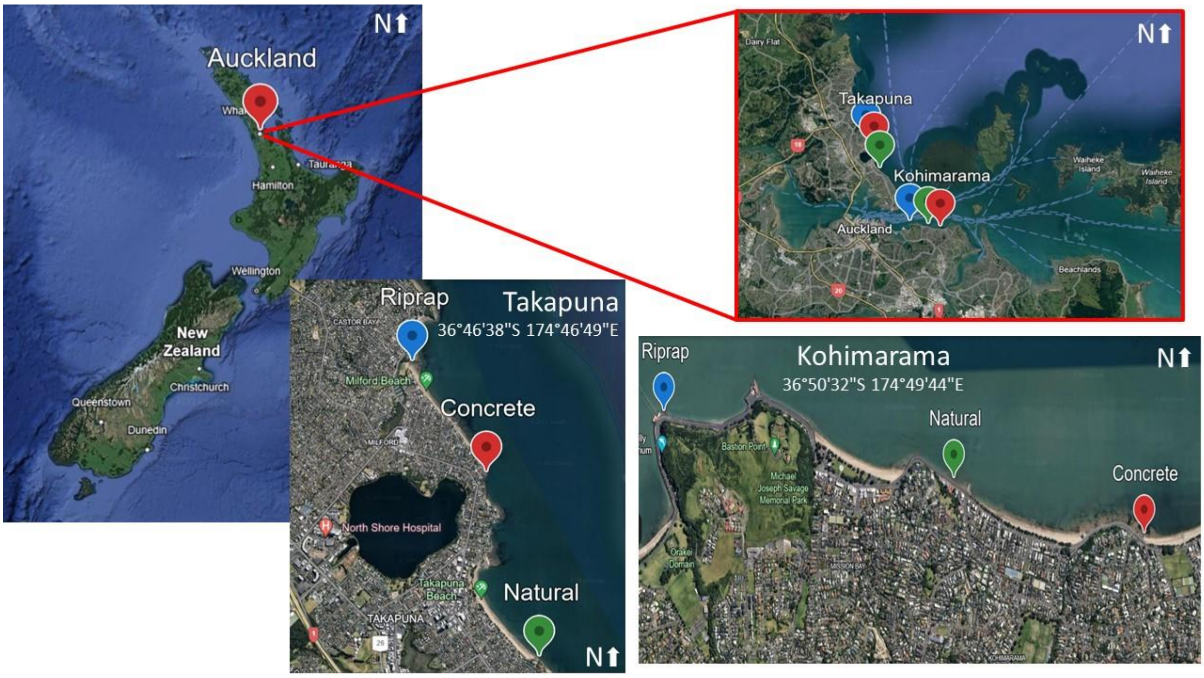


Figure 2.1: Reference map for three levels of habitat treatment (indicated by the coloured pins) at two locations (Kohimarama and Takapuna).

2.3.2 Sampling Method

Two locations, Kohimarama and Takapuna, were sampled monthly during low tides between July 2019 and January 2021. At each location, quadrats (10 x 10 cm) were randomly placed above 10 replicate pools no more than 120mm deep at the mid-tide level (between 0.7 and 1.5m above the Mean Low Water Springs), of three different substrates (concrete, riprap and natural; Figure 2.2); in accordance with Firth et al. (2015)). The concrete structure sampled at Takapuna was an abandoned concrete boat ramp with small indentations caused by weathering, while at Kohimarama there are artificially constructed concrete groynes with pools carved into them. These artificial groynes were constructed in 2009, however it is unclear when the riprap substrates and concrete boat ramp were constructed. The locations sampled have all three substrates within 3.5 kilometres of each other. Additionally, both locations are areas of high urbanisation where coastal defence is vital for protecting the expensive infrastructure around those areas. Two disturbance events; smothering by rocks or sand, and desiccation, occurred in all three substrate types among the two locations. Desiccation was recorded when pools contained less than 10mm of water, and smothering was recorded when loose sand or rocks completely covered the pool.

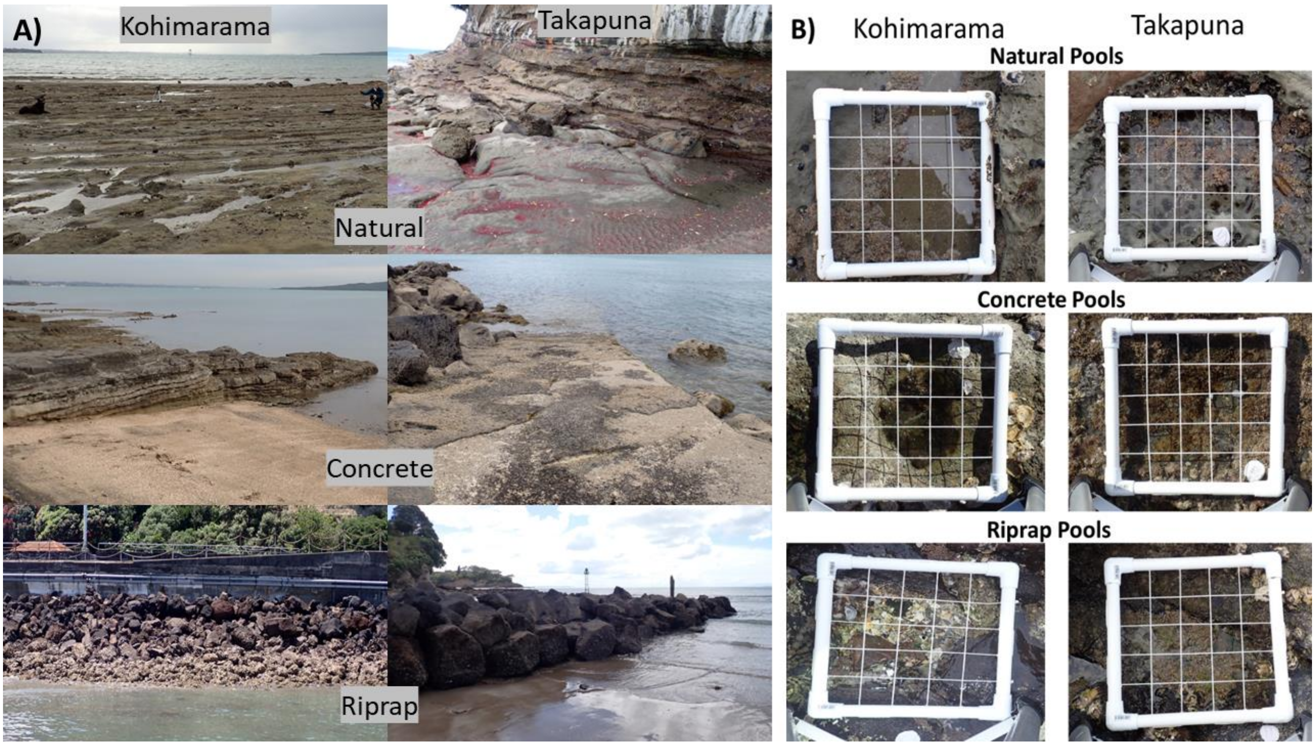


Figure 2.2: Substrates sampled in this experiment. A: Overview of habitat types. B: Sample of rockpools observed in each substrate.

2.3.3 Response Variables

During sample collection, the abundance of mobile macroscopic organisms observed (e.g. snails, crabs) and the percentage cover of canopy and sub-canopy space occupying sessile macroscopic organisms (e.g. sponges, algae, barnacles, oysters) were recorded. Pool area was recorded in the initial site exploration, although was not recorded throughout the study so was not included in this analysis. Species were identified down to the lowest possible taxonomic level and any obvious stress responses (e.g. bleaching or mushrooming of limpets) were noted. Species were also assigned a functional group, with algal functional groups following guidelines set by Arenas et al. (2006). A multiprobe (HANNA HI98194 pH/EC/DO multiparameter) and temperature gun (Fluke 568 IR thermometer) was also used to record details about pH, temperature (inside and outside pools (°C)), dissolved oxygen and salinity (PSU) of each pool, however these measurements are yet to be analysed.

2.3.4 Analysis

To examine differences in the biodiversity of pools we fitted a joint species distribution model using the Hierarchical Modelling of Species Communities (HMSC) framework of Ovaskainen et al. (2017) implemented in the Bayesian framework using the HMSC 3.0-13 R package (Tikhonov et al. 2022). To account for differences in form and function between unitary and colonial organisms found in rockpools, we focused on analysing the presence or absence of taxa in replicate pools across the 18-month experimental period.

In our analyses, the response variable was the presence-absence of taxa. Accordingly, we assumed a binomial error distribution and fit a generalized linear mixed model using a probit link function. The fixed effects were location with two levels: Kohimarama and Takapuna, habitat with three levels: concrete, natural and riprap and disturbance with three levels: smothered, desiccated or normal. Rockpool was fitted as a random effect to account for repeated measures on each pool. Day was fitted as a random effect to account for variation in taxa prevalence across the duration of the experiment. Last, sample was fitted as a random effect to account for correlations in taxa prevalence in each sampling event. We also examined if the relationship between taxa prevalence and the fixed effects differed among functional groups by including functional group as a trait measured at the taxa level.

Model fitting, evaluation, and cross-validation

We used the default priors recommended for HMSC models for both the fixed and random effects (Ovaskainen and Abrego 2020) and ran four parallel Monte Carlo Markov chains (MCMCs) with 500 iterations, a burn-in of 5000 iterations and a thinning interval of 500 iterations resulting in 2000 posterior samples for each chain. To evaluate chain mixing and convergence quantitatively, we computed potential scale-reduction factors for the model parameters (Gelman et al. 2014) and confirmed model convergence by confirming that the potential scale reduction factor was centred on a value of 1 (Gelman and Rubin 1992). To determine the fit of the model to the data we computed area-under-curve (AUC) statistics and coefficients of discrimination (Tjur r^2) for each taxa (Pearce and Ferrier 2000, Tjur 2009).

Variance partitioning and residual taxa associations

We partitioned the variance in taxa prevalence explained by each of the fixed and random effects following Ovaskainen et al. (2017). We also estimated residual taxa-associations matrices at each level of the random effects and scaled these to correlations. We then determined if these associations were significant by examining if the 95% highest posterior density interval of the correlation overlapped zero. Plots of the residual association were produced using the corrplot function in the corrplot R package (Wei and Simko 2021).

Planned comparisons

We used a custom script based on the constructGradient function of HMSC, to determine the significance of the habitat, location and disturbance on pool richness and functional group prevalence. We then assessed whether taxa richness and functional group prevalence was different among locations, habitats and levels of disturbance. If the 95% highest posterior density (HPD) interval for the difference in taxa richness or functional group prevalence of each planned comparison did not overlap zero, we interpreted this as evidence of a significant difference in taxa richness or functional group prevalence between levels of location, habitat or disturbance.

2.4 Results

2.4.1 HMSC model convergence and variance partitioning

A total of 66 taxa were recorded in pools across two locations (Kohimarama and Takapuna) and three substrates (natural, concrete and riprap) surveyed. Of these, 52 were recorded in concrete pools, 55 were recorded in natural pools, and 54 were recorded in riprap pools. Predatory animals contributed the greatest number of taxa (14 taxa), followed by filter feeders (13 taxa), grazers and sub-canopy algae (9 taxa), scavengers (7 taxa), turf algae (6 taxa), encrusting algae, deposit feeders and canopy algae (2 taxa) and detritivores (1 taxa). The fit of the model to the data was excellent with a mean AUC of 0.931 (Appendix 1.1A). Additionally, the fit of the model to the data did not vary with taxa prevalence (Appendix 1.2), although our ability to differentiate between taxa presences and absences was not strong (mean TjurR2 = 0.158, Appendix 1.1B). Potential scale-reduction factors for the parameter estimates in the HMSC model were centred on 1 indicating good convergence of the model (Appendix 1.3). The variance partitioning shows that disturbance (27.3%) explains most of the variation in taxa prevalence (Figure 2.3). Habitat type (23.3%), rockpool (20.8%) and location (16.4%) are also important for some species, but not so important for others when explaining taxa prevalence (Figure 2.3). While the random effects, day (6.5%) and sample (5.8%) play very minor roles in explaining differences in taxa prevalence (Figure 2.3). Additionally, there was no strong functional group bias in the proportion of the variation attributable to fixed or random effects in this experiment.

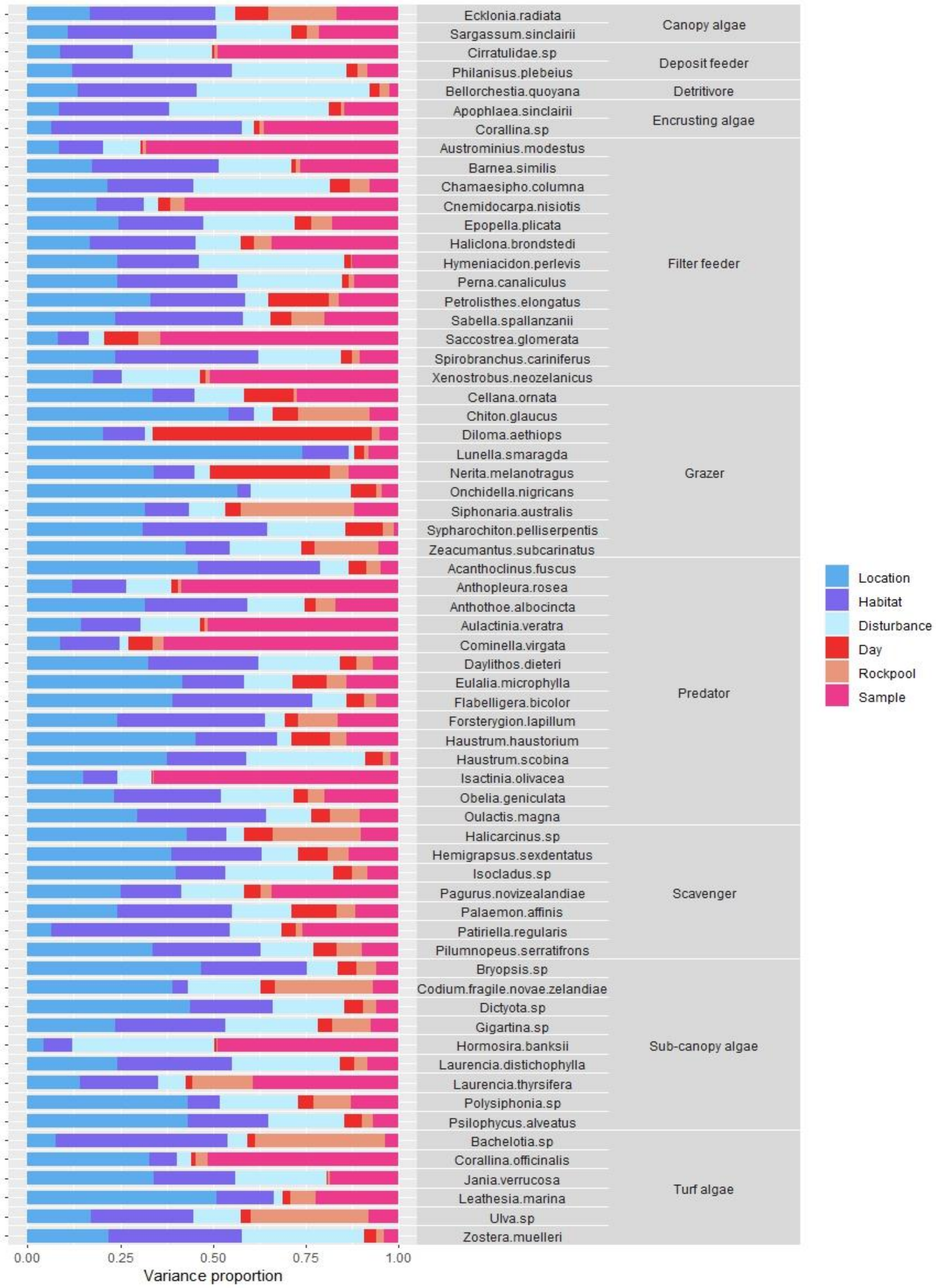


Figure 2.3: Variance partitioning among the fixed (habitat, disturbance and location) and random (day, rockpool and sample) effects in the model. Cool colours represent fixed effects and warm colours represent random effects.

2.4.2 Assessing differences in taxa richness

Normal pools hosted on average three times as many taxa ($\bar{x}$ = 3.350, HPD = 2.007, 4.979) compared to those that had been disturbed, either by desiccation ($\bar{x}$ = 1.013, HPD = 0.245, 1.869) or smothering ($\bar{x}$ = 0.545, HPD = 0.066, 1.287). Smothering caused the greatest reduction in taxa richness with six times less taxa in smothered pools compared with normal pools. There was no difference in taxa richness between locations, although there was a notable difference between habitat types in desiccated pools, with artificial pools ($\bar{x}$ = 1.167, HPD = 0.329, 2.062) hosting 1.6 times as many taxa than natural pools ($\bar{x}$ = 0.705, HPD = 0.078, 1.483, Table 2.1).

Substrate	Location	Disturbance	$\bar{x}$	HPD (95% confidence interval)
Concrete	Kohimarama	Smothered	0.856	0.125 – 1.744
		Normal	3.533	2.390 – 5.023
		Desiccated	1.576	0.534 – 2.588
	Takapuna	Smothered	0.809	0.130 – 1.667
		Normal	3.976	2.545 – 5.712
		Desiccated	1.317	0.430 – 2.249
Natural	Kohimarama	Smothered	0.342	0.014 – 1.025
		Normal	2.398	1.291 – 3.530
		Desiccated	0.742	0.094 – 1.482
	Takapuna	Smothered	0.343	0.029 – 1.006
		Normal	3.581	2.011 – 5.687
		Desiccated	0.668	0.061 – 1.484
Riprap	Kohimarama	Smothered	0.380	0.037 – 1.026
		Normal	2.821	1.547 – 4.185
		Desiccated	0.867	0.152 – 1.661
	Takapuna	Smothered	0.531	0.059 – 1.256
		Normal	3.789	2.258 – 5.736
		Desiccated	0.907	0.198 – 1.751

Table 2.1: Mean taxa richness (and 95% HPD intervals) in each combination of location, habitat and disturbance.

2.4.3 Assessing differences in taxa prevalence

Our analyses also revealed differences in functional group prevalence among levels of habitat and disturbance but not location. Encrusting algae ($\bar{x}$ = 0.067, HPD = <0.001, 0.192) and grazers ($\bar{x}$ = 0.296, HPD = 0.136, 0.460) favoured riprap habitats over natural habitats, provided pool conditions were normal (encrusting algae: $\bar{x}$ = 0.004, HPD = <0.001, 0.016; grazers: $\bar{x}$ = 0.175, HPD = 0.058, 0.312). Although encrusting algae thrived even when riprap pools were desiccated ($\bar{x}$ = 0.141, HPD = <0.001, 0.493). Filter feeders tended to favour natural pools (x= 0.146, HPD = 0.018, 0.424) over concrete pools ($\bar{x}$ = 0.054, HPD = 0.001, 0.189), while grazers favoured normal pool conditions ($\bar{x}$ = 0.220, HPD = 0.096, 0.363) compared to desiccated pools ($\bar{x}$ = 0.037, HPD = <0.001, 0.136) when in concrete habitats (Table 2.2).

Functional Group	Substrate	Location	Disturbance	$\bar{x}$	HPD (95% confidence interval)
Encrusting algae	Concrete	Kohimarama	Smothered	0.011	<0.001-0.048
			Normal	0.008	<0.001-0.037
			Desiccated	0.010	<0.001-0.052
		Takapuna	Smothered	0.104	<0.001-0.419
			Normal	0.043	<0.001-0.118
			Desiccated	0.049	<0.001-0.222
	Natural	Kohimarama	Smothered	0.003	<0.001-0.007
			Normal	0.002	<0.001-0.009
			Desiccated	0.004	<0.001-0.017
		Takapuna	Smothered	0.016	<0.001-0.078
			Normal	0.005	<0.001-0.023
			Desiccated	0.013	<0.001-0.062
	Riprap	Kohimarama	Smothered	0.096	<0.001-0.455
			Normal	0.055	<0.001-0.178
			Desiccated	0.104	<0.001-0.416
		Takapuna	Smothered	0.188	<0.001-0.626
			Normal	0.079	<0.001-0.207
			Desiccated	0.177	<0.001-0.571
Filter feeder	Concrete	Kohimarama	Smothered	0.047	<0.001-0.216
			Normal	0.035	0.001-0.106
			Desiccated	0.060	<0.001-0.222
		Takapuna	Smothered	0.054	<0.001-0.2
			Normal	0.057	0.007-0.134
			Desiccated	0.071	<0.001-0.257
	Natural	Kohimarama	Smothered	0.111	<0.001-0.46
			Normal	0.087	0.011-0.218
			Desiccated	0.121	<0.001-0.432
		Takapuna	Smothered	0.179	<0.001-0.54
			Normal	0.205	0.096-0.335
			Desiccated	0.174	<0.001-0.56
	Riprap	Kohimarama	Smothered	0.090	<0.001-0.41
			Normal	0.043	0.001-0.129
			Desiccated	0.103	<0.001-0.396
		Takapuna	Smothered	0.065	<0.001-0.268
			Normal	0.058	0.005-0.144
			Desiccated	0.089	<0.001-0.34
Grazer	Concrete	Kohimarama	Smothered	0.036	<0.001-0.156
			Normal	0.183	0.07-0.309
			Desiccated	0.025	<0.001-0.095
		Takapuna	Smothered	0.090	<0.001-0.324
			Normal	0.257	0.122-0.416
			Desiccated	0.049	<0.001-0.177
	Natural	Kohimarama	Smothered	0.034	<0.001-0.158
			Normal	0.180	0.055-0.305
			Desiccated	0.037	<0.001-0.14
		Takapuna	Smothered	0.051	<0.001-0.224
			Normal	0.169	0.06-0.32
			Desiccated	0.052	<0.001-0.201
	Riprap	Kohimarama	Smothered	0.080	<0.001-0.314
			Normal	0.287	0.127-0.445
			Desiccated	0.073	<0.001-0.258
		Takapuna	Smothered	0.092	<0.001-0.327
			Normal	0.306	0.146-0.475
			Desiccated	0.078	<0.001-0.256

Table 2.2: Mean prevalence (and 95% HPD intervals) in each combination of location, habitat and disturbance for the functional groups: encrusting algae, filter feeder and grazer. For a complete table of means and HPD intervals of functional group prevalence see Appendix 1.4.

2.4.4 Assessing residual-taxa associations.

Assessing the influence of the random effects in our model indicated residual taxa associations at the level of day, rockpool and sample after accounting for all other variables in the model. At the level of day, there were two main clusters of positively associated taxa and the taxa in these clusters were negatively associated with taxa in the opposing cluster indicating the existence of alternate taxa compositions among days (Figure 2.4). One cluster included eight taxa with a mixture of smaller algae and grazers, while the other cluster included a grazing chiton and filter-feeding oyster. At the level of rockpool, we found two major assemblages present in rockpools (Figure 2.5). One cluster included eight taxa with a mixture of predators, scavengers and smaller algae, while the other cluster contained nine taxa that were predominantly filter feeders and grazers. Given that the matrix on the residual taxa associations at the level of sample is almost diagonal (Figure 2.6), indicating very low residual correlations among taxa, we conclude that the factors included in our model have collectively explained most of the co-variation in taxa prevalence present in our data (Ovaskainen et al. 2017, Ovaskainen and Abrego 2020)

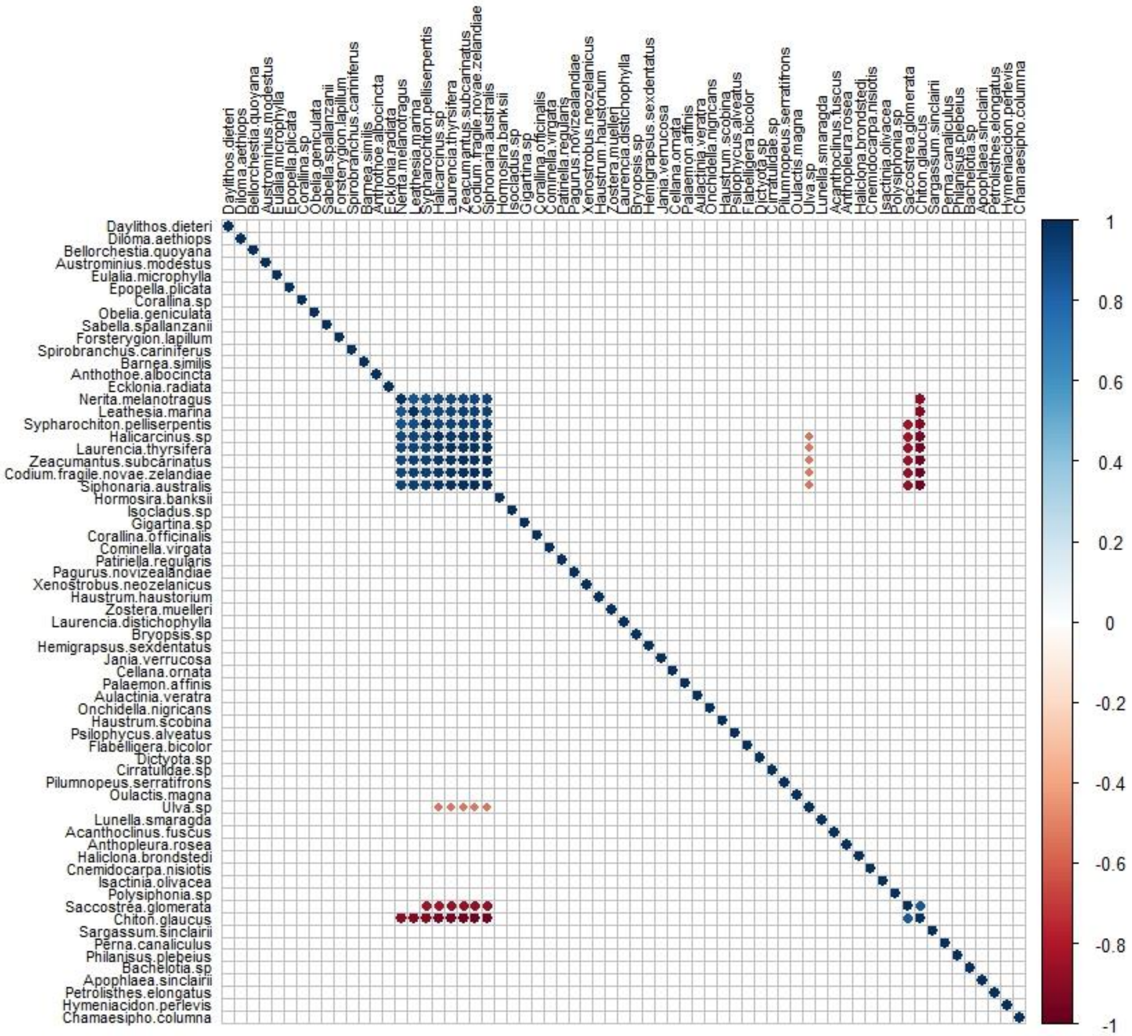


Figure 2.4: Significant residual taxa associations at the level of days. Negative associations are represented with warmer colours while positive associations are represented with cooler colours. The order of the rows and columns has been determined by hierarchical clustering to allow taxa in the same cluster to be plotted together.

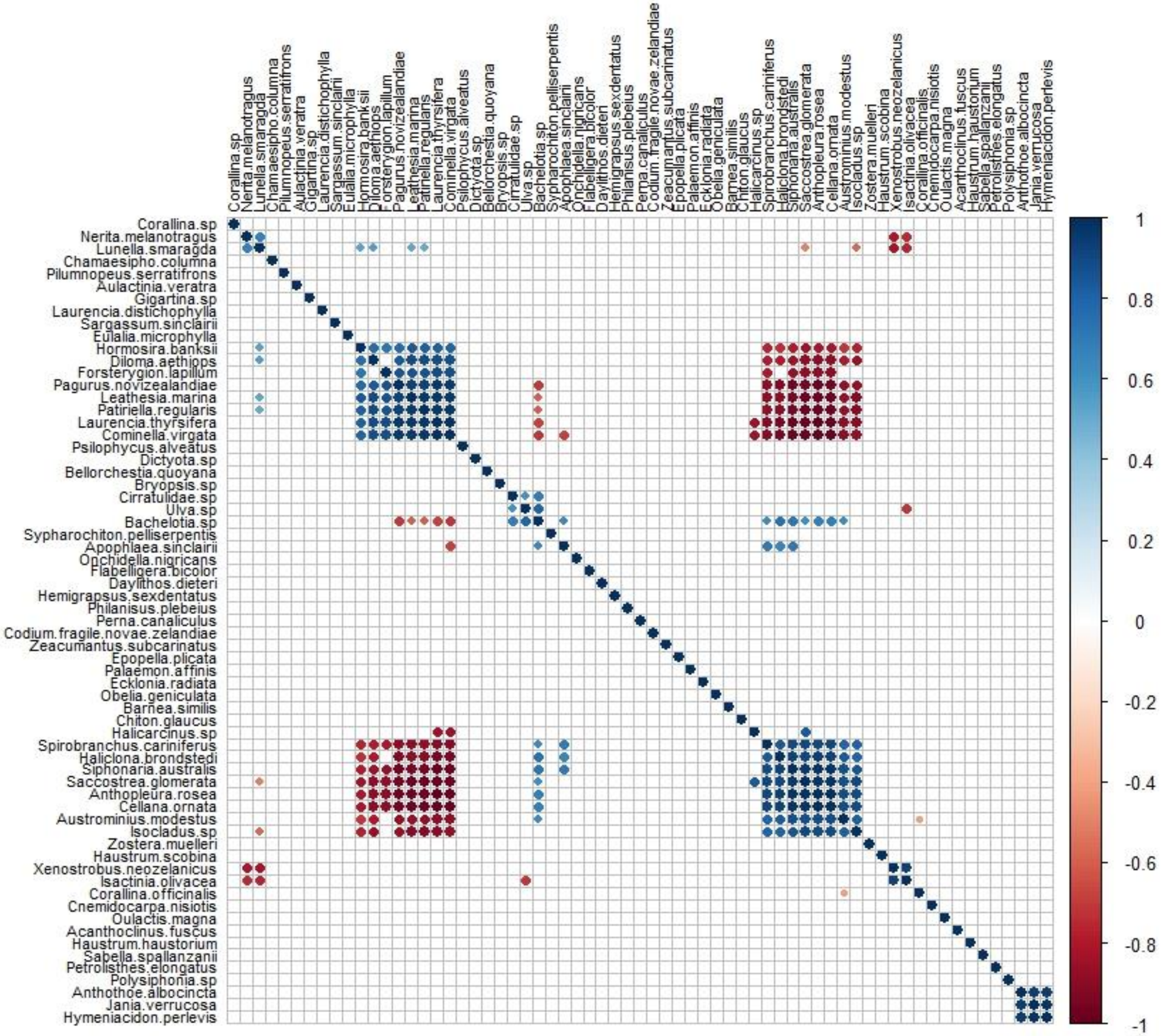


Figure 2.5: Significant residual taxa associations at the level of rockpool. Negative associations are represented with warmer colours while positive associations are represented with cooler colours. The order of the rows and columns has been determined by hierarchical clustering to allow taxa in the same cluster to be plotted together.

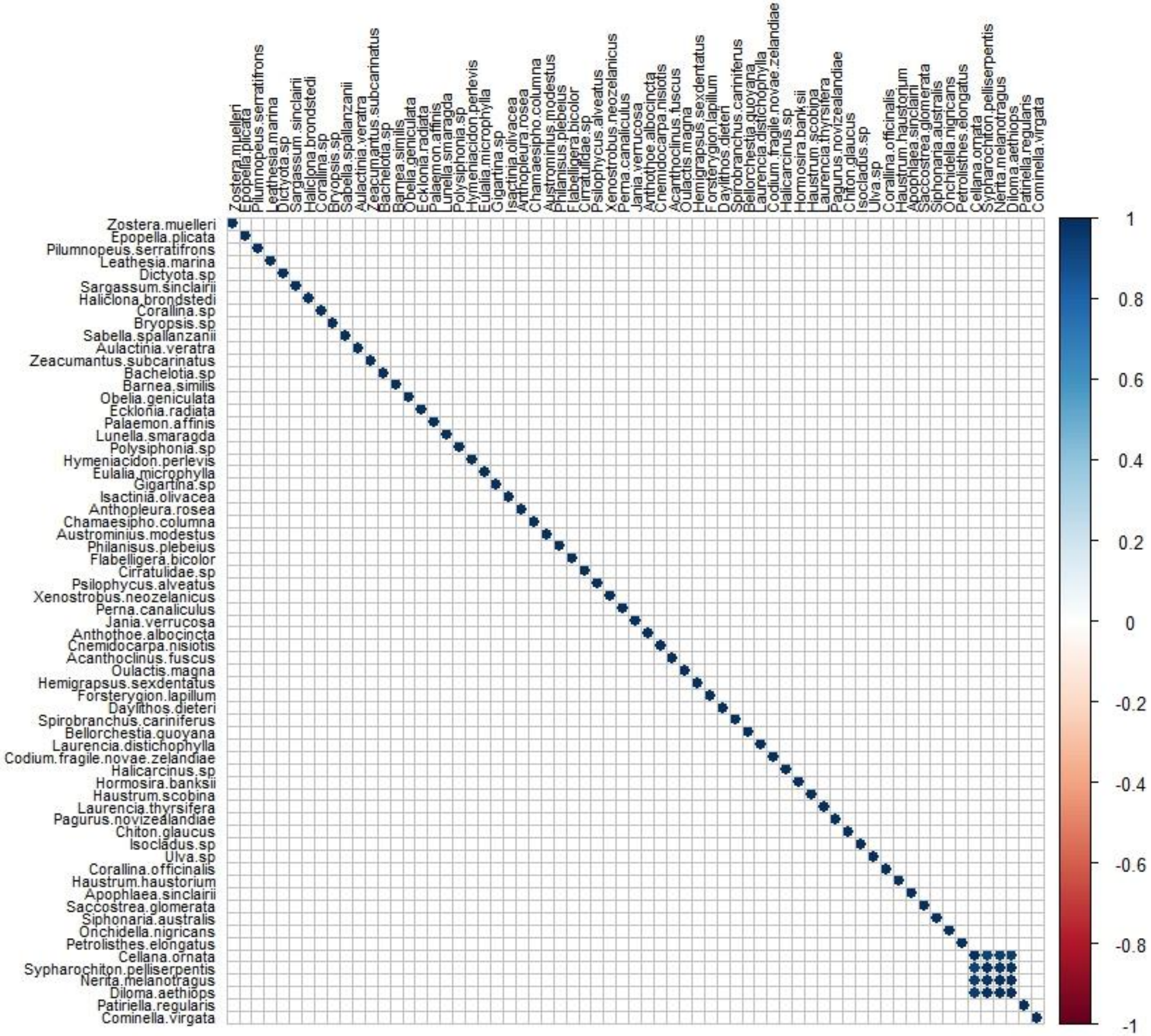


Figure 2.6: Significant residual taxa associations at the level of sample. Negative associations are represented with warmer colours while positive associations are represented with cooler colours. The order of the rows and columns has been determined by hierarchical clustering to allow taxa in the same cluster to be plotted together.

2.5 Discussion

Despite the ability of artificial structures to support numerous organisms, they are generally thought to support lower biodiversity than nearby natural rocky habitats (Chapman and Bulleri 2003, Firth et al. 2013a, Firth et al. 2015). However, my results indicated for rockpool ecosystems in Auckland, New Zealand, both artificial structures (riprap and concrete) support a similar taxa richness and functional group prevalence compared with natural substrates. In the intertidal zone, thermal and desiccation stresses have long been implicated in setting distributional limits (Wolcott 1973, Harley 2003) and the persistence of organisms can be contingent on the availability of microhabitat refugia from such stressors (Firth 2011). Not surprisingly, disturbance events had the most influence on taxa richness and functional group prevalence, with smothering events having the greatest negative effect on taxa richness.

Riprap is one of the most common coastal defence strategies implemented globally (Floerl et al. 2021). As a coastal defence strategy riprap functions well in reducing erosion caused by wave action; however, the frequency of disturbance events in this habitat can be a challenge for intertidal organisms. Our results suggest that riprap is similar to the natural substrate in terms of richness and functional group prevalence, and interestingly encrusting and grazing organisms seemed to prefer the riprap habitat compared with natural substrates when pool conditions were normal. During the survey three riprap pools across the two locations were permanently lost due to shifting of the boulders demonstrating how unstable these habitats can be. In future, if riprap is continued to be used as the preferred coastal defence strategy employed in New Zealand, an increase in permanent water-retaining features and fixing permanent pool habitats amongst the boulders should be implemented to increase the availability and stability of suitable habitats for intertidal organisms (Moschella et al. 2005). Given that richness was similar between riprap and natural habitats, securing some boulders with pools carved into them, could greatly increase the number of stable pool niches available in that environment, thus increasing taxa richness and diversity on these coastal defence substrates potentially beyond that of natural substrates.

When pools were desiccated, we found a higher taxa richness on concrete substrates compared with natural substrates, although grazers preferred natural substrates in dry conditions. A similar study concluded the primary explanation for the concrete substrates having lower taxa richness when compared to natural was a lack of heterogeneity and the overall number of water-retaining features (Firth et al. 2013b). The overall surface of the concrete ramp at Takapuna appears to have been affected by honeycomb weathering and is littered with small indentations among the larger pools, in addition, the ramp has a very flat sloping gradient. Meanwhile, the eco-engineered groyne at Kohimarama has high structural complexity between pools and has a completely horizontal orientation. Natural substrates on the other hand were a matrix of sand and horizontal rocky ledges. This greatly affects the water-retaining features of both concrete structures, and the substrate surface likely remains damp as the tide retreats, providing a continuous hard substrate for organisms compared with natural habitats. This would allow some mobile organisms more time to move between pools without risking desiccation and mortality and could explain why both concrete structures supported a higher taxa richness when pools were desiccated (Firth et al. 2013b, Firth et al. 2016a).

Research has shown artificial structures in the marine environment can be more inviting to nonindigenous species as many exotic species are able to establish populations more readily on artificial structures (Inglis et al. 2005, Arévalo et al. 2007, Glasby et al. 2007, Bulleri and Chapman 2010, Mayer-Pinto et al. 2015). This in turn can have detrimental effects on the natural biodiversity of these areas and surrounding ecosystems. We observed one nonindigenous species, the Mediterranean Fan Worm (*Sabella spallanzanii*), in both the natural and concrete habitats over the experimental period, although its presence was rare. This filter feeding organism appeared in New Zealand in 2008 and has since spread rapidly and is now commonly found in intertidal and shallow subtidal environments around New Zealand (Read et al. 2011). Interestingly, we found that filter feeders were more common on natural habitats over concrete. This indicates that the artificial habitats studied here may not be as inviting for nonindigenous species as in other studies and locations.

Residual taxa associations within pools unveiled intriguing clusters of taxa assemblages, shedding light on microscale variations in ecological positioning. When examining the residual taxa associations among pools we discovered two clusters of taxa assemblages present in pools and negative associations between taxa in different clusters. Further examination of these clusters revealed a cluster of higher intertidal species such as barnacles (*Austrominius modestus*), calcareous tube worms (*Spirobranchus cariniferus*), limpets (*Cellana ornata*) and oysters (*Saccostrea glomerata*). While the second cluster included species that are typically found at lower tidal heights including more predatory species such as starfish (*Patiriella regularis*), triplefins (*Forsterygion lapillum*) and whelks (*Cominella virgata*). This underscores how seemingly identical pools at the same tidal height can exhibit stark similarities to distinct high or low intertidal environments due to subtle microscale differences in position, orientation, and slope.

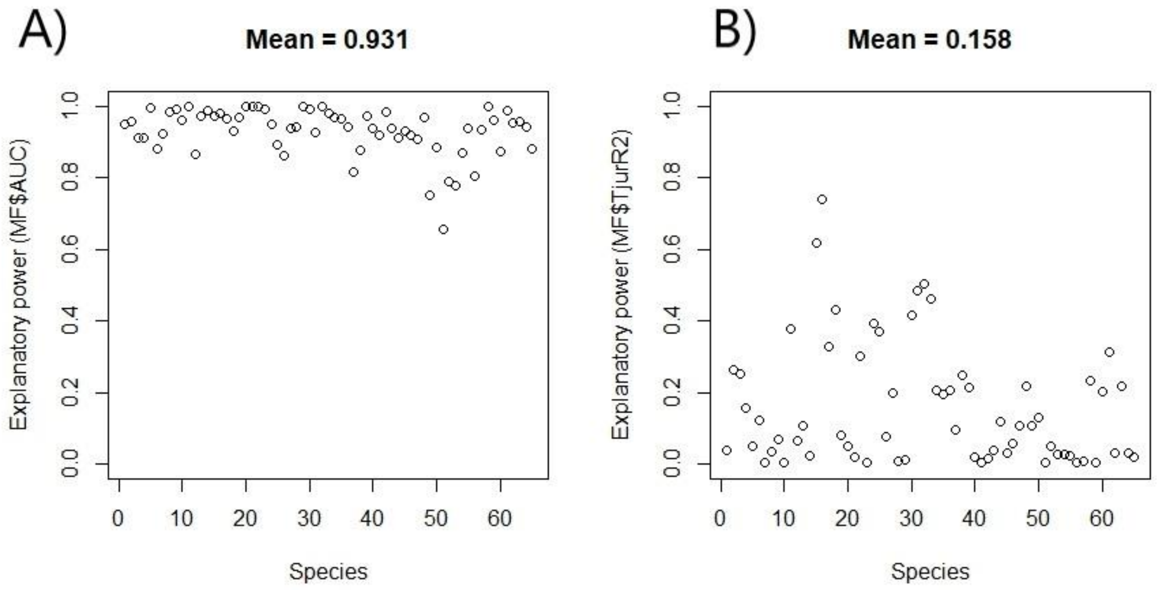
Many sessile organisms found on or in association with pools create biogenic habitats around them (e.g. mussels, barnacles, sponges) further enhancing microhabitat heterogeneity and diversity in an environment (Moschella et al. 2005, Chapman and Blockley 2009, Browne and Chapman 2011, Chapman and Underwood 2011, Klein et al. 2011, Firth et al. 2014b). Interestingly we discovered two clusters of taxa that were positively associated within each cluster, but between clusters were negatively associated through time (Figure 2.4). The composition of the larger cluster suggests that the growth of small algae may act as a biogenic habitat that encourages the arrival of grazing taxa into those pools. In contrast, the smaller cluster comprised of a grazing chiton (*Chiton glaucus*) and filter-feeding oyster (*S. glomerata*). It is possible that the oyster can outcompete the smaller algae but experience seasonal die-offs which allow smaller algae species to colonise pools, the oysters then provide a refuge for the chiton effectively decoupling the abundances of these two clusters of taxa.

Some studies suggest enhancing eco-engineered structures may also increase their effectiveness when recruiting new species (Aguilera et al. 2014). Incorporating more microhabitats by introducing more holes and crevices onto an artificial structure may improve the function of that substrate in the environment by allowing more niches to be occupied by a range of species (Aguilera et al. 2014, Ng et al. 2015). A promising area of future research involves the seeding of artificial structures with biogenic species such as bivalves to enhance the biodiversity and overall ecosystem services of artificial structures (Coleman and Connell 2001, Wilhelmsson et al. 2006, Clynick et al. 2007, Perkol-Finkel et al. 2012, Dafforn et al. 2015, Strain et al. 2018).

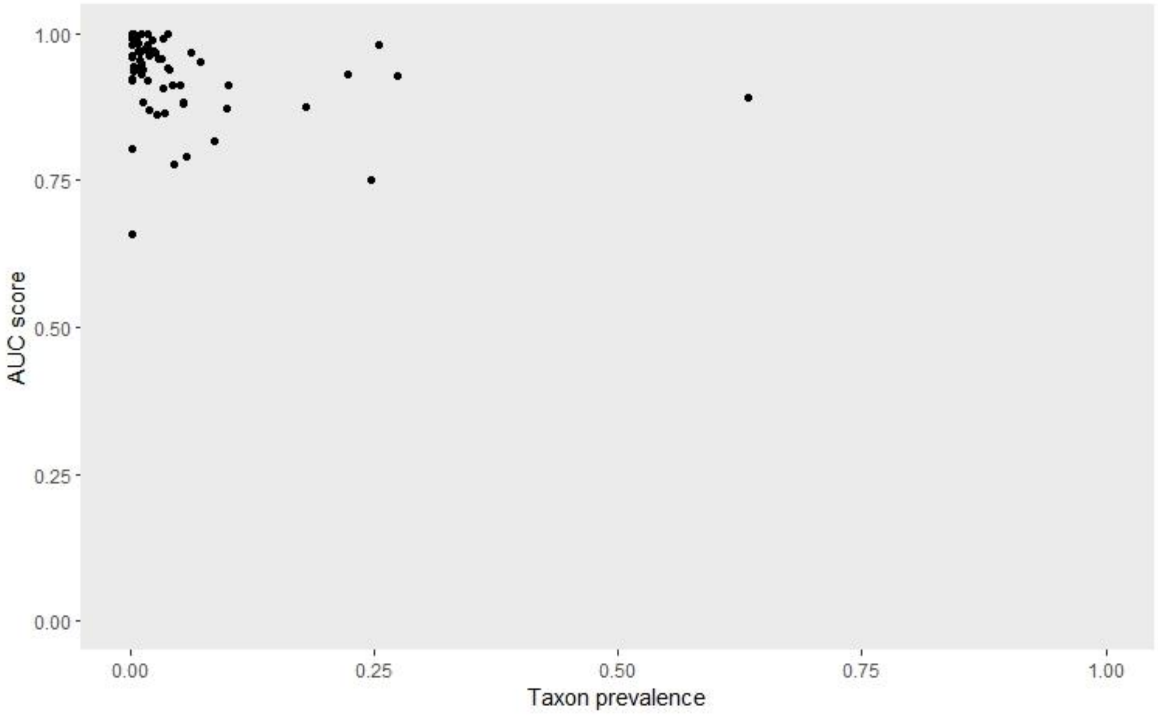
Being able to minimise any significant changes to natural assemblages of organisms when deploying artificial structures in the marine environment is a priority (Bulleri 2005, Salauddin et al. 2021). Future research needs to focus on developing a better understanding of the ecology of riprap environments, ensuring analysis of the effect of disturbance in those habitats compared with natural and other artificial rocky shores (Schiel et al. 2021). One further focus could be to examine the effect of seeding artificial structures with biogenic species and look to increase the number of available microhabitats by increasing the number of crevices and holes in the substrate and securing permanent boulders and pools. By developing a thorough understanding of the mechanisms that influence species assemblage in these artificial environments, the design and functionality of these structures can be improved to ensure their benefit and worth in aiding human development and the conservation and management of natural habitats (Bulleri 2005, Aguilera et al. 2014, Jebakumar et al. 2021, Salauddin et al. 2021).

Chapter Two Appendices:

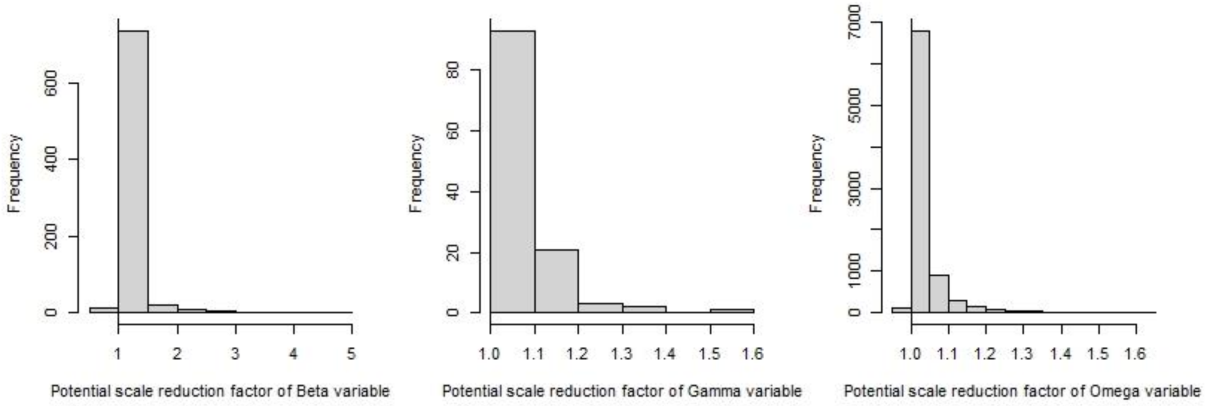
Appendix 1: Supplementary figures



Appendix 1.1: An evaluation of the explanatory power of the model. Panels A and B show the ability of the model to discriminate presences (count > 0) from absences (count = 0) in terms of AUC (A) and Tjur R^2 (B).



Appendix 1.2: The explanatory power of the HMSC model in terms of differential taxon prevalence. This plot shows the ability of the model to discriminate high abundances from low abundances in locations where species are present, measured with AUC.



Appendix 1.3: MCMC convergence diagnostics for the parameter estimates evaluated in terms of the potential scale reduction factor. A) represents the Beta variable (i.e. the fixed effects), B) represents the Gamma variable (i.e. the functional groups), C) represents the Omega variable (i.e. the random effects).

Functional Group	Substrate	Location	Disturbance	$\bar{x}$	HPD (95% confidence interval)
Canopy algae	Concrete	Kohimarama	Smothered	0.003	<0.001-0.013
			Normal	0.001	<0.001-0.003
			Desiccated	0.001	<0.001-0.003
		Takapuna	Smothered	0.001	<0.001-0.002
			Normal	0.000	<0.001-0.001
			Desiccated	0.000	<0.001-0.001
	Natural	Kohimarama	Smothered	0.034	<0.001-0.205
			Normal	0.010	<0.001-0.047
			Desiccated	0.008	<0.001-0.045
		Takapuna	Smothered	0.020	<0.001-0.104
			Normal	0.009	<0.001-0.048
			Desiccated	0.008	<0.001-0.03
	Riprap	Kohimarama	Smothered	0.060	<0.001-0.278
			Normal	0.010	<0.001-0.032
			Desiccated	0.016	<0.001-0.096
		Takapuna	Smothered	0.011	<0.001-0.059
			Normal	0.003	<0.001-0.012
			Desiccated	0.005	<0.001-0.022
Deposit feeder	Concrete	Kohimarama	Smothered	0.001	<0.001-0.002
			Normal	0.0003	0-0.0003
			Desiccated	0.0004	0-0.0003
		Takapuna	Smothered	0.009	<0.001-0.049
			Normal	0.002	<0.001-0.007
			Desiccated	0.003	<0.001-0.012
	Natural	Kohimarama	Smothered	0.007	<0.001-0.02
			Normal	0.001	<0.001-0.004
			Desiccated	0.002	<0.001-0.003
		Takapuna	Smothered	0.049	<0.001-0.325
			Normal	0.016	<0.001-0.09
			Desiccated	0.015	<0.001-0.083
	Riprap	Kohimarama	Smothered	0.017	<0.001-0.08
			Normal	0.002	<0.001-0.009
			Desiccated	0.004	<0.001-0.016
		Takapuna	Smothered	0.059	<0.001-0.304
			Normal	0.014	<0.001-0.059
			Desiccated	0.019	<0.001-0.11
Detritivore	Concrete	Kohimarama	Smothered	0.003	<0.001-0.015
			Normal	0.0003	<0.001-0.001
			Desiccated	0.0004	<0.001-0.001
		Takapuna	Smothered	0.044	<0.001-0.221
			Normal	0.007	<0.001-0.02
			Desiccated	0.009	<0.001-0.053
	Natural	Kohimarama	Smothered	0.000	<0.001-0.001
			Normal	0.000	<0.001-0.0001
			Desiccated	0.000	<0.001-0.0001
		Takapuna	Smothered	0.013	<0.001-0.064
			Normal	0.001	<0.001-0.004
			Desiccated	0.002	<0.001-0.009
	Riprap	Kohimarama	Smothered	0.007	<0.001-0.037
			Normal	0.001	<0.001-0.002
			Desiccated	0.001	<0.001-0.003
		Takapuna	Smothered	0.071	<0.001-0.318
			Normal	0.009	<0.001-0.023

			Desiccated	0.014	<0.001-0.082
Encrusting algae	Concrete	Kohimarama	Smothered	0.011	<0.001-0.048
			Normal	0.008	<0.001-0.037
			Desiccated	0.010	<0.001-0.052
		Takapuna	Smothered	0.104	<0.001-0.419
			Normal	0.043	<0.001-0.118
			Desiccated	0.049	<0.001-0.222
	Natural	Kohimarama	Smothered	0.003	<0.001-0.007
			Normal	0.002	<0.001-0.009
			Desiccated	0.004	<0.001-0.017
		Takapuna	Smothered	0.016	<0.001-0.078
			Normal	0.005	<0.001-0.023
			Desiccated	0.013	<0.001-0.062
	Riprap	Kohimarama	Smothered	0.096	<0.001-0.455
			Normal	0.055	<0.001-0.178
			Desiccated	0.104	<0.001-0.416
		Takapuna	Smothered	0.188	<0.001-0.626
			Normal	0.079	<0.001-0.207
			Desiccated	0.177	<0.001-0.571
Filter feeder	Concrete	Kohimarama	Smothered	0.047	<0.001-0.216
			Normal	0.035	0.001-0.106
			Desiccated	0.060	<0.001-0.222
		Takapuna	Smothered	0.054	<0.001-0.2
			Normal	0.057	0.007-0.134
			Desiccated	0.071	<0.001-0.257
	Natural	Kohimarama	Smothered	0.111	<0.001-0.46
			Normal	0.087	0.011-0.218
			Desiccated	0.121	<0.001-0.432
		Takapuna	Smothered	0.179	<0.001-0.54
			Normal	0.205	0.096-0.335
			Desiccated	0.174	<0.001-0.56
	Riprap	Kohimarama	Smothered	0.090	<0.001-0.41
			Normal	0.043	0.001-0.129
			Desiccated	0.103	<0.001-0.396
		Takapuna	Smothered	0.065	<0.001-0.268
			Normal	0.058	0.005-0.144
			Desiccated	0.089	<0.001-0.34
Grazer	Concrete	Kohimarama	Smothered	0.036	<0.001-0.156
			Normal	0.183	0.07-0.309
			Desiccated	0.025	<0.001-0.095
		Takapuna	Smothered	0.090	<0.001-0.324
			Normal	0.257	0.122-0.416
			Desiccated	0.049	<0.001-0.177
	Natural	Kohimarama	Smothered	0.034	<0.001-0.158
			Normal	0.180	0.055-0.305
			Desiccated	0.037	<0.001-0.14
		Takapuna	Smothered	0.051	<0.001-0.224
			Normal	0.169	0.06-0.32
			Desiccated	0.052	<0.001-0.201
	Riprap	Kohimarama	Smothered	0.080	<0.001-0.314
			Normal	0.287	0.127-0.445
			Desiccated	0.073	<0.001-0.258
		Takapuna	Smothered	0.092	<0.001-0.327
			Normal	0.306	0.146-0.475

			Desiccated	0.078	<0.001-0.256
Predator	Concrete	Kohimarama	Smothered	0.132	0.002-0.384
			Normal	0.090	0.024-0.213
			Desiccated	0.029	<0.001-0.111
		Takapuna	Smothered	0.209	0.003-0.513
			Normal	0.160	0.046-0.325
			Desiccated	0.055	<0.001-0.203
	Natural	Kohimarama	Smothered	0.178	0.002-0.591
			Normal	0.162	0.018-0.418
			Desiccated	0.035	<0.001-0.159
		Takapuna	Smothered	0.379	0.006-0.818
			Normal	0.253	0.066-0.437
			Desiccated	0.102	<0.001-0.491
	Riprap	Kohimarama	Smothered	0.185	0.001-0.526
			Normal	0.133	0.023-0.359
			Desiccated	0.035	<0.001-0.132
		Takapuna	Smothered	0.251	0.005-0.651
			Normal	0.229	0.057-0.417
			Desiccated	0.073	<0.001-0.331
Sub-canopy algae	Concrete	Kohimarama	Smothered	0.227	<0.001-0.654
			Normal	0.154	0.003-0.287
			Desiccated	0.168	<0.001-0.459
		Takapuna	Smothered	0.023	<0.001-0.132
			Normal	0.028	<0.001-0.113
			Desiccated	0.020	<0.001-0.114
	Natural	Kohimarama	Smothered	0.347	<0.001-0.877
			Normal	0.184	0.003-0.388
			Desiccated	0.253	<0.001-0.719
		Takapuna	Smothered	0.030	<0.001-0.177
			Normal	0.021	<0.001-0.09
			Desiccated	0.027	<0.001-0.161
	Riprap	Kohimarama	Smothered	0.164	<0.001-0.618
			Normal	0.118	0.005-0.298
			Desiccated	0.117	<0.001-0.459
		Takapuna	Smothered	0.010	<0.001-0.047
			Normal	0.018	<0.001-0.058
			Desiccated	0.008	<0.001-0.042
Scavenger	Concrete	Kohimarama	Smothered	0.041	<0.001-0.142
			Normal	0.024	0.005-0.048
			Desiccated	0.019	<0.001-0.074
		Takapuna	Smothered	0.087	<0.001-0.29
			Normal	0.054	0.015-0.094
			Desiccated	0.044	<0.001-0.159
	Natural	Kohimarama	Smothered	0.034	<0.001-0.158
			Normal	0.031	0.003-0.072
			Desiccated	0.020	<0.001-0.098
		Takapuna	Smothered	0.060	<0.001-0.24
			Normal	0.066	0.016-0.117
			Desiccated	0.036	<0.001-0.167
	Riprap	Kohimarama	Smothered	0.065	<0.001-0.239
			Normal	0.030	0.005-0.064
			Desiccated	0.032	<0.001-0.13
		Takapuna	Smothered	0.094	<0.001-0.312
			Normal	0.053	0.014-0.09

			Desiccated	0.051	<0.001-0.182
Turf algae	Concrete	Kohimarama	Smothered	0.500	0.017-0.873
			Normal	0.506	0.305-0.695
			Desiccated	0.688	0.372-0.965
		Takapuna	Smothered	0.380	0.003-0.781
			Normal	0.391	0.206-0.548
			Desiccated	0.699	0.365-0.965
	Natural	Kohimarama	Smothered	0.251	<0.001-0.748
			Normal	0.342	0.103-0.56
			Desiccated	0.519	0.078-0.904
		Takapuna	Smothered	0.203	<0.001-0.669
			Normal	0.256	0.065-0.426
			Desiccated	0.571	0.111-0.966
	Riprap	Kohimarama	Smothered	0.235	<0.001-0.687
			Normal	0.321	0.113-0.534
			Desiccated	0.514	0.104-0.889
		Takapuna	Smothered	0.159	<0.001-0.561
			Normal	0.230	0.078-0.366
			Desiccated	0.487	0.073-0.874

Appendix 1.4: Mean functional group prevalence (and 95% HPD intervals) in each combination of location, habitat and disturbance.

Chapter Three: Kelp canopy and adhesives enhance the success of kelp reforestation using Green Gravel

3.1 Abstract

Kelp forests provide habitat and support extraordinary levels of biodiversity, yet they are facing global declines, including in New Zealand. Restoration efforts are crucial to counteract this decline, and a promising approach to address kelp forest decline involves seeding small gravel with kelp spores and cultivating them in the laboratory through the microsporophyte stage before transplanting to the restoration site (termed Green Gravel). This chapter explores the efficacy of different Green Gravel methodologies for restoring collapsed *Ecklonia radiata* forests and investigates the impact of environmental conditions on gravel retention and sporophyte length. Although it was not surprising to find that gluing gravel to the substrate significantly improved gravel retention, what was surprising was sporophyte lengths on placed gravel were initially 100mm less than glued gravel sporophytes, but similar by the end of the experiment. Despite three times lower retention of placed Green Gravel compared with glued Green Gravel, an overall retention of 20% after 14 months for placed gravel still offers restoration potential, especially for community groups where there might be greater limitations on using adhesives compared with the production of Green Gravel. During the first 5-7 months of development, sporophyte lengths were greater in urchin-barren environments, while in the subsequent 7-9 months, sporophyte lengths were greater within an *E. radiata* canopy. It is not clear if this pattern was a consequence of developmental stage, disturbance, or season as the early burst of growth in the barren habitats occurred in autumn and winter whereas the late burst of growth in kelp forest habitats occurred in summer and spring when irradiance and temperatures are higher. This study underscores the importance of considering habitat characteristics, season, and the engineering effects of adult kelp when implementing restoration techniques. Future research should optimize transplanting densities and assess long-term restoration outcomes across seasons, investigating the effect of wave energy and disturbances, and the effectiveness of complementary tools like attachment methods. Due to the relative ease of implementation, Green Gravel offers promise as a tool for community-led active marine restoration and ameliorating some of the challenges our declining kelp forests face.

3.2 Introduction

Being among the most prolific primary producers on Earth, kelp forests play a foundational role in rocky reef communities through their physical structure and abiotic influence (Dayton 1985, Steneck et al. 2002, Bennett et al. 2016, Teagle et al. 2017, Filbee-Dexter et al. 2022). The estimated economic value of the biodiversity, climate regulation, coastal protection, and provision of food, consumable products and other services (Velimirov et al. 1977, Abdullah et al. 2017, Blamey and Bolton 2018, Filbee-Dexter et al. 2022) that kelp ecosystems support, is estimated in the millions of dollars per kilometre of coastline (Bennett et al. 2016, Blamey and Bolton 2018, Eger et al. 2021). Furthermore, once these habitats are established, there are positive feedback mechanisms that favour their long-term persistence, providing valuable, long-term benefits (Filbee-Dexter and Scheibling 2014, Layton et al. 2020).

Regrettably, despite the global rise in commercial kelp aquaculture (Coleman et al. 2022), wild kelp forests are presently undergoing alarming declines (Fujita 2011, Johnson et al. 2011, Moy and Christie 2012, Krumhansl et al. 2016, Blamey and Bolton 2018, Martínez et al. 2018, Wernberg et al. 2019b, Filbee-Dexter et al. 2020, Tait et al. 2021). Kelp decline is a growing concern and although the deterioration of these forests is fuelled by various factors, it is primarily the overharvesting of keystone species, coastal development, pollution and a changing climate that have been highlighted as the key contributors (Johnson et al. 2011, Bennett et al. 2016, Krumhansl et al. 2016, Filbee-Dexter and Wernberg 2018, Vergés et al. 2019). As kelp communities deteriorate, ecosystems undergo a phase shift to areas dominated by turf-algae (Filbee-Dexter and Wernberg 2018) or urchin barrens (Shears and Babcock 2002, Filbee-Dexter and Scheibling 2014, Ling et al. 2015), further hindering the natural recruitment and development of juvenile kelp (Layton et al. 2019a, Coleman et al. 2020), and increasing the likelihood of a permanent phase shift from dense kelp forest to a turf or barren dominated state.

Ecklonia radiata, the dominant laminarian kelp species along the North-East coast of New Zealand (Shears and Babcock 2007), is the most widely distributed kelp on our planet, predominantly forming monospecific forests (Wernberg et al. 2019a). Flourishing in rocky reefs and shallow waters up to approximately 40 meters in depth, this eco-engineer is even found at depths of up to 90 meters in certain regions (Nelson et al. 2015). Sustaining growth on the reef for up to a decade (Novaczek 1984), *E. radiata* plays a pivotal role in delivering valuable ecosystem services to the rocky reef community (Wernberg et al. 2019a). However, similar to other kelp forests worldwide, these vital ecosystems are presently facing decline, alarming coastal and indigenous communities as once-thriving kelp forests transform into desolate, barren landscapes dominated by crustose coralline algae and sea urchins (predominantly *Evechinus chloroticus*).

In light of these challenges, active and passive restoration are the two main approaches employed for restoring damaged or degraded ecosystems, each striving to achieve restoration goals through contrasting methods (Walters and Holling 1990). Active restoration involves direct intervention to promote the growth of a desired species, such as by transplanting kelp into the ecosystem or managing populations of grazing urchins (Eger et al. 2022a, Eger et al. 2022b). In contrast, passive restoration relies on natural processes promoting ecosystem recovery, by reducing or removing sources of stress and disturbance to allow the ecosystem to recover on its own (e.g. improving water quality: Foster and Schiel 2010, limiting kelp harvest: Fujita 2011, and reducing fishing pressure: Hopf et al. 2022). The choice between passive and active restoration depends on a careful assessment of the specific ecosystem, the extent and severity of degradation, resource availability, and restoration project objectives (Eger et al. 2022a).

The restoration of kelp forests holds both positive and negative implications, necessitating careful consideration before intervention, both at local and global scales (Eger et al. 2022a). Active restoration of kelp forests, if feasible and appropriate, could prevent further loss of kelp forests and enhance population resilience (Aitken and Whitlock 2013, Fredriksen et al. 2020, Cebrian et al. 2021, Gleason et al. 2021, Eger et al. 2022b). Nonetheless, restoration projects should always take into account the multitude of stressors affecting kelp ecosystems and how these will affect restoration efforts (Eger et al. 2022a). Given the difficulty of passive restoration when phase shifts have occurred, the initial adoption of an active restoration approach appears promising to rebuild lost forest populations (Cebrian et al. 2021) transitioning into passive restoration as the ecosystem begins to recover (Eger et al. 2022a).

A novel restoration approach utilizing "Green Gravel" has been developed at the Institute of Marine Research in Norway, aiming to overcome some limitations associated with active kelp forest restoration (Fredriksen et al. 2020). The process involves seeding kelp spores directly onto small gravel, which develop into sporophytes in a nursery environment before being transplanted onto the reef. This gravel acts as a weight for the sporophytes, allowing them to establish holdfasts and naturally cement to the reef. Green Gravel shows promise as an affordable, accessible, and easily upscaled method for kelp restoration, potentially aiding in the "future-proofing" of vulnerable kelp ecosystems (Fredriksen et al. 2020). Evaluating the efficacy of using Green Gravel as an active restoration tool in New Zealand can provide valuable insights for community groups wanting to take proactive approaches to rejuvenate areas displaying signs of kelp degradation.

Here, we examined the effectiveness of using different methodologies to seed *E. radiata* on small gravel to create Green Gravel, as well as varying techniques for transplanting the Green Gravel onto the reef. Specifically, we assessed the effect of depth, habitat and attachment method, on gravel retention and sporophyte length on Green Gravel. We hypothesised that sporophytes would exhibit increased length in shallow sites with higher light available (Smith et al. 2020), yet retention of green gravel would be compromised in such areas due to heightened susceptibility to disturbance from concentrated swell conditions. Attaching gravel using an adhesive would positively impact the retention of Green Gravel by minimising disruption to both the gravel and developing sporophytes, facilitating holdfast attachment to the reef. Additionally, sporophytes transplanted within a kelp canopy would have greater length due to the ecosystem engineering effects of adult E. radiata facilitating juvenile development, while Green Gravel transplanted in barrens may have lower retention due to being more exposed to wave action (Layton et al. 2019b).

3.3 Methods

3.3.1 Study Design

Cultivation of Ecklonia radiata

The cultivation of *Ecklonia radiata* can be divided into four distinct stages: zoospore release, gametophyte growth, fertilization, and sporophyte growth. For the purposes of this thesis, we focus on two stages: zoospore release and sporophyte growth. The cultivation protocol followed the New England Seaweed Culture Handbook (Redmond 2014) with minor adjustments to enhance accessibility and eliminate the need for specialized laboratory equipment.

Experiments involved a combination of *E. radiata* sori (reproductive kelp tissue) obtained through SCUBA diving and freshly beach-cast sori, collected from Ti Point, Matheson's Bay, and Omaha Beach in the North-East of New Zealand (Figure 3.1A). To initiate the desiccation process, the collected kelp tissue was placed in mesh bags and exposed to full sunlight for 2 hours. Ripe sori tissue (Figure 3.1B) was gently wiped with paper towels to remove epibionts before further desiccation in the dark at 17°C for 120 minutes. The sori were then transferred to culture tanks with a base layer of small gravel (2-4cm diameter; Figure 3.1C) and filled with filtered seawater (to 1 µm) sourced from local beaches. Each tank received a single air stone to encourage gentle water movement and gas diffusion. The culture tanks containing sori and gravel were then placed in a 17°C water bath overnight, with a complete water change the following morning and Provasoli Enriched Seawater Media (PES) added at a dose of 20ml/L (Redmond 2014).

The growth rate of sporophytes is influenced by day length, irradiance, temperature, and nutrient availability (Praeger et al. 2022). During the initial 4-week period, the gravel was placed in static culture tanks maintained at a constant temperature of 17°C (Figure 3.1C). Fortnightly water changes were carried out, accompanied by nutrient supplementation (20ml/L of PES) to ensure standardized growth conditions. A single light source with a photosynthetic photon flux density of approximately 30µmol/s/m2 was used for each tank during this period, and gradually increased to two light sources with a total of 50µmol/s/m2 over the first two months of cultivation, while maintaining a consistent 16:8hr light:dark photoperiod.

To acclimate sporophytes to natural environments before transplantation into the field, the seeded Green Gravel was transitioned to flow-through culture tank systems after approximately 40 days in the static culture tanks (Figure 3.1D). Additional flow was introduced using small pickup filters to stimulate dynamic oceanic conditions, enhancing gas exchange and waste removal (Hurd 2000). To mitigate rising pH due to kelp respiration and reduce the bioload in the flow-through system, sporophyte coverage on the gravel was manually reduced by approximately 50% on each Green Gravel, 10 days after the transition to the flow-through, using a scalpel blade. Green Gravel was transplanted once sporophytes were larger than 20mm, after spending 108 days in the culture tanks (Figure 3.1E and 3.1F).

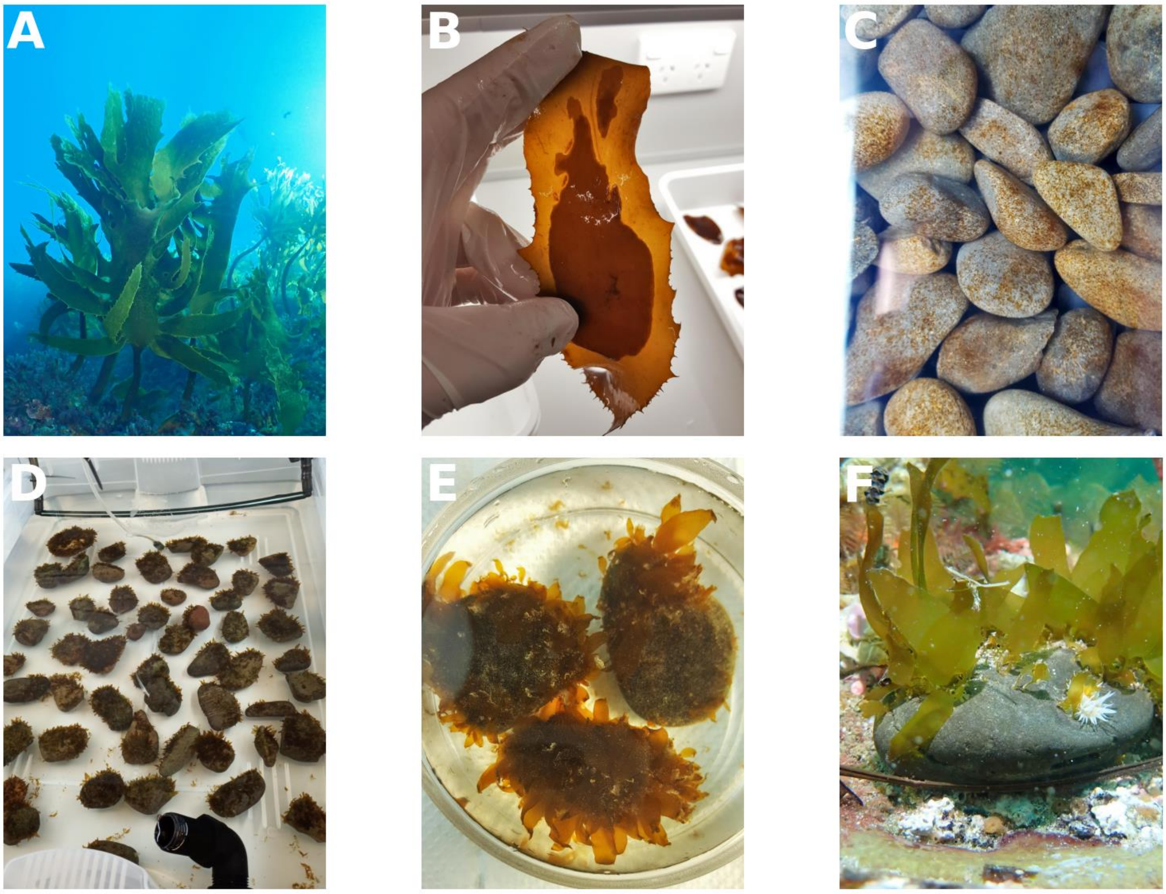


Figure 3.1: Process of creating Green Gravel. A: Collect ripe sorus tissue from adult *Ecklonia radiata* from beach cast kelp or from the sea, B: Clean sorus tissue and start desiccation process, C: Seed gravel by soaking desiccated sorus tissue in seawater above gravel – this image is taken one month after seeding gravel when sporophytes were 2-4mm, D: Flow-through culture tanks with additional flow and water volume, E: Sporophytes ready for transplant, F: Sporophytes one month after transplant into the field.

Sporophyte Settlement Study

A factorial experiment (*n* =140) was employed to investigate the potential influence of gravel type at four levels (river pebble, scoria, white chip, and roading chip) and cleaning method at three levels (mechanically washed, hand washed, and sterilised) on the coverage of *E. radiata* sporophytes after 90 days. Mechanically washed gravel underwent a household dishwasher cycle without detergent, sterilised gravel were briefly submerged in 95% ethanol, followed by thorough rinsing in distilled water for 5 minutes, and hand washed gravel were rinsed manually in freshwater for 5 minutes. All gravel used were 2-4cm in diameter, and samples of the four gravel types were purchased from a local gardening store (Figure 3.2). We measured sporophyte length from the base of the stipe to the top of the central lamina, excluding any eroding tissue and counted the number of sporophytes growing on each gravel.

Figure 3.2: Rock types used in cleaning method trial. A: Scoria, B: River pebbles, C: Roading chip, D: White chip.

Field Study Design

A total of 312 river pebbles, seeded in two batches using the simplified kelp cultivation technique described above, were transplanted to Ti Point reef, Auckland. The site is characterised by small barren patches embedded within a kelp forest. Ti Point reef is located adjacent to an estuary entrance, influenced heavily by freshwater draining from the surrounding catchment causing periods of high sedimentation and low light. We intended to collect fortnightly data on both batches of Green Gravel however, we were restricted with weather and only managed to collect eleven measurements with batch one and three measurements for batch two.

The first batch of Green Gravel (*n* =192) was transplanted in April 2022, with the first set of measurements starting 16 days after transplantation and ending on day 420, after approximately 14 months in the field. A factorial experiment was implemented to investigate the potential influence of depth at two levels (5m and 8m), habitat at two levels (on barren reef and within the kelp canopy; Figure 3.3), and attachment at two levels (glued and placed) on sporophyte length and retention of *E. radiata* Green Gravel. Green Gravel was either glued to the reef using a two-part epoxy (Splash Zone A-788) or placed into small divots within the reef structure to prevent them from sliding off the rock surface too easily. There were two replicate plots for each combination of factors giving 16 plots in total. Plots for the two levels of depth were separated by 50m of each other, plots for the two levels of habitat were separated by 25m, plots for the two levels of attachment were separated by 10m. Twelve Green Gravel were transplanted into each combination of levels in our experimental design.

The second batch of Green Gravel (*n* =120) was transplanted in September 2022, with the first measurements collected 13 days after transplanting and finishing on day 259, just over 8 ½ months later. A factorial experiment was implemented to investigate the potential influence of habitat at two levels (on barren reef and within the kelp canopy; Figure 3.3) and attachment at two levels (glued and placed) on sporophyte length and retention of *E. radiata* Green Gravel. There were three replicate plots for each combination of factors giving 12 plots in total. Depth was not considered in this experiment due to the smaller batch size and all gravel was transplanted at 8m. Habitat and attachment remained consistent with plots separated by 10m. Ten Green Gravel were transplanted into each combination of levels in our experimental design.

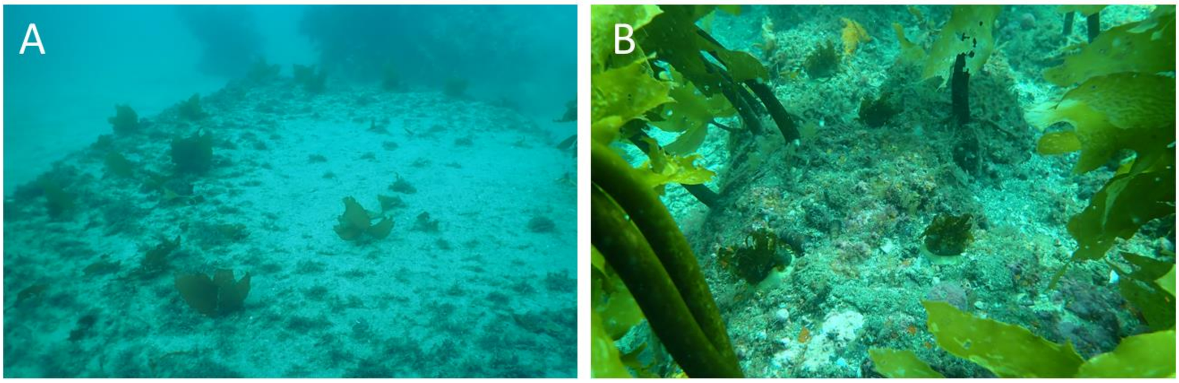


Figure 3.3: Habitat types for Green Gravel deployments: Barren areas (A) and within kelp forest canopies (B)

To assess the size of *E. radiata* sporophytes for both batches of Green Gravel within the first 90 days in the laboratory environment before transplantation to the field, length measurements (in mm) of sporophytes were obtained by taking photographs using Zeiss Axiocam 105 colour camera with the Leica DM IL LED Inverted Laboratory Microscope and processed in ZenBlue Ver.2.6 (Zeiss 2018).

In the field, we measured the length of largest sporophyte on each gravel from the base of the stipe to the top of the central lamina using a ruler. If the gravel was devoid of kelp but still present, a value of 0 was assigned for sporophyte length; however, if the gravel was completely lost a length was not recorded for that sample. Placed gravel moved considerably during the experiment, and so confidently identifying individual gravel and treating these data as repeated measures on individuals was challenging. Similarly, taking length measurements of sporophytes without disturbing placed Green

Gravel was challenging in the early stages, therefore, to encourage attachment, length data for placed gravel was only captured after 99 days in the field.

Temperature and light data were collected using HOBO pendant loggers for six months (October – March) during the experiment (Onset Computer Corporation 2022). Loggers were bolted to the reef both within the kelp canopy and on barren reef adjacent to the treatment plots. Temperature remained consistent across treatment plots, but lighting conditions differed between habitats, with a daily mean LUX of 246 among the kelp canopy and 1434 in barren areas. All seedlings were grown in a common garden in the laboratory and then randomly allocated to the treatment plots.

3.3.2 Sporophyte Settlement Analysis

To assess the potential influence of gravel type and cleaning method on the number of sporophytes, a linear model was used. The response variable was the number of sporophytes on each Green Gravel, with cleaning method and gravel type as fixed effects and the interaction between these variables included. Given that the mean number of sporophytes per gravel was 11.84, a linear model assuming a Gaussian error distribution was used for simplicity rather than a generalised linear model using a Poisson error distribution. Given that there were no sporophytes detected on any of the gravel types in the sterilised treatment after 90 days, the analysis below only included hand and mechanically washed gravel for the cleaning treatment.

3.3.3 Field study analysis

To evaluate the effects of depth, habitat, and attachment on the retention of Green Gravel and sporophyte length post-transplantation, mixed-effects COX proportional hazards models using the coxme (Therneau 2022) and survival (Therneau 2023) packages and linear mixed-effects models using the lme4 (Bates et al. 2015) package were used, respectively.

In the COX proportional hazards model, habitat, depth (for batch one only) and attachment were treated as fixed effects, with plot treated as a random effect. The response variable was binary where 0 indicated the retention of a Green Gravel pebble and 1 indicated a loss of either the kelp on the Green Gravel, or the gravel itself. In the linear mixed effects models, habitat, depth, attachment method and days were treated as fixed effects, and two-way interactions between variables were included, with plot as a random effect. Lastly, to examine the differences in sporophyte lengths among batches we fit a linear mixed effects model treating days and batch, and their interaction as fixed effects, with plot included as a random effect.

To compare mixed-effects COX models and assess how the addition or removal of predictor variables and interactions affected the model fit, log-likelihood ratio tests using the ‘anova’ function in the base package were used. For sporophyte length analyses, a backward model selection by single-term deletions were performed using the ‘drop1’ function in the base package. All analyses were conducted using R version 4.3.1. (R Core Team 2023) and Rstudio, using ggplot2 (Wickham et al. 2016) and survminer (Kassambara et al. 2021) packages to plot the results.

3.4 Results

3.4.1. Effect of Cleaning Treatment and Gravel Type on Sporophyte Settlement

Sterilising gravel in ethanol resulted in complete batch failure despite thoroughly rinsing gravel in distilled water after exposure to ethanol; consequently, the sterilised level of the cleaning treatment was removed from further analyses. We found a significant main effect of gravel type on the number of sporophytes ($F_{3, 95}$ = 2608.56, $p < 0.001$), but no significant main effect of cleaning method ($\bar{x}$ = 1.983, Tukey’s 95% CI: -2.25 to 6.217, $F_{1, 98}$ = 94.41, $p > 0.05$) or significant interaction between gravel type and cleaning method ($F_{3, 92}$ = 605.41, $p > 0.05$; Figure 3.4). Estimated marginal means and post-hoc Tukey tests revealed that the mean number of sporophytes on white chip gravel was not significantly different from river pebbles ($\bar{x}$ = -7.32, Tukey’s 95% CI: -15.05 to 0.41). Considering that river pebbles are more readily available and typically more cost-effective than white chip, we decided to use hand-rinsed, river pebbles for all subsequent experiments.

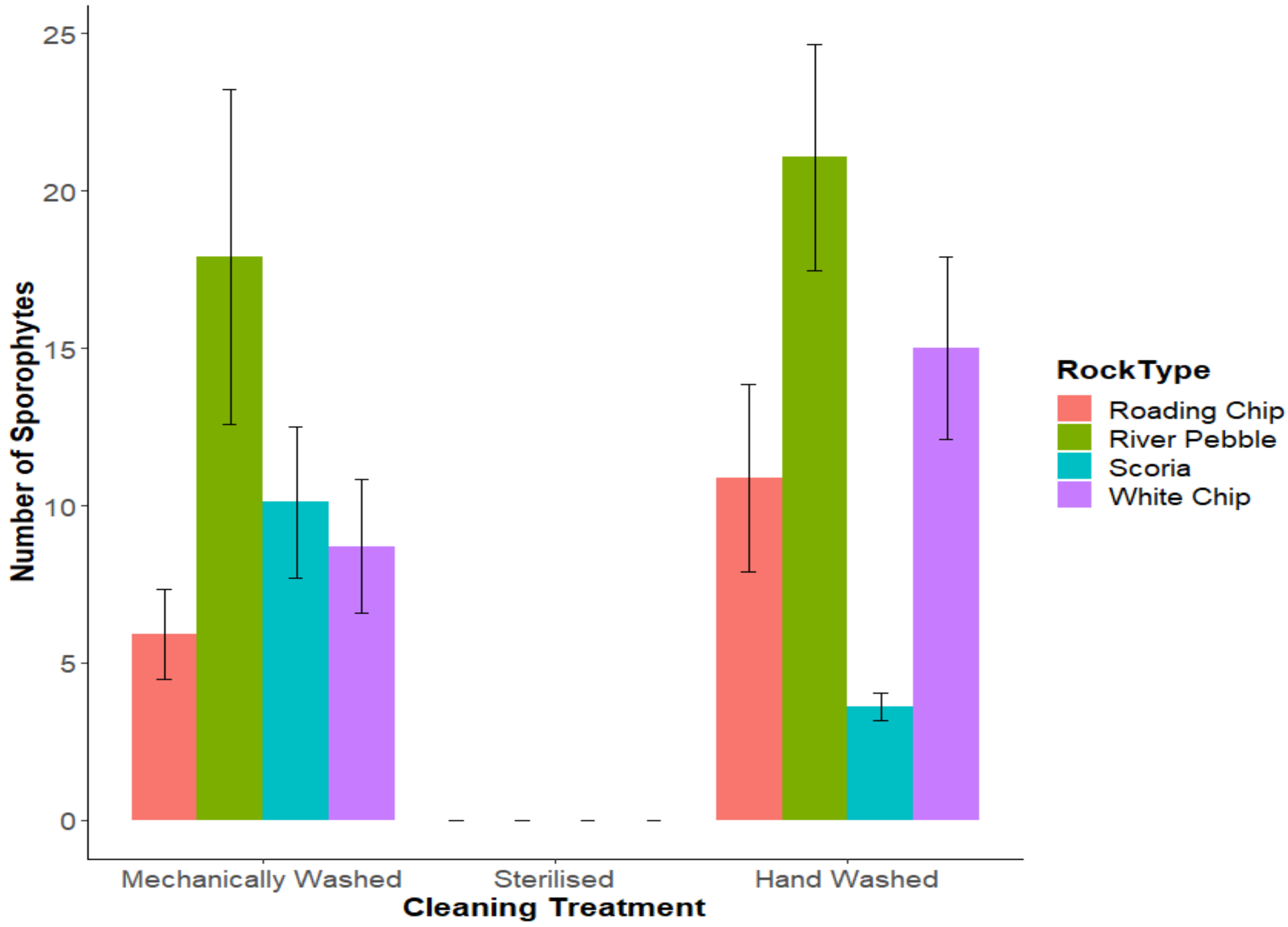


Figure 3.4: Mean (±SE) number of sporophytes of *Ecklonia radiata* on different gravel types (roading chip, river pebble, scoria, white chip, *n* =140) exposed to different cleaning treatments before seeding (mechanically washed, sterilised and hand washed).

3.4.2 Effect of attachment, depth, and habitat on gravel retention

In the first 90 days after seeding in the laboratory, the mean sporophyte length was 34.4mm (±0.61), and sporophytes exhibited an average growth rate of 0.38mm/day.

Analysis of the first batch of Green Gravel indicated that gravel retention was not influenced by habitat (χ^2_1= 2.3936, $p > 0.05$) or depth (χ^2_1= 0.0177, $p > 0.05$) but varied between attachment methods, with glued gravel having a higher estimated retention probability compared to placed gravel (χ^2_1= 9.9264, $p < 0.001$; Figure 3.5). In the second batch, we observed notable disparities in gravel retention between attachment methods across the two habitats (Figure 3.6). The retention probability was similar for placed gravel between habitats (Kelp: 0.21 ±0.07; Barren: 0.12 ±0.05) whereas glued Green Gravel within the kelp canopy had greater retention probability than glued Green Gravel in barren habitats (Kelp: 0.852 ±0.06; Barren: 0.51 ±0.09).

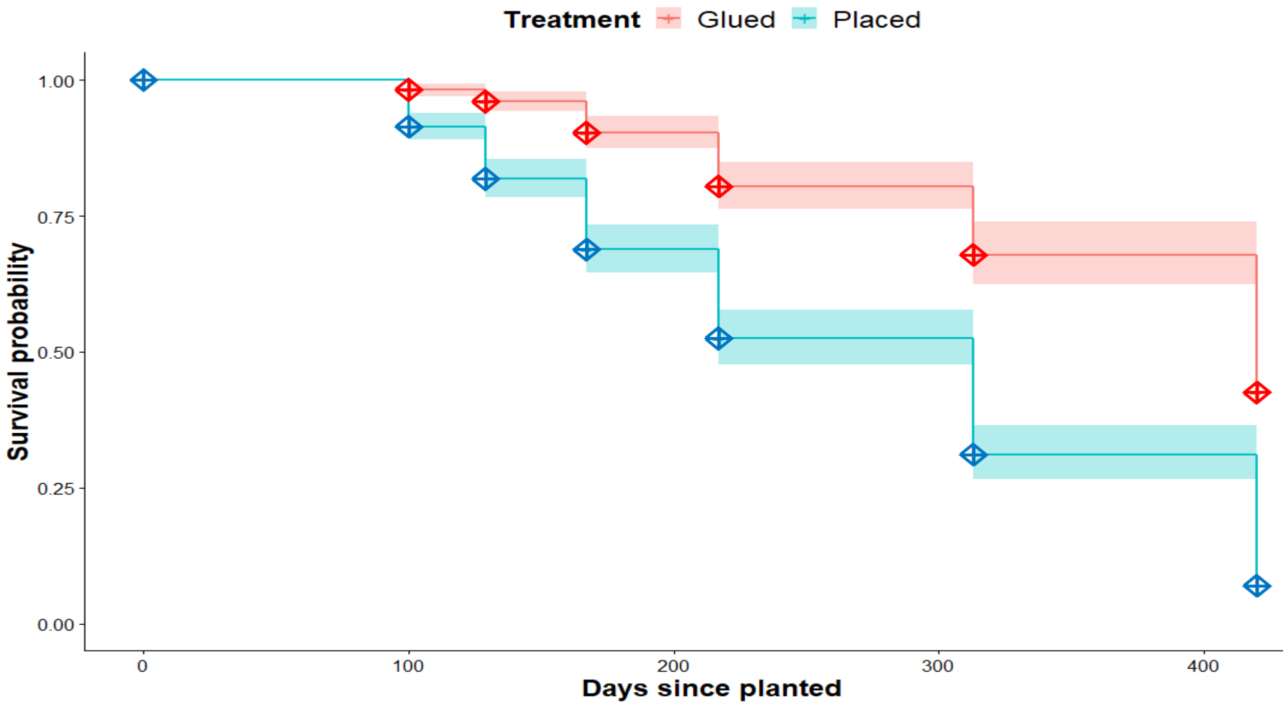


Figure 3.5: COX proportional hazards plot showing the estimated survival probabilities (±95% confidence intervals indicated by shading) for glued and placed Green Gravel treated in batch one (*n* =192) over the experimental period (April 2022 – June 2023).

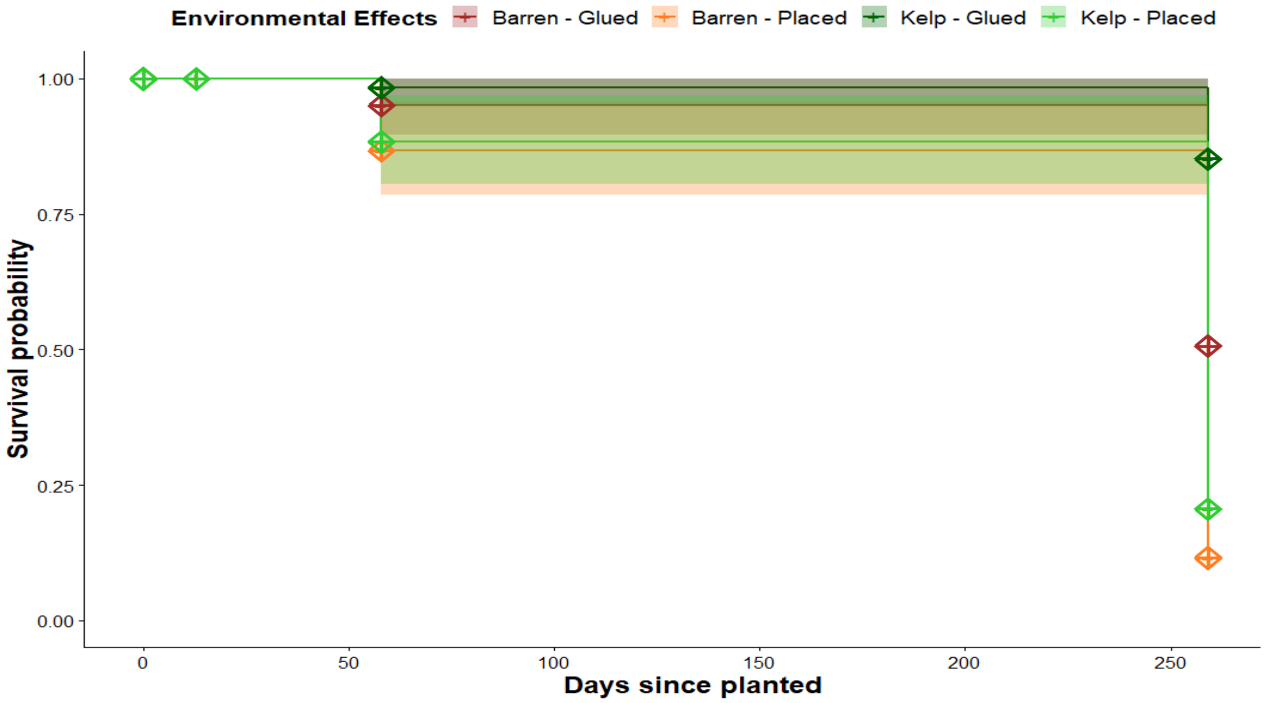


Figure 3.6: COX proportional hazards plot showing the estimated survival probabilities (±95% confidence intervals indicated by shading) for glued and placed Green Gravel in barren habitats and within the kelp canopy, treated in batch two (*n* =120) over the experimental period (October 2022 – June 2023).

3.4.3 Effect of attachment, depth, and habitat on sporophyte length of *Ecklonia radiata* on Green Gravel

After 14 months in the field, 50% of retained gravel from the first batch harboured reproductive kelp with an average length of 368.7mm (±13.06), growing at an average rate of 0.77mm/day, and the tallest sporophyte reaching 610mm (Figure 3.7). Analysis of glued Green Gravel over the 14 months revealed no significant effect of depth ($\chi^2_1 = 2.777$, p-value > 0.05) on sporophyte length, but a significant interaction between days and habitat ($\chi^2_1 = 4.568$, p-value = 0.033). Specifically, sporophytes in barren environments initially experienced rapid growth, while the sporophytes transplanted within the kelp canopy exhibited greater late growth (Figure 3.8). The analysis of both glued and placed Green Gravel also indicated a similar effect of habitat on mean sporophyte length ($\chi^2_1 = 11.881$, p-value < 0.001), favouring barren habitats in the early stages of transplantation (Figure 3.9), with the glued sporophytes in kelp habitats surpassing the barren sporophytes faster than the placed group ($\chi^2_1 = 14.43$, p-value < 0.001).

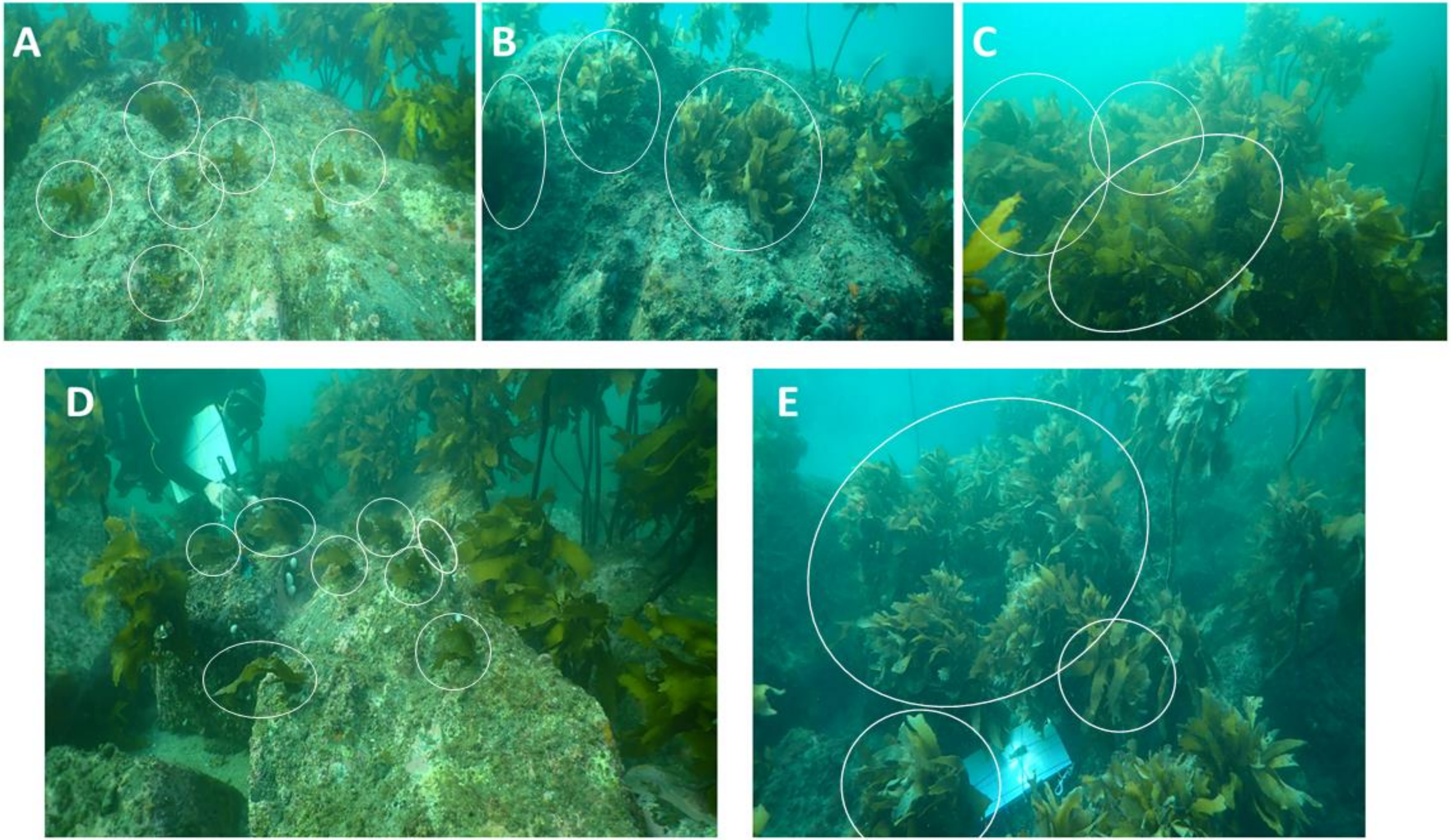


Figure 3.7: Green Gravel growth over 14 months in two plots. A, B and C represent plot one while D and E represent plot two. Green gravel is circled in each photo.

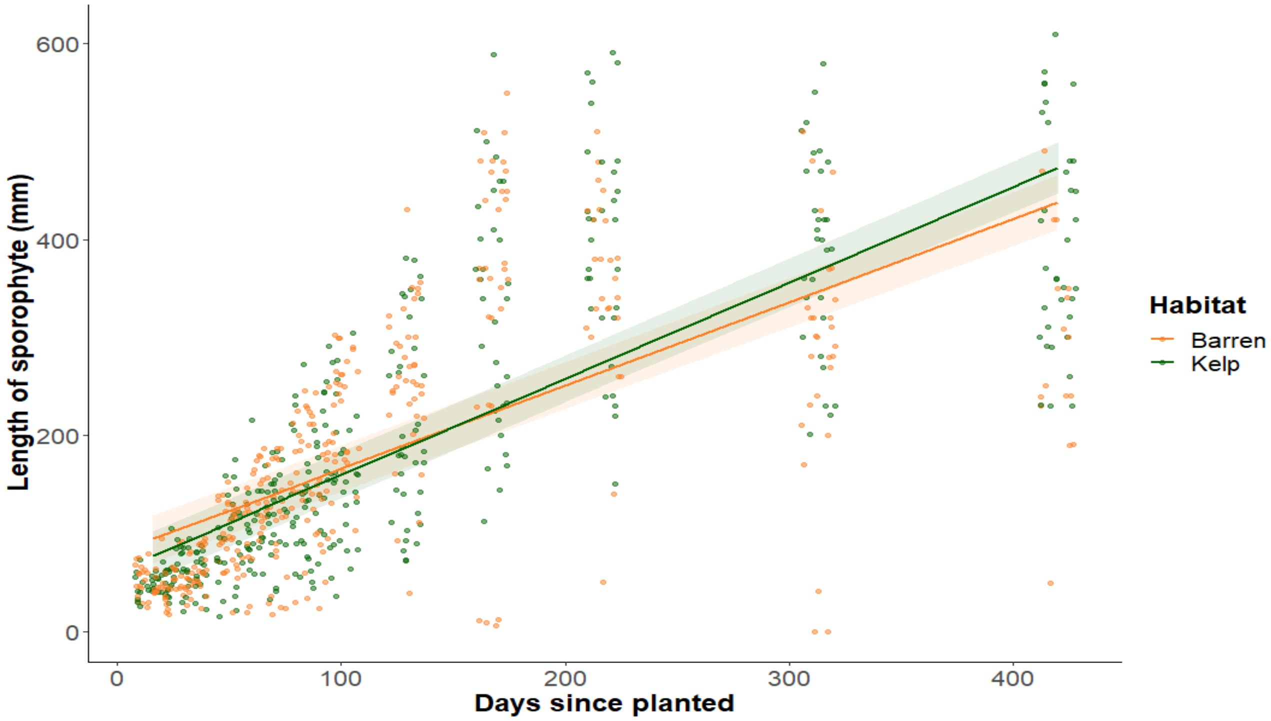


Figure 3.8: Effect of habitat on changes in sporophyte length (±95% confidence intervals indicated by shading) for glued batch one sporophytes (*n* =192), sampled between days 16 (April 2022) and 420 (June 2023) since transplanting.

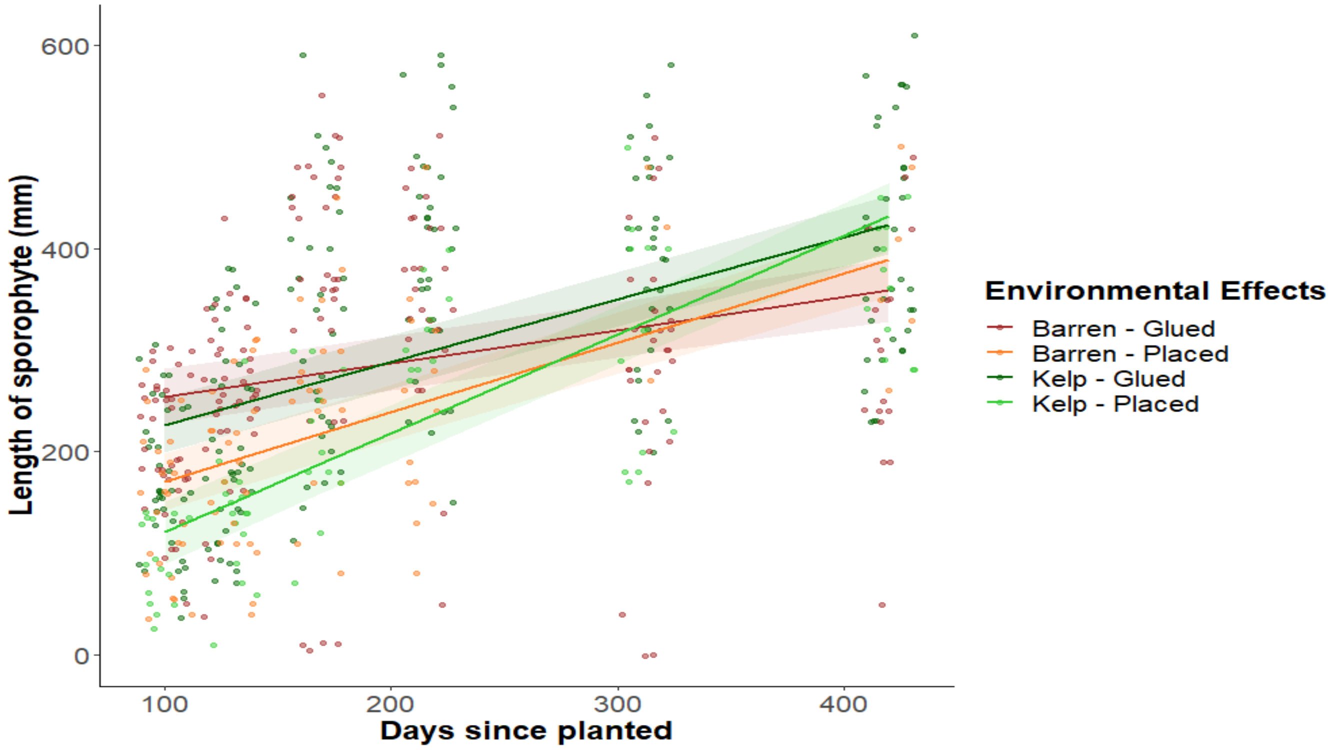


Figure 3.9: Effect of habitat and attachment method on changes in sporophyte length (±95% confidence intervals indicated by shading) for batch one sporophytes (*n* =192), sampled between days 99 (August 2022) and 420 (June 2023) since transplanting.

After approximately 8 ½ months in the field, sporophytes in the second batch of Green Gravel reached an average length of 117.5mm (±16.76), with an average growth rate of 0.33mm/day, and the tallest sporophyte measuring 270mm. Unfortunately, due to several, severe weather events during January and February 2023 (including cyclone Gabrielle), shortly after transplanting the second batch, a considerable number of Green Gravel samples were lost from the study site limiting our ability to comprehensively analyse differences between habitat and attachment methods: 100% loss of glued Green Gravel in barrens, 97% loss of Green Gravel placed within the kelp canopy, 90% loss placed Green Gravel in barrens, and 47% loss of glued Green Gravel within the kelp canopy. Nevertheless, over the first 8 ½ months following transplant to the field, we found sporophytes in batch 2 growing significantly less than those in the first batch for glued Green Gravel transplanted within the kelp canopy ($\chi^2_1 = 272.96$, p-value < 0.001; Figure 3.10).

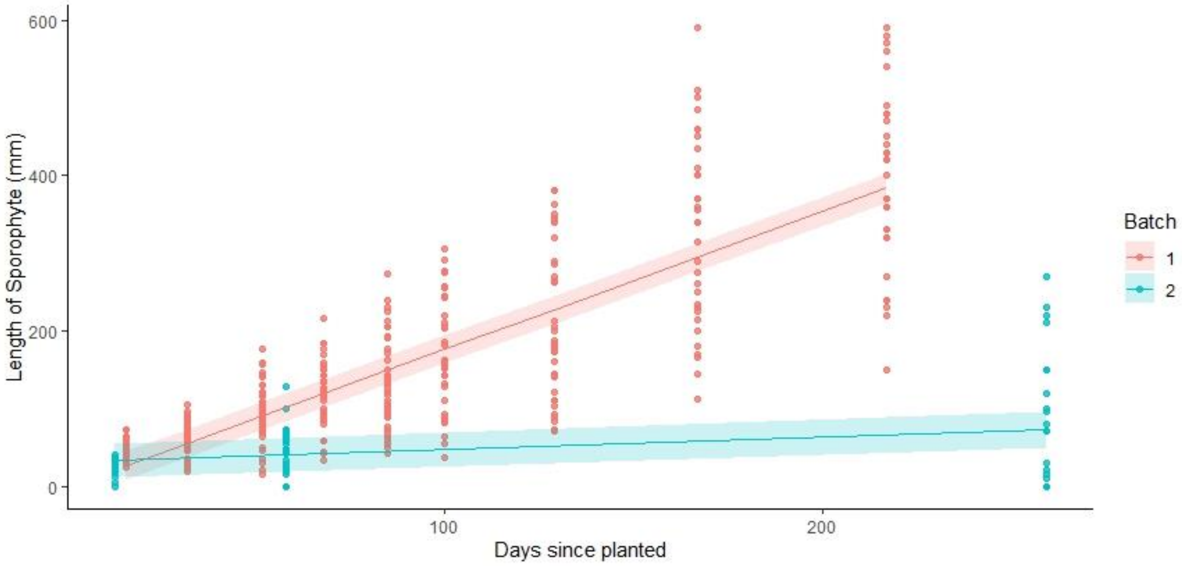


Figure 3.10: Effect of batch on the changes in sporophyte length (±95% confidence intervals indicated by shading) for glued Green Gravel in kelp habitats between days 13 and 259 since transplanting. Time measured in “days since planting” as batches were transplanted at different times of the year - batch one transplanted in April 2022 (*n* =192), batch two transplanted in September 2022 (*n* =120).

3.5 Discussion

The results of this study underscore the importance of attachment and habitat in determining the retention of Green Gravel and the length of seeded *Ecklonia radiata* sporophytes. Contrary to our initial hypothesis, depth did not impact the sporophyte length, and interestingly, it did not influence the retention of Green Gravel either. Not surprisingly, attachment emerged as the most significant factor influencing gravel retention and sporophyte length on the Green Gravel. Analysis of the first batch of

Green Gravel revealed notable differences in percent of retention, with the glued group (62%) exhibiting higher retention rates compared to the placed group (22%). Interestingly however, over the first 8 months, glued Green Gravel grew approximately 100mm longer than the placed gravel; however, by the end of the experiment, the length measurements became similar between the attachment methods. This suggests that placed Green Gravel experienced greater movement and thereby disturbance within the first few months, impacting the initial length and retention of sporophytes compared to the glued gravel, but once haptera were able to anchor the gravel to the reef, kelp on placed Green Gravel compensated for this slower initial growth with greater growth, reaching a similar size as glued gravel at the end of the experiment.

Unfortunately, due to several, severe weather events soon after planting batch two, causing major disturbance and gravel loss, we could not fully analyse the effect of habitat and attachment on the length measurements of the second batch. Instead, we focused on analysing the changes in sporophyte length for glued Green Gravel transplanted within the kelp canopy from both batches. Analysis of the two batches revealed significant differences in sporophyte length, with batch one sporophytes growing longer than batch two sporophytes in the first 8 ½ months. It is possible that the initial disturbance, soon after transplantation negatively impacted the length of batch two sporophytes (Eger et al. 2022a). However, it could also be a result of the season each batch was transplanted. Miller et al. (2011) and Fairhead and Cheshire (2004) found a seasonal growth pattern for *Ecklonia radiata* in Southern New Zealand and South Australia having maximum growth and productivity in late winter/spring but minimal during autumn. Meanwhile, Wernberg and Vanderklift (2010) described a summer maxima and winter minima for growth and productivity of *Ecklonia radiata* in Western Australia. Given batch one was transplanted in autumn and kelp growth in the first 8 ½ months was predominantly through winter/early spring, they grew faster than batch two which were transplanted in spring and grew predominantly through the late spring/summer. These disparities suggest that the timing of transplantation may influence growth and productivity and may vary by location, therefore further research on the impact of seasonality is warranted to determine the best time to transplant Green Gravel to optimize sporophyte establishment and growth.

Adhesives are commonly used in coral restoration when transplanting propagules and can be an effective tool for ensuring the success of transplants (Garrison and Ward 2012, Omori 2019, Boström-Einarsson et al. 2020), particularly in more exposed locations (Westermeier et al. 2014). Our results highlight the effectiveness of the glued treatment in promoting gravel retention. The placed treatment demonstrated some success for the Green Gravel, albeit with 3-times lower retention rates and with slower initial growth compared with the glued treatment group. By the end of the experiment, sporophytes were similar lengths between treatment groups, indicating that placed Green Gravel is a viable alternative for community groups unable to purchase adhesives or prevented from using them due to legislation. Gluing 156 green gravel to the reef at Ti Point for this experiment required approximately 400ml of Splash Zone A-788 two-part epoxy and took approximately 45 minutes longer during surface preparation and an extra 45 minutes to adhere the green gravel underwater. The ease of producing Green Gravel in large quantities and its scalability (Fredriksen et al. 2020), along with the utilization of locally sourced materials, makes it a valuable asset for small community groups engaged in kelp restoration efforts. Furthermore, observations we made of Green Gravel specimens that drifted from their original transplanted sites onto sandflats and continued to thrive, raise intriguing possibilities. Drifting Green Gravel may contribute to dispersal, potentially enhancing restoration outcomes by aiding the colonization of degraded reefs near restoration sites (Wernberg et al. 2019a, Fredriksen et al. 2020).

Differences in sporophyte lengths between kelp and barren habitats, regardless of attachment method, are consistent with previous studies that found adult *Ecklonia radiata* facilitated the growth and development of juvenile conspecifics (Layton et al. 2019b). The first batch of Green Gravel transplanted in barren environments exhibited rapid growth, while sporophytes within the kelp canopy had slower growth immediately after transplantation. The greater light available in barren habitats after transplantation may have contributed to the initial growth spurt of sporophytes in those areas (Miller et al. 2011). However, later in sporophyte development, this pattern reversed, with sporophytes transplanted within the kelp canopy growing longer than those transplanted in the barrens. This period coincided with the most light-intensive period of the year, with LUX readings approximately six times greater in the barren habitat compared to the kelp habitat. It is possible that light levels were too high in the barren habitat stunting photosynthetic capabilities (Sampath-Wiley et al. 2008). The exposure of both batches of Green Gravel to storm events during the final months of the experiment likely removed the majority of batch two gravel and may have also impacted the Green Gravel in the barren habitat, negatively affecting both sporophyte length and gravel retention (Wernberg et al. 2019a, Eger et al. 2022a). Future research on the optimal timing for transplanting Green Gravel to foster the establishment of *Ecklonia radiata* sporophytes on reefs, mitigating wave-action disturbances by timing transplants during seasons of calm weather (Graham et al. 2022) or taking advantage of periods of maximal productivity for enhanced growth and rapid haptera attachment of the Green Gravel to the reef (Fairhead and Cheshire 2004, Wernberg and Vanderklift 2010, Miller et al. 2011) will provide valuable insights.

Proximity to existing adult conspecifics was identified as a significant factor influencing gravel retention and sporophyte length, indicating that the most effective kelp restoration efforts could aim to expand remnant kelp forests rather than commence in the centres of large barren areas or simultaneously transplant adult kelp alongside Green Gravel. Encouragingly, 50% of retained Green Gravel hosted reproductive sporophytes 14 months after transplant, implying that populations transplanted for restoration could produce offspring within two years, making this a feasible timeline for community-based restoration projects (Eger et al. 2022a). Nonetheless, further investigations should focus on assessing the optimal Green Gravel density for transplanting in various ecological contexts to determine the threshold density at which self-sustainability is achieved, thereby maximizing restoration efforts (Wernberg et al. 2020).

Involving and engaging the local community in ecosystem assessment and knowledge exchange play a crucial role in identifying restoration priorities and evaluating the efficacy of restoration endeavours (Vergés et al. 2020). Empowering community groups with restoration techniques is essential, as their active involvement in the process can lead to more successful outcomes compared to relying solely on the scientific community. The accessibility and scalability of the Green Gravel technique make it an achievable tool for small community groups to address the decline of kelp forests in their local areas. Green Gravel can be easily transported in large quantities and deployed straight from a boat onto targeted reefs for restoration, while only small amounts of donor seed material are required to produce significant batches of Green Gravel, which can be conveniently obtained through the partial removal of single blades with ripe sorus tissue without removing the entire adult *Ecklonia radiata* plant (Fredriksen et al. 2020). Rinsed river pebbles, which proved to be the most successful seeding substrate to maximise sporophyte numbers, are easily prepared and commonly found near kelp forests. Locally sourcing both substrate and kelp spores ensures minimal genetic pollution of kelp populations and acknowledges the cultural significance of using gravel belonging to the restoration site (Clapcott et al. 2018, Fredriksen et al. 2020).

In conclusion, the utilization of *Ecklonia radiata* Green Gravel as a simplified cultivation technique presents a promising approach for kelp restoration in New Zealand. Integrating this technique with other strategies, such as establishing protected areas, managing urchin populations, and improving water quality, in collaboration with the local community, can contribute to more successful restoration outcomes (Coleman and Goold 2019, Wernberg et al. 2019b). This offers hope that we can effectively counter the decline of kelp forests. Future research should focus on optimal transplanting densities, long-term outcomes of restoration efforts across seasons, the impact of wave energy and disturbances, and the effectiveness of complementary tools like attachment methods to enhance the deployment of Green Gravel for kelp forest restoration.

Chapter Four: General Discussion

In this thesis I examined the effects of engineered coastal structures for biodiversity and the restoration of kelp forests. In Chapter Two, I analysed differences in the biodiversity of rockpools by assessing whether species richness and functional group prevalence was different between natural substrates and two commonly used artificial coastal structures; riprap and concrete. Surprisingly, both riprap and concrete exhibit comparable taxa richness and functional group prevalence to natural substrates. However, disturbance events, particularly smothering, significantly diminish taxa richness in all habitats. Moreover, different taxa were associated with different categories of disturbance and habitat type. Contrary to previous studies, artificial structures showed resistance to nonindigenous species. Encrusting algae and grazers favoured riprap habitats, providing pool conditions were normal. While filter feeders tended to favour natural pools over concrete pools. In Chapter Three, I analysed the effectiveness of different methodologies to seed *Ecklonia radiata* on small gravel to create Green Gravel, as well as varying techniques for transplanting the Green Gravel onto the reef. Although it was not surprising to find that gluing gravel to the substrate significantly improved gravel retention, I was surprised that sporophyte lengths initially differed between attachment methods and habitats but were similar by the end of the experiment. It is not clear if this pattern was a consequence of developmental stage, disturbance, or season as the early burst of growth in barrens habitats occurred autumn and winter primarily on the glued gravel whereas the late burst of growth in kelp forest habitats occurred in summer and spring when irradiance and temperatures were higher, with sporophytes on placed gravel catching up to those on glued gravel. In this general discussion, I summarise the main results of my thesis, the implications of these findings, and discuss caveats and future research directions, pertinent to effective eco-engineering and kelp forest recovery.

Chapter Two of this thesis seeks to breakdown the complexity of biodiversity in rockpool habitats between natural and artificial substrates. Although the protection of natural habitats is important (Gaines et al. 2010), the rapidly increasing human population makes some coastal modification inevitable (Chapman and Blockley 2009, Browne and Chapman 2011). Therefore to combat biodiversity decline, eco-engineering emerges as a solution to balance coastal hardening's negative ecological impact with human needs (Chapman and Underwood 2011, Firth et al. 2016a, Mayer-Pinto et al. 2017). This chapter underscores the importance of microhabitat diversity in supporting species and ecosystem health on artificial structures, guiding eco-engineering strategies to optimize their ecological value while accommodating anticipated urbanization.

Effective coastal eco-engineering can be realized through well-functioning structures that both safeguard human interests and uphold natural biodiversity (Perkol-Finkel and Benayahu 2004). Formerly, artificial structures like concrete walls and riprap were perceived as ecological deserts (Gibson et al. 2007, Airoldi et al. 2015, Heery et al. 2017, Mayer-Pinto et al. 2018). However, current research, exemplified in Chapter Two, challenges this perspective. Overall, riprap and concrete substrates studied in this experiment exhibited comparable taxa richness and functional group prevalence to natural substrates. Research has shown artificial structures in the marine environment can be more inviting to nonindigenous species as many exotic species can establish populations more readily on artificial structures (Inglis et al. 2005, Arévalo et al. 2007, Bulleri and Chapman 2010, Mayer-Pinto et al. 2015). However, I found that filter feeders prefer natural habitats over concrete, and the only observation of an nonindigenous species was a filter-feeding organism (the Mediterranean Fan Worm – *Sabella spallanzanii;* (Read et al. 2011)), found in both concrete and natural substrates. This highlights the benefit of studying the effects of eco-engineered structures in their deployment environment, given that outcomes are likely to vary across locations.

The results from Chapter Two highlight that while substrate composition may have limited influence on biodiversity, it is important to understand how ecosystems respond to disturbance events to help guide effective conservation and management strategies of intertidal zones. Not surprisingly, disturbance events had the most influence on taxa richness and functional group prevalence, with smothering events having the greatest negative effect on taxa richness. The stress gradient hypothesis predicts that positive associations will be greatest in environments where biotic or abiotic stressors are greatest, and weakest in environmentally benign environments (Strain et al. 2018). Uncovering the composition of clusters when assessing residual species associations alluded to the importance of biogenic habitats in rockpool habitats. The growth of small algae species appeared to encourage the arrival of grazing taxa into those pools, and further increased the availability of microhabitats in these habitats, indicating the intricate connections between habitat-forming species and their associated taxa.

Fundamentally, any water-retaining feature introduced to coastal infrastructure increases habitat biodiversity, regardless of substrate composition (Firth et al. 2013b, Ostalé-Valriberas et al. 2018). Consequently, prevalent eco-engineering methods involve enhancing hard substrate surface area and complexity via additive (protruding structures) or subtractive (drilling, substrate removal) techniques (Chapman and Underwood 2011). Introducing additional holes and crevices onto an artificial structure can improve the function of that substrate, by increasing the availability of niches and encouraging new recruits into the habitat (Aguilera et al. 2014, Ng et al. 2015). Additive approaches have utilised both abiotic substrates such as flower-pot pools (Browne and Chapman 2011), and "seeding" with habitat-forming taxa such as barnacles, bivalves, canopy-forming algae, branching coralline algae or corals (Coleman and Connell 2001, Wilhelmsson et al. 2006, Clynick et al. 2007, Perkol-Finkel et al. 2012, Dafforn et al. 2015, Strain et al. 2018). Ideally, these features can be included in the design phase of eco-engineering on the coast; however, artificial substrates already in the environment can be modified to increase the number of water-retaining features or introduce biogenic species onto the substrate.

Interventions alleviating abiotic stressors, such as temperature and desiccation, can significantly impact the intertidal environment. While organism size can impact intervention efficacy, with microhabitat additions that match organism size being the most beneficial interventions (Strain et al. 2018). Furthermore, intervention effects vary with time, and are contingent on recruitment, mobility, and community successional stage (Firth et al. 2016b). The effectiveness of some interventions may only become apparent after colonisation has occurred (Evans 2016), and while seeding of structures may speed up succession, it may not change the composition of the community at equilibrium (Ferse et al. 2013). By developing a thorough understanding of the mechanisms that influence species assemblage in these artificial environments, the design and functionality of these structures can be improved to ensure their benefit and worth in aiding human development while conserving natural habitats (Bulleri 2005, Aguilera et al. 2014, Jebakumar et al. 2021, Salauddin et al. 2021).

Chapter Three of this thesis serves as a foundation for comprehending the complexities of kelp restoration in New Zealand. It is within this context of dire need, that innovative restoration strategies like Green Gravel transplantation become imperative (Fredriksen et al. 2020). The overarching goal of this chapter was to explore the impact of various factors on the retention and growth of *Ecklonia radiata* sporophytes using Green Gravel, contributing to the broader understanding of successful kelp restoration strategies.

Adhesives are a pivotal tool used in coral restoration (Garrison and Ward 2012, Omori 2019, Boström-Einarsson et al. 2020), particularly in more exposed locations (Westermeier et al. 2014). Glued Green Gravel were three times more likely to be retained compared to placed gravel. Furthermore, although sporophyte lengths among glued and placed Green Gravel were comparable at the end of the experiment, glued Green Gravel sporophytes were approximately 100mm larger than placed Green Gravel sporophytes during the first 8 months in the field. This suggests that placed Green Gravel experienced greater movement and thereby disturbance within the first few months, impacting the initial length and retention of sporophytes compared to the glued gravel, but once haptera were able to anchor the gravel to the reef, kelp on placed Green Gravel compensated for this slower initial growth with greater growth, reaching a similar size as glued gravel at the end of the experiment. These results indicate that placing Green Gravel is still valuable for restoration efforts, especially for community groups where there might be greater limitations on using adhesives compared with the production of Green Gravel. The ease of producing Green Gravel in large quantities and its scalability (Fredriksen et al. 2020), along with the utilization of locally sourced materials, makes Green Gravel a valuable asset for small community groups engaged in kelp restoration efforts.

Differences in sporophyte lengths between kelp and barren habitats, regardless of attachment method, are consistent with previous studies that found adult *Ecklonia radiata* facilitated the growth and development of juvenile conspecifics (Layton et al. 2019b). The sporophytes on the first batch of Green Gravel transplanted within the kelp canopy had slower growth initially but, greater overall growth across the experiment, compared with sporophytes on Green Gravel transplanted into barren habitats. Proximity to existing adult conspecifics was a significant factor influencing gravel retention and sporophyte length, indicating that effective kelp restoration efforts should aim to expand remnant kelp forests rather than commence in the centres of large barren areas, alternatively, simultaneously transplant adult kelp alongside Green Gravel. Additionally, drifting Green Gravel may potentially enhance restoration outcomes by aiding the colonization of degraded reefs, through spore dispersal, near restoration sites (Wernberg et al. 2019a, Fredriksen et al. 2020).

Chapter Three also highlighted the influence of light availability and storm events on sporophyte growth, emphasizing the need for optimized transplanting strategies that account for seasonal variation and wave disturbances. Despite varying observations of seasonal growth patterns for *Ecklonia radiata* globally (Fairhead and Cheshire 2004, Wernberg and Vanderklift 2010, Miller et al. 2011), I observed greater growth during winter/early spring and delayed growth during late spring/summer. These disparities suggest that the timing of transplantation may influence growth and productivity and may vary by location, therefore further research on the impact of seasonality is warranted to determine the best time to transplant Green Gravel in each location to optimize sporophyte establishment and growth. Encouragingly, 50% of retained Green Gravel hosted reproductive sporophytes 14 months after transplant, implying that populations transplanted for restoration could produce offspring within two years, making this a feasible timeline for community-based restoration projects (Eger et al. 2022a).

By integrating innovative techniques like Green Gravel transplantation with broader conservation efforts, such as protected area establishment and urchin population management, collaborative restoration initiatives can be effective in countering kelp forest decline (Eger et al. 2022a). Community engagement and involvement are emphasized as crucial components of kelp restoration (Vergés et al. 2020), with the accessibility and scalability of the Green Gravel technique making it an ideal tool for small community-based restoration projects. By addressing the challenges facing kelp ecosystems through innovative restoration strategies, collaboration between scientific communities and local stakeholders can pave the way for the resurgence of these vital marine habitats.

4.1 Limitations

A major limitation to the rockpool study, occurred during the selection of replicate pools to measure. I selected replicate pools during a benign environmental period (during July and August), however during stressful summer periods, some of these pools became quite shallow, with some pools only containing millimetres of seawater. In the future I would recommend choosing replicate pools during periods when pools are likely to be the most desiccated, to ensure they remain pools across 12 months. The selected pools were also already established with intertidal communities before my experiment. Therefore, there was no way to control for past events that may have dictated the community composition or successional stage of each pool. Additionally, the replicated habitats for the artificial substrates were deployed into the environment at separate times, meaning I could not ensure the pool communities measured, were at a similar successional stage across habitats and locations at the start of sampling.

During these experiments there were times when samples of rockpools and Green Gravel were displaced, limiting my ability to comprehensively assess the effect of these disturbances in this experiment. During the rockpool survey three riprap pools across the two locations were permanently lost due to the shifting of the boulders and smaller rocks within this habitat matrix, demonstrating how unstable these habitats can be and the difficulties involved with studying a system of high disturbance. Additionally, due to several, severe weather events during January and February 2023 (including cyclone Gabrielle), shortly after transplanting the second batch of Green Gravel, a considerable number of those samples were lost from the study site limiting my ability to comprehensively analyse differences between habitat and attachment methods between the two batches of Green Gravel transplanted in different seasons.

Another limitation for the Green Gravel experiment is the use of only one study location. Using the reef at Ti Point, tells us a lot about the success of Green Gravel in that particular habitat type, but it is only through further trials at multiple different locations, with different environmental conditions, that we will gain a comprehensive understanding of the success of Green Gravel for kelp restoration. Ti Point is not considered an urchin-barren or turf-dominated environment, instead it is characterised by a mosaic of emergent barrens and turf communities embedded within a kelp forest.

The reason for choosing Ti Point as a location for this work was because this mosaic of habitat types allowed us to pair kelp and barren treatments in close proximity but also because it offered an oceanic site where strong easterly swells would run parallel to the coast rather than perpendicular to it, minimising wave disturbance. Future studies in locations where barren and turf habitats dominate as well as sites with more or less wave exposure will provide a greater understanding of the long-term viability of Green Gravel as a kelp restoration method.

4.2 Final Thoughts

Despite their distinct focal points, both chapters share a commitment to understanding and preserving coastal ecosystems. While Chapter Two delves into the complexities of biodiversity dynamics on natural and modified coasts, Chapter Three explores active restoration of species with disproportionately strong effects on ecosystems to drive ecological recovery. Both chapters also emphasize the importance of biotic and abiotic interactions. Chapter Two prompts us to reevaluate our perception of artificial structures, offering an alternate view that these structures can harbour comparable biodiversity to natural habitats. Meanwhile, Chapter Three ushers in a new era of restoration strategies, highlighting the potential of Green Gravel transplantation as a scalable approach to ecosystem restoration. Both chapters beckon for further research, encouraging the exploration of novel methodologies and the refinement of existing practices.

Further exploration could delve into the mechanisms driving taxa prevalence and how disturbance events influence community dynamics in rockpool environments. In particular, given the broad use of riprap as coastal defence in New Zealand, future research needs to focus on developing a better understanding of the ecology of riprap environments, ensuring analysis of the effect of disturbance in those habitats compared with natural and other artificial rocky shores. Long-term monitoring will help shed light on the stability of artificial habitats over time. In future, if riprap is continued to be used as the preferred coastal defence strategy employed in New Zealand, an increase in permanent water-retaining features and fixing of permanent pool habitats amongst the boulders should be implemented to increase the availability of suitable habitats for intertidal organisms (Moschella et al. 2005). By securing some boulders with pools carved into them, it could greatly increase the number of stable pool niches available in that environment, thus increasing taxa richness and diversity on these coastal defence substrates. One further focus could be to examine the effect of seeding artificial structures with biogenic species to increase the number of available microhabitats (Aguilera et al. 2014, Ng et al. 2015).

For kelp restoration using Green Gravel, further research on the impact of seasonality on sporophyte growth, in various geographic locations, could provide valuable insights for optimizing transplantation timing. Accelerating the establishment of *Ecklonia radiata* sporophytes on the reef by timing transplants during seasons of calm weather to mitigate wave-action disturbances (Graham et al. 2022) or taking advantage of periods of maximal productivity (Fairhead and Cheshire 2004, Wernberg and Vanderklift 2010, Miller et al. 2011) will enhance the success of restoration efforts. Additionally, Chapter Three underscores the need for continued investigation into the effectiveness of complementary tools, such as attachment methods, to enhance Green Gravel transplantation, especially in areas of high flow.

In final reflection, this thesis emerges as a beacon of hope amid the storm of challenges that engulf kelp ecosystems and urbanised coastal environments. Through Green Gravel transplantation and innovative eco-engineering on the coast, scientific expertise converges with local engagement, embodying the promise that coastal urbanisation can benefit both humans and coastal organisms and that restoration of kelp forests is achievable. The journey that lies ahead necessitates interdisciplinary collaboration, ecological insight, and an unwavering commitment to safeguarding the future of these invaluable marine ecosystems.

Literature Cited

Abdullah, M. I., S. Fredriksen, and H. Christie. 2017. The impact of the kelp (*Laminaria hyperborea*) forest on the organic matter content in sediment of the west coast of Norway. Marine Biology Research 13:151-160.

Aguilera, M. A., B. R. Broitman, and M. Thiel. 2014. Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. Marine pollution bulletin 87:257-268.

Airoldi, L., M. W. Beck, L. B. Firth, A. B. Bugnot, P. D. Steinberg, and K. A. Dafforn. 2021. Emerging solutions to return nature to the urban ocean. Annual Review of Marine Science 13:445-477.

Airoldi, L., X. Turon, S. Perkol-Finkel, and M. Rius. 2015. Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. Diversity and Distributions 21:755-768.

Aitken, S. N., and M. C. Whitlock. 2013. Assisted gene flow to facilitate local adaptation to climate change. Annual Review of Ecology, Evolution, and Systematics 44:367-388.

Alder, A., A. Jeffs, and J. Hillman. 2022. Timing mussel deployments to improve reintroduction success and restoration efficiency. Marine Ecology Progress Series 698:69-83.

Alder, A., A. Jeffs, and J. R. Hillman. 2021. Considering the use of subadult and juvenile mussels for mussel reef restoration. Restoration Ecology 29.

Anderson, M. J., C. E. Diebel, W. M. Blom, and T. J. Landers. 2005. Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at different taxonomic resolutions. Journal of Experimental Marine Biology and Ecology 320:35-56.

Arenas, F., I. Sánchez, S. J. Hawkins, and S. R. Jenkins. 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. Ecology 87:2851-2861.

Arévalo, R., S. Pinedo, and E. Ballesteros. 2007. Changes in the composition and structure of Mediterranean rocky-shore communities following a gradient of nutrient enrichment: descriptive study and test of proposed methods to assess water quality regarding macroalgae. Marine pollution bulletin 55:104-113.

Arranz, V., L. Liggins, and J. D. Aguirre. 2022. Metabarcoding hyperdiverse kelp holdfast communities on temperate reefs: An experimental approach to inform future studies. Environmental DNA 4:492-509.

Babcock, R. C., S. Kelly, N. T. Shears, J. W. Walker, and T. J. Willis. 1999. Changes in community structure in temperate marine reserves. Marine Ecology Progress Series 189:125-134.

Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. Lafferty, T. R. Mcclanahan, and G. R. Russ. 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. Proceedings of the National Academy of Sciences 107:18256-18261.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecological monographs 81:169-193.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-48.

Beaumont, N., M. Austen, S. Mangi, and M. Townsend. 2008. Economic valuation for the conservation of marine biodiversity. Marine pollution bulletin 56:386-396.

Bellou, N., E. Papathanassiou, S. Dobretsov, V. Lykousis, and F. Colijn. 2012. The effect of substratum type, orientation and depth on the development of bacterial deep-sea biofilm communities grown on artificial substrata deployed in the Eastern Mediterranean. Biofouling 28:199-213.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. Nature 429:827-833.

Benedetti-Cecchi, L., and F. Cinelli. 1996. Patterns of disturbance and recovery in littoral rock pools: nonhierarchical competition and spatial variability in secondary succession. Marine Ecology Progress Series 135:145-161.

Benedetti-Cecchi, L., F. Pannacciulli, F. Bulleri, P. Moschella, L. Airoldi, G. Relini, and F. Cinelli. 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Marine Ecology Progress Series 214:137-150.

Benjamin, E. D. 2023. Assessing the potential to restore green-lipped mussels in Pelorus Sound/Te Hoiere, New Zealand. ResearchSpace@Auckland.

Bennett, S., T. Wernberg, S. D. Connell, A. J. Hobday, C. R. Johnson, and E. S. Poloczanska. 2016. The ‘Great Southern Reef’: social, ecological and economic value of Australia’s neglected kelp forests. Marine and Freshwater Research 67:47-56.

Bergen, S. D., S. M. Bolton, and J. L. Fridley. 2001. Design principles for ecological engineering. Ecological Engineering 18:201-210.

Blamey, L. K., and J. J. Bolton. 2018. The economic value of South African kelp forests and temperate reefs: past, present and future. Journal of Marine Systems 188:172-181.

Boström-Einarsson, L., R. C. Babcock, E. Bayraktarov, D. Ceccarelli, N. Cook, S. C. Ferse, B. Hancock, P. Harrison, M. Hein, and E. Shaver. 2020. Coral restoration–A systematic review of current methods, successes, failures and future directions. PLOS ONE 15.

Browne, M. A., and M. G. Chapman. 2011. Ecologically informed engineering reduces loss of intertidal biodiversity on artificial shorelines. Environmental science & technology 45:8204-8207.

Browne, M. A., and M. G. Chapman. 2014. Mitigating against the loss of species by adding artificial intertidal pools to existing seawalls. Marine Ecology Progress Series 497:119-129.

Bulleri, F. 2005. Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Marine Ecology Progress Series 287:53-65.

Bulleri, F., and L. Airoldi. 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile ssp. tomentosoides*, in the north Adriatic Sea. Journal of applied ecology 42:1063-1072.

Bulleri, F., L. Benedetti-Cecchi, S. Acunto, F. Cinelli, and S. J. Hawkins. 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. Journal of Experimental Marine Biology and Ecology 267:89-106.

Bulleri, F., and M. Chapman. 2004. Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. Marine biology 145:381-391.

Bulleri, F., M. Chapman, and A. Underwood. 2005. Intertidal assemblages on seawalls and vertical rocky shores in Sydney Harbour, Australia. Austral Ecology 30:655-667.

Bulleri, F., and M. G. Chapman. 2010. The introduction of coastal infrastructure as a driver of change in marine environments. Journal of applied ecology 47:26-35.

Bulleri, F., B. K. Eriksson, A. Queirós, L. Airoldi, F. Arenas, C. Arvanitidis, T. J. Bouma, T. P. Crowe, D. Davoult, and K. Guizien. 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. Plos Biology 16.

Burt, J., A. Bartholomew, P. Usseglio, A. Bauman, and P. Sale. 2009. Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? Coral reefs 28:663-675.

Burt, J. A., D. A. Feary, G. Cavalcante, A. G. Bauman, and P. Usseglio. 2013. Urban breakwaters as reef fish habitat in the Persian Gulf. Marine pollution bulletin 72:342-350.

Butchart, S. H., M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, J. E. Baillie, B. Bomhard, C. Brown, and J. Bruno. 2010. Global biodiversity: indicators of recent declines. science 328:1164-1168.

Cacabelos, E., I. Gestoso, P. Ramalhosa, L. Riera, A. I. Neto, and J. Canning-Clode. 2019. Intertidal assemblages across boulders and rocky platforms: a multi-scaled approach in a subtropical island. Marine Biodiversity 49:2709-2723.

Cacabelos, E., G. M. Martins, R. Thompson, A. C. Prestes, J. M. N. Azevedo, and A. I. Neto. 2016. Material type and roughness influence structure of inter-tidal communities on coastal defenses. Marine Ecology 37:801-812.

Cardinale, B. J. 2011. Biodiversity improves water quality through niche partitioning. Nature 472:86-89.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, and D. A. Wardle. 2012. Biodiversity loss and its impact on humanity. Nature 486:59-67.

Cebrian, E., L. Tamburello, J. Verdura, G. Guarnieri, A. Medrano, C. Linares, B. Hereu, J. Garrabou, C. Cerrano, and C. Galobart. 2021. A roadmap for the restoration of Mediterranean macroalgal forests. Frontiers in Marine Science 8.

Chapman, M., and D. Blockley. 2009. Engineering novel habitats on urban infrastructure to increase intertidal biodiversity. Oecologia 161:625-635.

Chapman, M., and F. Bulleri. 2003. Intertidal seawalls—new features of landscape in intertidal environments. Landscape and urban planning 62:159-172.

Chapman, M., and A. Underwood. 2011. Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. Journal of Experimental Marine Biology and Ecology 400:302-313.

Chapman, M., A. Underwood, and M. A. Browne. 2018. An assessment of the current usage of ecological engineering and reconciliation ecology in managing alterations to habitats in urban estuaries. Ecological Engineering 120:560-573.

Chapman, M. G. 2012. Restoring intertidal boulder-fields as habitat for "Specialist" and "Generalist" animals. Restoration Ecology 20:277-285.

Cieraad, E., S. Walker, R. Price, and J. Barringer. 2015. An updated assessment of indigenous cover remaining and legal protection in New Zealand's land environments. New Zealand Journal of Ecology 39:309-315.

Clapcott, J., J. Ataria, C. Hepburn, D. Hikuroa, A.-M. Jackson, R. Kirikiri, and E. Williams. 2018. Mātauranga Māori: shaping marine and freshwater futures. Pages 457-466. Taylor & Francis.

Clynick, B., M. Chapman, and A. Underwood. 2007. Effects of epibiota on assemblages of fish associated with urban structures. Marine Ecology Progress Series 332:201-210.

Coleman, M. A., and S. D. Connell. 2001. Weak effects of epibiota on the abundances of fishes associated with pier pilings in Sydney Harbour. Environmental biology of fishes 61:231-239.

Coleman, M. A., and H. D. Goold. 2019. Harnessing synthetic biology for kelp forest conservation. Journal of phycology 55:745-751.

Coleman, M. A., G. Wood, K. Filbee-Dexter, A. J. Minne, H. D. Goold, A. Vergés, E. M. Marzinelli, P. D. Steinberg, and T. Wernberg. 2020. Restore or redefine: Future trajectories for restoration. Frontiers in Marine Science 7:237.

Coleman, S., A. T. S. Gelais, D. W. Fredriksson, T. Dewhurst, and D. C. Brady. 2022. Identifying scaling pathways and research priorities for kelp aquaculture nurseries using a techno-economic modeling approach. Frontiers in Marine Science 9.

Coombes, M. A., E. C. La Marca, L. A. Naylor, and R. C. Thompson. 2015. Getting into the groove: opportunities to enhance the ecological value of hard coastal infrastructure using fine-scale surface textures. Ecological Engineering 77:314-323.

Courtenay, G., D. R. Smith, and W. Gladstone. 2012. Occupational health issues in marine and freshwater research. Journal of Occupational Medicine and Toxicology 7:1-11.

Cuadrado, D. G., E. A. Gómez, and S. S. Ginsberg. 2005. Tidal and longshore sediment transport associated to a coastal structure. Estuarine, Coastal and Shelf Science 62:291-300.

Cummings, V., J. Hewitt, J. Halliday, and G. Mackay. 2007. Optimizing the success of *Austrovenus stutchburyi* restoration: Preliminary investigations in a New Zealand estuary. Journal of Shellfish Research 26:89-100.

Dafforn, K. A., T. M. Glasby, L. Airoldi, N. K. Rivero, M. Mayer-Pinto, and E. L. Johnston. 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. Frontiers in Ecology and the Environment 13:82-90.

Davies, K., A. A. Murchie, V. Kerr, and C. Lundquist. 2018. The evolution of marine protected area planning in Aotearoa New Zealand: Reflections on participation and process. Marine Policy 93:113-127.

Dayton, P. K. 1985. Ecology of kelp communities. Annual review of ecology and systematics 16:215-245.

Deloitte. 2023. New Zealand Ports and Freight Yearbook 2023. Navigating the new normal.

Díaz, S. M., J. Settele, E. Brondízio, H. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. Brauman, and S. Butchart. 2019. The global assessment report on biodiversity and ecosystem services: Summary for policy makers.

Dugan, J., L. Airoldi, M. Chapman, S. Walker, T. Schlacher, E. Wolanski, and D. McLusky. 2011. 8.02-Estuarine and coastal structures: environmental effects, a focus on shore and nearshore structures. Treatise on estuarine and coastal science 8:17-41.

Eckman, J. E., D. O. Duggins, and A. T. Sewell. 1989. Ecology of under story kelp environments. I. Effects of kelps on flow and particle transport near the bottom. Journal of Experimental Marine Biology and Ecology 129:173-187.

Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, M. A. Becerro, A. T. Bernard, and J. Berkhout. 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506:216-220.

Eger, A., C. Layton, T. McHugh, M. Gleason, and N. Eddy. 2022a. Kelp restoration guidebook: lessons learned from kelp projects around the world. The Nature Conservancy.

Eger, A., E. M. Marzinelli, H. Christie, C. W. Fagerli, D. Fujita, A. P. Gonzalez, S. W. Hong, J. H. Kim, L. C. Lee, and T. A. McHugh. 2022b. Global kelp forest restoration: past lessons, present status, and future directions. Biological Reviews 97:1449-1475.

Eger, A. M., E. Marzinelli, R. Baes, C. Blain, L. Blamey, P. E. Carnell, C. G. Choi, M. Hessing-Lewis, K. Y. Kim, and J. Lorda. 2021. The economic value of fisheries, blue carbon, and nutrient cycling in global marine forests.

Evans, A. J. 2016. Artificial coastal defence structures as surrogate habitats for natural rocky shores: giving nature a helping hand. Aberystwyth University.

Evans, A. J., L. B. Firth, S. J. Hawkins, E. S. Morris, H. Goudge, and P. J. Moore. 2015. Drill-cored rock pools: an effective method of ecological enhancement on artificial structures. Marine and Freshwater Research 67:123-130.

Fairhead, V. A., and A. C. Cheshire. 2004. Seasonal and depth related variation in the photosynthesis–irradiance response of *Ecklonia radiata* (Phaeophyta, Laminariales) at West Island, South Australia. Marine biology 145:415-426.

Ferse, S. C., M. M. Nugues, S. B. Romatzki, and A. Kunzmann. 2013. Examining the use of mass transplantation of brooding and spawning corals to support natural coral recruitment in Sulawesi/Indonesia. Restoration Ecology 21:745-754.

Filbee-Dexter, K., and R. E. Scheibling. 2014. Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Marine Ecology Progress Series 495:1-25.

Filbee-Dexter, K., and T. Wernberg. 2018. Rise of turfs: a new battlefront for globally declining kelp forests. BioScience 68:64-76.

Filbee-Dexter, K., T. Wernberg, S. Grace, J. Thormar, S. Fredriksen, C. Narvaez, C. Feehan, and K. Norderhaug. 2020. Marine heatwaves and the collapse of marginal North Atlantic kelp forests. Scientific reports 10.

Filbee-Dexter, K., T. Wernberg, R. Barreiro, M. A. Coleman, T. de Bettignies, C. J. Feehan, J. N. Franco, B. Hasler, I. Louro, and K. M. Norderhaug. 2022. Leveraging the blue economy to transform marine forest restoration. Journal of Phycology 58:198-207.

Firth, L., R. Thompson, K. Bohn, M. Abbiati, L. Airoldi, T. Bouma, F. Bozzeda, V. Ceccherelli, M. Colangelo, and A. Evans. 2014a. Between a rock and a hard place: environmental and engineering considerations when designing coastal defence structures. Coastal Engineering 87:122-135.

Firth, L. B., L. Airoldi, F. Bulleri, S. Challinor, S. Y. Chee, A. J. Evans, M. E. Hanley, A. M. Knights, K. O'Shaughnessy, and R. C. Thompson. 2020. Greening of grey infrastructure should not be used as a Trojan horse to facilitate coastal development. Journal of applied ecology 57:1762-1768.

Firth, L. B., K. A. Browne, A. M. Knights, S. J. Hawkins, and R. Nash. 2016a. Eco-engineered rock pools: a concrete solution to biodiversity loss and urban sprawl in the marine environment. Environmental Research Letters 11.

Firth, L. B., Hawkins, S.J. . 2011. Introductory comments - Global change in marine ecosystems: Patterns, processes and interactions with regional and local scale impacts. Journal of Experimental Marine Biology and Ecology 400:1-6.

Firth, L. B., A. M. Knights, D. Bridger, A. Evans, N. Mieskowska, P. J. Moore, N. E. O'Connor, E. V. Sheehan, R. C. Thompson, and S. J. Hawkins. 2016b. Ocean sprawl: challenges and opportunities for biodiversity management in a changing world.

Firth, L. B., N. Mieszkowska, R. C. Thompson, and S. J. Hawkins. 2013a. Climate change and adaptational impacts in coastal systems: the case of sea defences. Environmental Science: Processes & Impacts 15:1665-1670.

Firth, L. B., M. Schofield, F. J. White, M. W. Skov, and S. J. Hawkins. 2014b. Biodiversity in intertidal rock pools: Informing engineering criteria for artificial habitat enhancement in the built environment. Marine Environmental Research 102:122-130.

Firth, L. B., R. C. Thompson, F. J. White, M. Schofield, M. W. Skov, S. P. Hoggart, J. Jackson, A. M. Knights, and S. J. Hawkins. 2013b. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. Diversity and Distributions 19:1275-1283.

Firth, L. B., F. J. White, M. Schofield, M. E. Hanley, M. T. Burrows, R. C. Thompson, M. W. Skov, A. J. Evans, P. J. Moore, and S. J. Hawkins. 2015. Facing the future: the importance of substratum features for ecological engineering of artificial habitats in the rocky intertidal. Marine and Freshwater Research 67:131-143.

Fisheries New Zealand. 2022. Aquatic Environment and Biodiversity Annual Review 2021. Page 779

Floerl, O., J. Atalah, A. B. Bugnot, M. Chandler, K. A. Dafforn, L. Floerl, A. Zaiko, and R. Major. 2021. A global model to forecast coastal hardening and mitigate associated socioecological risks. Nature Sustainability 4:1060-1067.

Foster, M. S., and D. R. Schiel. 2010. Loss of predators and the collapse of southern California kelp forests: Alternatives, explanations and generalizations. Journal of Experimental Marine Biology and Ecology 393:59-70.

Francis, R. A., and J. Lorimer. 2011. Urban reconciliation ecology: the potential of living roofs and walls. Journal of Environmental Management 92:1429-1437.

Fredriksen, S., K. Filbee-Dexter, K. M. Norderhaug, H. Steen, T. Bodvin, M. A. Coleman, F. Moy, and T. Wernberg. 2020. Green gravel: a novel restoration tool to combat kelp forest decline. Scientific reports 10.

Fujita, D. 2011. Management of kelp ecosystem in Japan. CBM-Cahiers de Biologie Marine 52:499.

Gacia, E., M. P. Satta, and D. Martín. 2007. Low crested coastal defence structures on the Catalan coast of the Mediterranean Sea: how they compare with natural rocky shores. Scientia Marina 71:259-267.

Gaines, S. D., C. White, M. H. Carr, and S. R. Palumbi. 2010. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences 107:18286-18293.

Garrison, V. H., and G. Ward. 2012. Transplantation of storm-generated coral fragments to enhance Caribbean coral reefs: A successful method but not a solution. Revista de Biología Tropical 60:59-70.

Gelman, A., J. Hwang, and A. Vehtari. 2014. Understanding predictive information criteria for Bayesian models. Statistics and computing 24:997-1016.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical science 7:457-472.

Gibson, R., R. Atkinson, and J. Gordon. 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology: an annual review 45:345-405.

Glasby, T. 2000. Surface composition and orientation interact to affect subtidal epibiota. Journal of Experimental Marine Biology and Ecology 248:177-190.

Glasby, T., and S. Connell. 2001. Orientation and position of substrata have large effects on epibiotic assemblages. Marine Ecology Progress Series 214:127-135.

Glasby, T., S. Connell, M. Holloway, and C. Hewitt. 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? Marine Biology 151, 887–895.

Gleason, M., J. Caselle, W. Heady, V. Saccomanno, J. Zimmerman, T. McHugh, and N. Eddy. 2021. A structured approach for kelp restoration and management decisions in California. Arlington, VA: The Nature Conservancy.

Graham, T. D., R. L. Morris, E. M. Strain, and S. E. Swearer. 2022. Identifying key factors for transplantation success in the restoration of kelp (*Ecklonia radiata*) beds. Restoration Ecology 30:e13536.

Griggs, G. B., and K. Fulton-Bennett. 1988. Rip rap revetments and seawalls and their effectiveness along the central California coast. Shore and Beach 56:3-11.

Harley, C. D. 2003. Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. Ecology 84:1477-1488.

Heery, E. C., M. J. Bishop, L. P. Critchley, A. B. Bugnot, L. Airoldi, M. Mayer-Pinto, E. V. Sheehan, R. A. Coleman, L. H. Loke, and E. L. Johnston. 2017. Identifying the consequences of ocean sprawl for sedimentary habitats. Journal of Experimental Marine Biology and Ecology 492:31-48.

Heron, S. F., C. M. Eakin, F. Douvere, K. L. Anderson, J. C. Day, E. Geiger, O. Hoegh-Guldberg, R. Van Hooidonk, T. Hughes, and P. Marshall. 2017. Impacts of climate change on World Heritage coral reefs: a first global scientific assessment.

Hillebrand, H., and B. Matthiessen. 2009. Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecology Letters 12:1405-1419.

Holloway, P., and R. Field. 2020. Can rock-rubble groynes support similar intertidal ecological communities to natural rocky shores? Land 9:131.

Hopf, J. K., J. E. Caselle, and J. W. White. 2022. No-take marine protected areas enhance the benefits of kelp-forest restoration for fish but not fisheries. Ecology letters 25:1665-1675.

Hughes, A. R., B. D. Inouye, M. T. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. Ecology letters 11:609-623.

Hurd, C. L. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology 36:453-472.

Ido, S., and P.-F. Shimrit. 2015. Blue is the new green–ecological enhancement of concrete based coastal and marine infrastructure. Ecological Engineering 84:260-272.

Inglis, G. 2001. Criteria for selecting New Zealand ports and other points of entry that have a high risk of invasion by new exotic marine organisms. Report prepared for the New Zealand Ministry of Fisheries. National Institute of Water and Atmospheric Research, Christchurch.

Inglis, G., N. Gust, I. Fitridge, O. Floerl, B. Hayden, and G. Fenwick. 2005. Port of Auckland: baseline survey for non-indigenous marine species. NIWA report prepared for Biosecurity New Zealand Post-clearance Directorate for Project ZBS2000-04.

Iveša, L., M. Chapman, A. Underwood, and R. Murphy. 2010. Differential patterns of distribution of limpets on intertidal seawalls: experimental investigation of the roles of recruitment, survival and competition. Marine Ecology Progress Series 407:55-69.

Jebakumar, J. P. P., G. Nandhagopal, S. Ragumaran, V. Ravichandran, and C. Ramakritinan. 2021. Artificial coastal defence structures–A surrogate of natural rocky structure to enhance coastal biodiversity. Journal of Earth System Science 130:127.

Johnson, C. R., S. C. Banks, N. S. Barrett, F. Cazassus, P. K. Dunstan, G. J. Edgar, S. D. Frusher, C. Gardner, M. Haddon, and F. Helidoniotis. 2011. Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. Journal of Experimental Marine Biology and Ecology 400:17-32.

Jones, C. G., J. L. Gutiérrez, J. E. Byers, J. A. Crooks, J. G. Lambrinos, and T. S. Talley. 2010. A framework for understanding physical ecosystem engineering by organisms. Oikos 119:1862-1869.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos:373-386.

Jones, P. 2014. Governing marine protected areas: resilience through diversity. Routledge.

Kassambara, A., M. Kosinski, and P. Biecek. 2021. survminer: Drawing Survival Curves using'ggplot2'. R package.

Kim, H. H., Y. W. Ko, K. M. Yang, G. Sung, J. H. Kim, H. H. Kim, Y. W. Ko, K. M. Yang, G. Sung, and J. H. Kim. 2017. Effects of disturbance timing on community recovery in an intertidal habitat of a Korean rocky shore. Algae 32:325-336.

Kingsford, R. T., J. E. Watson, C. J. Lundquist, O. Venter, L. Hughes, E. Johnston, J. Atherton, M. Gawel, D. A. Keith, and B. G. Mackey. 2009. Major conservation policy issues for biodiversity in Oceania. Conservation Biology 23:834-840.

Klein, J. C., A. Underwood, and M. Chapman. 2011. Urban structures provide new insights into interactions among grazers and habitat. Ecological Applications 21:427-438.

Knapp, S., O. Schweiger, A. Kraberg, H. Asmus, R. Asmus, T. Brey, S. Frickenhaus, J. Gutt, I. Kühn, and M. Liess. 2017. Do drivers of biodiversity change differ in importance across marine and terrestrial systems—Or is it just different research communities' perspectives? Science of the Total Environment 574:191-203.

Kovalenko, K. E., S. M. Thomaz, and D. M. Warfe. 2012. Habitat complexity: approaches and future directions. Hydrobiologia 685:1-17.

Kriegisch, N., S. Reeves, C. Johnson, and S. Ling. 2019. Top-down sea urchin overgrazing overwhelms bottom-up stimulation of kelp beds despite sediment enhancement. Journal of Experimental Marine Biology and Ecology 514:48-58.

Krumhansl, K. A., D. K. Okamoto, A. Rassweiler, M. Novak, J. J. Bolton, K. C. Cavanaugh, S. D. Connell, C. R. Johnson, B. Konar, and S. D. Ling. 2016. Global patterns of kelp forest change over the past half-century. Proceedings of the National Academy of Sciences 113:13785-13790.

Layton, C., M. J. Cameron, V. Shelamoff, P. A. Fernández, D. Britton, C. L. Hurd, J. T. Wright, and C. R. Johnson. 2019a. Chemical microenvironments within macroalgal assemblages: Implications for the inhibition of kelp recruitment by turf algae. Limnology and Oceanography 64:1600-1613.

Layton, C., M. A. Coleman, E. M. Marzinelli, P. D. Steinberg, S. E. Swearer, A. Vergés, T. Wernberg, and C. R. Johnson. 2020. Kelp forest restoration in Australia. Frontiers in Marine Science 7:74.

Layton, C., V. Shelamoff, M. J. Cameron, M. Tatsumi, J. T. Wright, and C. R. Johnson. 2019b. Resilience and stability of kelp forests: The importance of patch dynamics and environment-engineer feedbacks. PLOS ONE 14.

Ling, S., C. Johnson, S. Frusher, and K. Ridgway. 2009. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. Proceedings of the National Academy of Sciences 106:22341-22345.

Ling, S., R. Scheibling, A. Rassweiler, C. Johnson, N. Shears, S. Connell, A. Salomon, K. Norderhaug, A. Pérez-Matus, and J. Hernández. 2015. Global regime shift dynamics of catastrophic sea urchin overgrazing. Philosophical Transactions of the Royal Society B: Biological Sciences 370.

Liversage, K., and M. Chapman. 2018. Coastal ecological engineering and habitat restoration: incorporating biologically diverse boulder habitat. Marine Ecology Progress Series 593:173-185.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. Hooper, M. Huston, D. Raffaelli, and B. Schmid. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. science 294:804-808.

Mangialajo, L., M. Chiantore, and R. Cattaneo-Vietti. 2008. Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. Marine Ecology Progress Series 358:63-74.

Marsden, I. D., and S. C. Adkins. 2010. Current status of cockle bed restoration in New Zealand. Aquaculture International 18:83-97.

Martínez, B., B. Radford, M. S. Thomsen, S. D. Connell, F. Carreño, C. J. Bradshaw, D. A. Fordham, B. D. Russell, C. F. D. Gurgel, and T. Wernberg. 2018. Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. Diversity and Distributions 24:1350-1366.

Martínez, M. L., A. Intralawan, G. Vázquez, O. Pérez-Maqueo, P. Sutton, and R. Landgrave. 2007. The coasts of our world: Ecological, economic and social importance. Ecological economics 63:254-272.

Martins, G. M., A. F. Amaral, F. M. Wallenstein, and A. I. Neto. 2009. Influence of a breakwater on nearby rocky intertidal community structure. Marine Environmental Research 67:237-245.

Martins, G. M., R. C. Thompson, A. I. Neto, S. J. Hawkins, and S. R. Jenkins. 2010. Enhancing stocks of the exploited limpet *Patella candei d'Orbigny* via modifications in coastal engineering. Biological Conservation 143:203-211.

Mayer-Pinto, M., V. Cole, E. L. Johnston, A. Bugnot, H. Hurst, L. Airoldi, T. Glasby, and K. Dafforn. 2018. Functional and structural responses to marine urbanisation. Environmental Research Letters 13:014009.

Mayer-Pinto, M., E. Johnston, P. Hutchings, E. Marzinelli, S. Ahyong, G. Birch, D. Booth, R. Creese, M. Doblin, and W. Figueira. 2015. Sydney Harbour: a review of anthropogenic impacts on the biodiversity and ecosystem function of one of the world's largest natural harbours. Marine and Freshwater Research 66:1088-1105.

Mayer-Pinto, M., E. L. Johnston, A. B. Bugnot, T. M. Glasby, L. Airoldi, A. Mitchell, and K. A. Dafforn. 2017. Building 'blue': an eco-engineering framework for foreshore developments. Journal of Environmental Management 189:109-114.

McLeod, I., D. Parsons, M. Morrison, S. Van Dijken, and R. Taylor. 2014. Mussel reefs on soft sediments: a severely reduced but important habitat for macroinvertebrates and fishes in New Zealand. New Zealand Journal of Marine and Freshwater Research 48:48-59.

McLeod, K. L., and H. M. Leslie. 2009. Why ecosystem-based management. Ecosystem-based management for the oceans:3-12.

Menge, B., L. Ashkenas, and A. Matson. 1983. Use of artificial holes in studying community development in cryptic marine habitats in a tropical rocky intertidal region. Marine biology 77:129-142.

Miller, K. I., C. O. Blain, and N. T. Shears. 2022. Sea urchin removal as a tool for macroalgal restoration: A review on removing “the spiny enemies”. Frontiers in Marine Science 9.

Miller, S. M., C. L. Hurd, and S. R. Wing. 2011. Variations in growth, erosion, productivity, and morphology of *Ecklonia radiata* (Alariaceae; laminariales) along a fjord in southern New Zealand. Journal of Phycology 47:505-516.

Morrison, M., E. G. Jones, M. Consalvey, and K. Berkenbusch. 2014. Linking marine fisheries species to biogenic habitats in New Zealand: a review and synthesis of knowledge. Ministry for Primary Industries Wellington.

Moschella, P., M. Abbiati, P. Åberg, L. Airoldi, J. Anderson, F. Bacchiocchi, F. Bulleri, G. E. Dinesen, M. Frost, and E. Gacia. 2005. Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. Coastal Engineering 52:1053-1071.

Moy, F. E., and H. Christie. 2012. Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. Marine Biology Research 8:309-321.

Nelson, W., K. Neill, R. D’Archino, T. Anderson, J. Beaumont, and J. Dalen. 2015. Beyond diving depths: deepwater macroalgae in the New Zealand region. Marine Biodiversity 45:797-818.

Ng, C. S. L., S. C. Lim, J. Y. Ong, L. M. S. Teo, L. M. Chou, K. E. Chua, and K. S. Tan. 2015. Enhancing the biodiversity of coastal defence structures: transplantation of nursery-reared reef biota onto intertidal seawalls. Ecological Engineering 82:480-486.

Norse, E. A., and L. B. Crowder. 2005. Marine conservation biology: the science of maintaining the sea's biodiversity.

Novaczek, I. 1984. Development and phenology of *Ecklonia radiata* at two depths in Goat Island Bay, New Zealand. Marine biology 81:189-197.

Omori, M. 2019. Coral restoration research and technical developments: what we have learned so far. Marine Biology Research 15:377-409.

Onset Computer Corporation. 2022. HOBO Pendant - Temperature/Light Data Logger (64K).

Ostalé-Valriberas, E., J. Sempere-Valverde, S. Coppa, J. García-Gómez, and F. Espinosa. 2018. Creation of microhabitats (tidepools) in ripraps with climax communities as a way to mitigate negative effects of artificial substrate on marine biodiversity. Ecological Engineering 120:522-531.

Ovaskainen, O., and N. Abrego. 2020. Joint species distribution modelling: With applications in R. Cambridge University Press.

Ovaskainen, O., G. Tikhonov, D. Dunson, V. Grøtan, S. Engen, B.-E. Sæther, and N. Abrego. 2017. How are species interactions structured in species-rich communities? A new method for analysing time-series data. Proceedings of the Royal Society B: Biological Sciences 284.

Papps, D., and S. Priestley. 2003. Project Manukau: coastal restoration using crenulated beaches. Pages 1296-1303 *in* New Zealand Coastal Society Conference (2003: Auckland, NZ). Institution of Engineers, Australia Barton, ACT.

Papps, D., and S. Priestley. 2005. Design and performance of replenishment projects on Auckland's eastern beaches. Pages 125-130 *in* Coasts and Ports 2005: Coastal Living-Living Coast; Australasian Conference; Proceedings. Institution of Engineers, Australia Barton, ACT.

Pearce, J., and S. Ferrier. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological modelling 133:225-245.

Perkol-Finkel, S., and Y. Benayahu. 2004. Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral reefs 23:195-205.

Perkol-Finkel, S., F. Ferrario, V. Nicotera, and L. Airoldi. 2012. Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures. Journal of applied ecology 49:1457-1466.

Petrella, V., E. Martinez, M. G. Anderson, and K. A. Stockin. 2012. Whistle characteristics of common dolphins (*Delphinus sp.*) in the Hauraki Gulf, New Zealand. Marine Mammal Science 28:479-496.

Pickett, S. T., J. Wu, and M. Cadenasso. 1999. Patch dynamics and the ecology of disturbed ground: a framework for synthesis. Ecosystems of the World:707-722.

Pister, B. 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. Marine biology 156:861-873.

Ponti, M., F. Fava, R. A. Perlini, O. Giovanardi, and M. Abbiati. 2015. Benthic assemblages on artificial reefs in the northwestern Adriatic Sea: Does structure type and age matter? Marine Environmental Research 104:10-19.

Praeger, C., M. Magnusson, and R. Lawton. 2022. Optimising the zoospore release, germination, development of gametophytes and formation of sporophytes of *Ecklonia radiata*. Journal of Applied Phycology 34:2535-2549.

R Core Team, R. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Read, G. B., G. Inglis, P. Stratford, and S. T. Ahyong. 2011. Arrival of the alien fanworm *Sabella spallanzanii*(Gmelin, 1791)(Polychaeta: Sabellidae) in two New Zealand harbours. Aquatic Invasions 6:273-279.

Redmond, S., L. Green, C. Yarish, , J. Kim, and C. Neefus. 2014. New England Seaweed Culture Handbook - Nursery Systems. Connecticut Sea Grant CTSG 14:92.

Revive Our Gulf. 2023. The Mussel Reef Restoration Trust

Rouse, H. L., R. G. Bell, C. J. Lundquist, P. E. Blackett, D. M. Hicks and D. N. King. 2017. Coastal adaptation to climate change in Aotearoa-New Zealand. Journal of Marine and Freshwater Research. 51:2, 183-222.

Salauddin, M., J. J. O'Sullivan, S. Abolfathi, and J. M. Pearson. 2021. Eco-engineering of seawalls—an opportunity for enhanced climate resilience from increased topographic complexity. Frontiers in Marine Science 8.

Sampath-Wiley, P., C. D. Neefus, and L. S. Jahnke. 2008. Seasonal effects of sun exposure and emersion on intertidal seaweed physiology: Fluctuations in antioxidant contents, photosynthetic pigments and photosynthetic efficiency in the red alga *Porphyra umbilicalis Kützing* (Rhodophyta, Bangiales). Journal of Experimental Marine Biology and Ecology 361:83-91.

Schiel, D. 2013. The other 93%: trophic cascades, stressors and managing coastlines in non-marine protected areas. New Zealand Journal of Marine and Freshwater Research 47:374-391.

Schiel, D. R., S. Gerrity, S. Orchard, T. Alestra, R. A. Dunmore, T. Falconer, M. S. Thomsen, and L. W. Tait. 2021. Cataclysmic disturbances to an intertidal ecosystem: loss of ecological infrastructure slows recovery of biogenic habitats and diversity. Frontiers in Ecology and Evolution 9.

Scyphers, S. B., S. P. Powers, K. L. Heck Jr, and D. Byron. 2011. Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. PLOS ONE 6.

Sea, M. A., J. R. Hillman, and S. F. Thrush. 2022. The influence of mussel restoration on coastal carbon cycling. Global change biology 28:5269-5282.

Sedano, F., C. Navarro-Barranco, J. Guerra-García, and F. Espinosa. 2020. Understanding the effects of coastal defence structures on marine biota: The role of substrate composition and roughness in structuring sessile, macro-and meiofaunal communities. Marine pollution bulletin 157.

Shears, N. T., and R. C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132:131-142.

Shears, N. T., and R. C. Babcock. 2007. Quantitative description of mainland New Zealand's shallow subtidal reef communities. Science & Technical Pub., Department of Conservation Wellington, NZ.

Small, C., and R. J. Nicholls. 2003. A global analysis of human settlement in coastal zones. Journal of coastal research:584-599.

Smith, K. E., M. T. Burrows, A. J. Hobday, N. G. King, P. J. Moore, A. Sen Gupta, M. S. Thomsen, T. Wernberg, and D. A. Smale. 2023. Biological impacts of marine heatwaves. Annual Review of Marine Science 15:119-145.

Smith, K. E., P. J. Moore, N. G. King, and D. A. Smale. 2022. Examining the influence of regional-scale variability in temperature and light availability on the depth distribution of subtidal kelp forests. Limnology and Oceanography, 67:314-328.

Smoothey, A., and M. Chapman. 2007. Small-scale variability in the dispersion of the sea urchin *Heliocidaris erythrogramma* among boulders. Marine Ecology Progress Series 340:89-99.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225-1239.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. The ecology of natural disturbance and patch dynamics 472.

Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. Environmental conservation 29:436-459.

Strain, E. M., C. Olabarria, M. Mayer-Pinto, V. Cumbo, R. L. Morris, A. B. Bugnot, K. A. Dafforn, E. Heery, L. B. Firth, and P. R. Brooks. 2018. Eco-engineering urban infrastructure for marine and coastal biodiversity: which interventions have the greatest ecological benefit? Journal of applied ecology 55:426-441.

Strain, E. M., P. D. Steinberg, M. Vozzo, E. L. Johnston, M. Abbiati, M. A. Aguilera, L. Airoldi, J. D. Aguirre, G. Ashton, and M. Bernardi. 2021. A global analysis of complexity–biodiversity relationships on marine artificial structures. Global Ecology and Biogeography 30:140-153.

Strain, E. M. A., V. R. Cumbo, R. L. Morris, P. D. Steinberg, and M. J. Bishop. 2020. Interacting effects of habitat structure and seeding with oysters on the intertidal biodiversity of seawalls. PloS one 15.

Tait, L. W., F. Thoral, M. H. Pinkerton, M. S. Thomsen, and D. R. Schiel. 2021. Loss of giant kelp, *Macrocystis pyrifera*, driven by marine heatwaves and exacerbated by poor water clarity in New Zealand. Frontiers in Marine Science 8:721087.

Tan, E. L.-Y., M. Mayer-Pinto, E. L. Johnston, and K. A. Dafforn. 2015. Differences in intertidal microbial assemblages on urban structures and natural rocky reef. Frontiers in Microbiology 6:1276.

Taylor, P. R., and M. M. Littler. 1982. The roles of compensatory mortality, physical disturbance, and substrate retention in the development and organization of a sand-influenced, rocky-intertidal community. Ecology 63:135-146.

Teagle, H., S. J. Hawkins, P. J. Moore, and D. A. Smale. 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. Journal of Experimental Marine Biology and Ecology 492:81-98.

Temmerman, S., P. Meire, T. J. Bouma, P. M. Herman, T. Ysebaert, and H. J. De Vriend. 2013. Ecosystem-based coastal defence in the face of global change. Nature 504:79-83.

Therneau, T. M. 2022. Mixed Effects Cox Models [R package coxme].

Therneau, T. M. 2023. Survival Analysis [R package survival].

Thomalla, F., and C. Vincent. 2003. Beach response to shore-parallel breakwaters at Sea Palling, Norfolk, UK. Estuarine, Coastal and Shelf Science 56:203-212.

Thomsen, M. S., A. H. Altieri, C. Angelini, M. J. Bishop, F. Bulleri, R. Farhan, V. M. Frühling, P. E. Gribben, S. B. Harrison, and Q. He. 2022. Heterogeneity within and among co-occurring foundation species increases biodiversity. Nature communications 13:581.

Thrush, S. F., J. E. Hewitt, G. A. Funnell, V. J. Cummings, J. Ellis, D. Schultz, D. Talley, and A. Norkko. 2001. Fishing disturbance and marine biodiversity: role of habitat structure in simple soft-sediment systems. Marine Ecology Progress Series 221:255-264.

Tikhonov, G., O. Ovaskainen, J. Oksanen, M. De Jonge, O. Opedal, and T. Dallas. 2022. Hmsc: Hierarchical Model of Species Communities. R Package, Version 3.0-13.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2-16.

Tjur, T. 2009. Coefficients of determination in logistic regression models—A new proposal: The coefficient of discrimination. The American Statistician 63:366-372.

Vaselli, S., F. Bulleri, and L. Benedetti-Cecchi. 2008. Hard coastal-defence structures as habitats for native and exotic rocky-bottom species. Marine Environmental Research 66:395-403.

Velimirov, B., J. Field, C. Griffiths, and P. Zoutendyk. 1977. The ecology of kelp bed communities in the Benguela upwelling system: analysis of biomass and spatial distribution. Helgoländer wissenschaftliche Meeresuntersuchungen 30:495-518.

Vergés, A., A. H. Campbell, G. Wood, L. Kajlich, A. M. Eger, D. Cruz, M. Langley, D. Bolton, M. A. Coleman, and J. Turpin. 2020. Operation Crayweed: Ecological and sociocultural aspects of restoring Sydney's underwater forests. Ecological Management & Restoration 21:74-85.

Vergés, A., E. McCosker, M. Mayer-Pinto, M. A. Coleman, T. Wernberg, T. Ainsworth, and P. D. Steinberg. 2019. Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. Functional Ecology 33:1000-1013.

Walters, C. J., and C. S. Holling. 1990. Large-scale management experiments and learning by doing. Ecology 71:2060-2068.

Wei, T., and V. Simko. 2021. R package "corrplot": Visualization of a Correlation Matrix Vienna.

Wernberg, T., M. A. Coleman, R. C. Babcock, S. Y. Bell, J. J. Bolton, S. D. Connell, C. L. Hurd, C. R. Johnson, E. M. Marzinelli, and N. T. Shears. 2019a. Biology and ecology of the globally significant kelp *Ecklonia radiata*. Oceanography and Marine Biology.

Wernberg, T., M. Couraudon-Réale, F. Tuya, and M. Thomsen. 2020. Disturbance intensity, disturbance extent and ocean climate modulate kelp forest understory communities. Marine Ecology Progress Series 651:57-69.

Wernberg, T., K. Krumhansl, K. Filbee-Dexter, and M. F. Pedersen. 2019b. Status and trends for the world's kelp forests. Pages 57-78 World seas: An environmental evaluation. Elsevier.

Wernberg, T., and M. A. Vanderklift. 2010. Contribution of temporal and spatial components to morphological variation in the kelp *Ecklonia* (Laminariales). Journal of Phycology 46:153-161.

Westermeier, R., P. Murúa, D. J. Patiño, L. Muñoz, C. Atero, and D. G. Müller. 2014. Repopulation techniques for *Macrocystis integrifolia* (Phaeophyceae: Laminariales) in Atacama, Chile. Journal of Applied Phycology 26:511-518.

Wickham, H., W. Chang, and M. H. Wickham. 2016. Package 'ggplot2'. Create elegant data visualisations using the grammar of graphics. Version 2:1-189.

Wilcox, M., S. Kelly, and A. Jeffs. 2018. Ecological restoration of mussel beds onto soft-sediment using transplanted adults. Restoration Ecology 26:581-590.

Wilhelmsson, D., T. Malm, and M. C. Öhman. 2006. The influence of offshore windpower on demersal fish. ICES Journal of Marine Science 63:775-784.

Wing, S. R., N. T. Shears, L. W. Tait, and D. R. Schiel. 2022. The legacies of land clearance and trophic downgrading accumulate to affect structure and function of kelp forests. Ecosphere 13.

Wolcott, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at" limiting factors". The Biological Bulletin 145:389-422.

Zeiss, C. 2018. ZEISS ZEN 2.6 (blue edition). Carl Zeiss Microscopy GmbH.

Zyserman, J. A., H. K. Johnson, B. Zanuttigh, and L. Martinelli. 2005. Analysis of far-field erosion induced by low-crested rubble-mound structures. Coastal Engineering 52:977-994.