Tīmata whakaora, kickstarting recovery -
Using bivalves to bioremediate degraded estuarine sediments

A thesis

submitted in fulfilment

of the requirements for the degree

of

Doctor of Philosophy in Biological Sciences

at

The University of Waikato

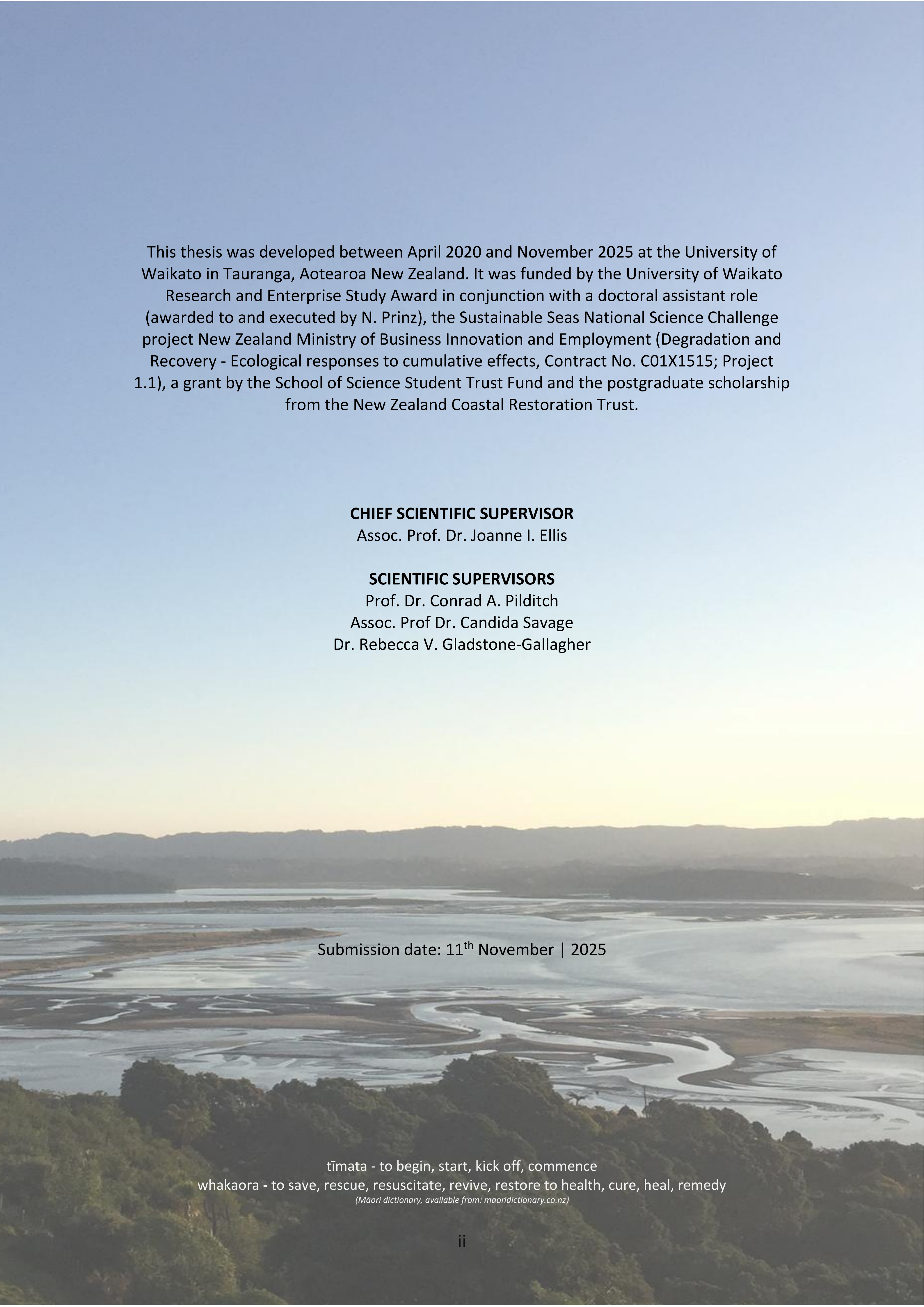
by

Natalie Prinz

2025

“I truly believe that nature has a fantastic ability to restore itself after being destroyed… Sometimes it restores itself slowly, over time. But now, because of the terrible harm we are causing on a daily basis, we need to step in and help in the restoration.”

Dr. Jane Goodall, The Book of Hope, 2021



This thesis was developed between April 2020 and November 2025 at the University of Waikato in Tauranga, Aotearoa New Zealand. It was funded by the University of Waikato Research and Enterprise Study Award in conjunction with a doctoral assistant role (awarded to and executed by N. Prinz), the Sustainable Seas National Science Challenge project New Zealand Ministry of Business Innovation and Employment (Degradation and Recovery - Ecological responses to cumulative effects, Contract No. C01X1515; Project 1.1), a grant by the School of Science Student Trust Fund and the postgraduate scholarship from the New Zealand Coastal Restoration Trust.

CHIEF SCIENTIFIC SUPERVISOR
Assoc. Prof. Dr. Joanne I. Ellis

SCIENTIFIC SUPERVISORS
Prof. Dr. Conrad A. Pilditch
Assoc. Prof Dr. Candida Savage
Dr. Rebecca V. Gladstone-Gallagher

Submission date: 11th November | 2025

tīmata - to begin, start, kick off, commence
whakaora - to save, rescue, resuscitate, revive, restore to health, cure, heal, remedy
(Māori dictionary, available from: maoridictionary.co.nz)

Abstract

Estuarine soft sediment ecosystems worldwide are increasingly threatened by anthropogenic, land-derived and marine stressors that compromise their health and functionality with cascading effects on ecosystem services that they provide. Once degraded, natural recovery can take years due to the loss of long-lived, functionally important benthic species. These species are important in maintaining internal feedback loops, thereby facilitating resilient communities that underpin critical ecosystem functions. In this thesis, I evaluated the role of two functionally distinct bivalve species, *Austrovenus stutchburyi*, a surface-dwelling suspension feeding bioturbator, and *Macomona liliana*, a deep-burrowing porewater-pressuriser, in supporting recovery of estuarine function following disturbance. Two field experiments in Tauranga Harbour, Aotearoa New Zealand were conducted, first a controlled disturbance-recovery translocation trial (after acute disturbance) and second, a large-scale translocation across a gradient of environmental (chronic) stress.
In the first experiment bivalves were added to defaunated plots in single and combined species treatments and compared to ambient and defaunated no-addition controls. Measurements were taken over a period of 389 days (one year) and included influence of bivalve additions on sediment properties, nutrient cycling, benthic metabolism (Chapter 2), and community composition recruitment (Chapter 3).

Results from the first research chapter (Chapter 2) demonstrate that *A. stutchburyi* consistently enhanced ecosystem function proxies, reducing sediment mud content, increasing oxygen consumption, and stimulating ammonium flux, even when survival was low, compared to unaided recovery. In contrast, *M. liliana* showed limited direct effects on the measured ecosystem functions and the co-addition of both species did not yield synergistic effects.

The second research chapter (Chapter 3) elucidates that the presence of *A. stutchburyi* also altered macrofaunal recovery trajectories and moderated the proliferation of opportunistic species, particularly in the absence of *M. liliana*. In contrast, *M. liliana* only treatments showed limited impact on functional recovery metrics but contributed to expected post-disturbance recruitment patterns by opportunists. Juveniles of both bivalve species settled in all treatments, *M. liliana* juveniles were enhanced in all defaunated treatments, whereas *A. stutchburyi* decreased but approached ambient after one year in all but *M. liliana* only treatments. While all treatments trended toward ambient community states over the course of one year, differences in recruitment patterns and functional diversity suggest that species additions only subtly altered recovery trajectories.

In the third research chapter (Chapter 4), *A. stutchburyi* was translocated across 9 sites within the Tauranga Harbour. Results showed that translocation success was not dependent on the overall stress-gradient or ambient *A. stutchburyi* densities. Translocation success did, however, vary with heavy metal (zinc) contamination after three months, even when concentrations were well below guideline thresholds. Effects of translocations on measures of ecosystem productivity could only be discerned in translocation sites with >44% clam retention, showing that increases in benthic metabolism and organic matter degradation are dependent on bivalve survival.

The synthesis of these chapters offers insights into the potential of using adult ecosystem engineering bivalves, particularly *A. stutchburyi*, to facilitate estuarine recovery and places this work in the broader context of restoration ecology with management implications. These findings highlight the importance of early reintroduction of ecosystem engineers to re-establish complex facilitatory feedbacks and support estuarine ecosystem recovery. However, successful restoration depends on environmental context, particularly the extent of stressor reduction needed to ensure translocation survival.

Preface

The main scientific work is presented in three research chapters (Chapters 2-4), which are individually submitted, or in preparation for publication in peer reviewed scientific journals. I co-developed the ideas and research questions, and was responsible for all field and laboratory work, data analysis, and writing of the manuscripts. Unless referenced otherwise, the following information is original and was developed and executed with the guidance support and supervision of my supervisory panel.

Chapter 2 is published in *Restoration Ecology*:
Prinz, N., Ellis, J. I., Thomson, T., Gladstone-Gallagher, R. V., Savage, C., & Pilditch, C. A. (2026). Bioturbating bivalves show potential to bioremediate degraded soft sediments by restoring ecosystem function. *Restoration Ecology*, e70393.

Chapters 3 is being prepared for submission to the *Journal of Experimental Marine Biology and Ecology (JEMBE)*.

Chapter 4 was accepted for submission to the special issue on Aquatic Ecosystem Restoration to the *New Zealand Journal of Marine and Freshwater Research (NZJMFR)* and is currently in review with the title 'Translocating clams for estuarine restoration: Retention is key for enhancing ecosystem functioning across a stressor gradient' by N Prinz, JI Ellis, L Rynkowski, T Thomson, RV Gladstone-Gallagher, C Savage, and CA Pilditch.

Findings will be shared with local iwi/hapū and the Bay of Plenty Regional Council.

Acknowledgements

"Ehara taku toa, i te toa takitahi, engari, he toa takitini" –

My strength is not mine alone, but the strength of many (Māori whakatauki)

Writing the acknowledgements make me feel so humble and grateful from the bottom of my heart for all the people who shared parts of my PhD journey. I arrived in Aotearoa New Zealand in 2020 just before the global lockdowns and knowing that I would be living here for at least 5 years seemed daunting - so many things can happen in 5 years. And they did.

Academic support - This journey would not have started without my two main supervisors Joanne Ellis and Conrad Pilditch, two excellent scientists and – even better – great people. Joanne, you made this all possible, you gave me the chance to come to Aotearoa. Thank you for being a role model for me and a female scientist I wish to be one day. Conrad, thank you for introducing me to your research and taking me under your wing. You are the ideal supervisor, and I learned an incredible amount of science and leadership from you. I am grateful for all the support that I got from you for all the scientific and extracurricular projects I wanted to squeeze in. My gratitude belongs to Rebecca Gladstone-Gallagher for being the most inspiring early-career researcher with the clearest mind and most empowering attitude. Thank you for standing by me through the roller coaster of PhD and motherhood. To Candida Savage for broadening my horizon outside the North Island perspective and sharing your knowledge with me.
To Drew Lohrer (NIWA/ESNZ) and Simon Thrush (University of Auckland) for lending me your incubation chamber equipment and providing a bulk of literature that I cited in this work. To Orlando Lam-Gordillo and Sabine Dittman for giving me purpose in my work towards the end of my PhD journey through your passion about, and insights into, the world of benthic macrofauna.
Being able to learn from this land and the tāngata whenua (people of the land) was probably the most important experience throughout this learning journey. Te Arahi Bryers and Kura Paul-Burke, tēnā rawa atu kōrua. The two of you guided me to connect to this place and learned the values and customs that I wish more people on this planet could live with. Te Arahi, I am very grateful that you introduced me to your culture from day one of being in Aotearoa. Kura, thank you for taking me into the heart of your hapū Ngāti Whakahemo, letting me learn and empowering me in so many ways. Your generosity and drive to support Youth, together with Jo Burke, taught me more than university alone could have.
To **Megan Ranapia** and **Vanessa Taikato** for being colleagues and sisters, for grounding me in this place and teaching me more about your estuaries than anyone else could have.
Thanks to Shaan Kingi (Ngāti Te Wai of Ngai te Rangi and Ngāti Ranginui) from the Tuapiro Marae who took the time to introduce me to the estuary of their hapū and blessed my field work with a karakia. To Reon and Gaston (Ngai Te Rangi) from Ōtawhiwhi marae for a beautiful wānanga that taught me a lot. To Kia Māia Ellis from the Tauranga Moana Customary Fisheries Trust for inviting us to speak about our project and engage in conversations about the interests to iwi around Te Awanui, Tauranga Moana.

To Margaret Barbour, Jo Lane, Hazel Needham, and Ian Duggan for trusting me to teach undergraduate students and letting me grow into a teaching role that you all are role-modelling par excellence.

Practical lab and field support - To Dr. Ariane Brandenburg for your continuous support in the CMFS laboratory and, along with Marika Obst, for playing board games and the life lessons, awesome chats, and always being there for me when a young mother needed it. Thanks to Soli Weiss and Eden Mutton for their unwavering support throughout my PhD between CMFS and campus. To Annette Rodgers, Holly Harvey-Wishart, and Grant Tempero for helping me in the Hamilton labs. **Elizabeth Copeland** for everything from day one of my employment with the University. You were always there for me, whether for questions or as a friend. Thank you for your trust and for letting me work so independently in the teaching labs. **Claire Shellem** for being the best friend in the PhD journey, for sharing my ups and downs, for being the aunty that took the little one for walks to give me hours to write, work, or just breathe.

Georgina Flowers, for being the senior PhD student who didn't mind spending hours and days teaching me methods and protocols, or showing me where to find equipment and how to do chamber work. I felt so grateful to have you share all your knowledge with me of how this working group operated. **Lolita Rynkowski**, for being my partner in crime - or rather - science. For making one of my chapters a joint project that made me feel part of a team and a bigger picture. I will always be so thankful for all your energy in the field and friendship inside and out of the PhD journey. **Jack Hamilton** you were always there for me as a friend and helped so much, especially in the field.

Thank you to all the volunteers (in addition to the **names in bold**) who helped me in the field and laboratory. Without you all this wouldn't have been possible.

For helping me in the field and with lab work: Rebecca Gibson, Johanna Gammal, Eva Prinz, Matthew Bennion, Steph Watson, Katherine Rowe, Siobhan Nuri, Elizabeth Harrison, Mingyu Liu, Ludwik Rynkowski, Edoardo Zelli, Mira Stenman, Bonnie Lewis, Ruben Muth, Minou Johari, Mo Razzaghi, Yanika Reiter, Olivia Dixon, Ethan Renner, Charmaine Eludo, Sanne Vaassen, Ian Thomson, Sourajit Sahoo, Maike Kaffenberger, Sinéad Nuri, Taylor Rawson, Jah-zia Tukaki-Smith, Te Hiringa Rawson, Harry Fearns, Carolina Aguirre, Franz Ferguson, Leeza Speranskaya, Jess Rutherford, Anita Lewis, Alex West, Caleb Crosby, Logan Kallam, and Dr. Maria Mugica, Silke Janssen, as well as Julia Bishop, Stef Hendra, Shanelle Kivell, and Vicky Alderson-Wallace from the Science Teaching Leadership Programme. To my fellow PhD friends, Akuhata Bailey-Winiata, Zoé Gibert, for the countless lunches and chats that made the day in the office worthwhile, and Mira Stenman, Brooke Ellis-Smith for the good chats when in Hamilton.

Providing opportunities - To the New Zealand Marine Sciences Society for allowing me to be part of the committee and help organise two conferences. To Dr. Julie Hall and the Sustainable Seas National Science Challenge Leadership team for allowing me to be part of something bigger and allowing me to represent the Youth.

To Tia Lush, Soraya Herbert, and Rachael Pratt from the STEMwana trust for giving me a voice as a young woman in STEM, letting me advocate for Science and for always supporting me to be out there with the people and children of the Tauranga community. I am deeply grateful to all the funders (page ii) and the Coastal Restoration Trust, for I will in the coming months be able to communicate this research in a meaningful way to iwi, hapū, and the community in Tauranga Moana.

Friends and Family - To the “Mount Familia” and friends in Mount Maunganui for being one of the best social networks I have ever had in my life. To my friends on other sides of the world, you have given me the important sense of belonging as like-minded people throughout time and space.

And now, thank you to my family, Susanne, Winfried, you raised me feeling loved and knowing that the sky, or the indefinite horizon of the sea, is the limit and you taught me to believe in myself. You gave me values and inner strength and are always there for me no matter how far away I am. Thank you Papa for giving me your explorer genes and always trying to find the most beautiful and adventurous things on this planet – it’s because of you that I am writing these lines. Mama, thank you for equipping me with emotional strength, communication skills and female self-confidence which is solely attributed to the way you role-modelled life. Thank you, especially for the privilege to study at universities abroad for so many years. To my sisters Tanja and Eva, how lucky am I to have you as the two most incredible young women by my side. Thank you for knowing all my faces but loving me no matter what, believing in me and always being there for me.

To Timothy Thomson for this life together, you are my all.

Finally, to Taio and your sibling who is getting ready to be born. I had a feeling that so much can develop in 5 (now nearly 6) years, and that you two came into this world was the best thing I could have ever wished for. Thank you for teaching me how to become the best version of myself.

I am deeply grateful to over 60.000 littleneck clams that were moved -
especially to the ones who gave their life for the sake of Science.
To the ones in a new home, keep making the
estuary more resilient.

Table of Contents

List of Figures

List of Tables

Top: Empty Austrovenus stutchburyi *and* Macomona liliana *shells. Bottom: Field work in the early hours of the day.*

Chapter 1

General Introduction

1.1 Background and introduction

1.1.1 Estuarine soft sediment systems

Estuarine soft sediment systems are one of the oceans ecologically and economically most valuable ecosystems. These habitats are highly productive, generate a range of ecosystem services like human nutrition and coastal protection, while playing a significant role in carbon storage, energy and nutrient cycling (Snelgrove, 1997; Barbier et al., 2011; Snelgrove et al., 2014). Infaunal communities in soft sediments are recognised as critical components underpinning these processes and mechanisms of energy and matter fluxes (Borja et al., 2010; Byers and Grabowski, 2014; De Juan et al., 2014).

Despite their importance, intertidal soft sediment habitats are increasingly subject to anthropogenic degradation (Halpern et al., 2008b). Their proximity to the land makes them susceptible to multiple local (runoff carrying nutrient and sediments, overharvesting of fauna) and global stressors (temperature increase, sea level rise, storm intensity), resulting in cumulative impacts on ecological processes (McLusky and Elliott, 2004; Adams, 2005; Thrush, Lundquist and Hewitt, 2005; Aubry and Elliott, 2006). As in other parts of the world, New Zealand's estuaries are subject to chronic stressors such as sedimentation, nutrient, and heavy metal contamination from terrestrial runoff with adverse impacts on water and sediment quality (Thrush, Lundquist and Hewitt, 2005; Sinner et al., 2011; Thrush et al., 2013a). These multiple stressors can create gradients within an estuarine system leading to varying levels of benthic health and functioning (Pratt et al., 2014; Norkko et al., 2015). Multiple cooccurring disturbances lead to habitat degradation, biodiversity loss, and in severe cases, ecological state shifts (Thrush et al., 2021). Degradation of estuarine soft sediment systems is often expressed through shifts in community structure, particularly the loss of large species that underpin key functions at the sediment-water interface.

1.1.2 Large ecosystem engineers – important players in recovery dynamics

The resilience of an ecosystem (the capacity of an ecosystem to absorb, adapt to, and recover from disturbances) and resistance to withstand a state shift is usually generated by ecological diversity, the interaction networks of species, and internal facilitatory feedback loops underpinned by species' functional traits (Thrush et al., 2014). Ecosystems in which these feedback loops are eroded can experience a state shift after disturbance, and although some might recover, it may take years before the system regains a similar level of functionality (Scheffer et al., 2012; Thrush et al., 2014). Large species, particularly ecosystem engineers (species significantly modifying, or maintaining habitat) such as in this context some bivalve species, are key drivers of facilitatory feedback loops, by acting as efficient bioturbators (sediment mixing species) and bioventilators (burrow ventilating species) of sediments, directly affecting biogeochemical cycling of intertidal sandflats (Norkko et al., 2013). Bioturbators can alter sediment erodibility, porosity, permeability, and grain size, thereby influencing all oxygen-dependent processes in the sediment (Meadows and Tait, 1989; Meadows, Tait and Hussain, 1990; Montserrat et al., 2008) and mediating inhospitable sediment conditions to form a biogenic habitat (Meysman, Middelburg and Heip, 2006; Hewitt and Cummings, 2013). For example, bioturbation can decrease nutrient loading from eutrophic sediments (Norkko et al., 2012) and increase solute fluxes and oxygen penetration depth in muddy sites (Dolbeth et al., 2019), which in turn increases species diversity and can mitigate multiple stressor effects on the system (Lenihan et al., 2018). Hence, one or two key species filling a particular functional role with their traits may be functionally more impactful than overall species diversity (Chapin III et al., 1997; Lohrer, Thrush and Gibbs, 2004; Sandwell, Pilditch and Lohrer, 2009; Norkko et al., 2015).

Acute disturbance and chronic stress in estuaries (combined or individually) generally leads to a loss of species, including these large individuals. Fast recolonisation by small opportunistic species results in communities dominated by species with limited capacity to modify the sediment structure or mediate ecosystem functions (Pearson and Rosenberg, 1978). Furthermore, once large species are lost their recolonisation of a disturbed area occurs slowly, taking years to return to pre-disturbance levels; or they fail to recover naturally to functionally significant sizes (Lohrer et al., 2010; van Colen et al., 2012; Norkko et al., 2013). This slow recovery and only partial re-establishment of function is termed hysteresis. When the pressure responsible for the regime shift is removed, the recovery rate often lags behind the rate of previous loss of functions (‘type I hysteresis’, Scheffer et al., 2001; Elliott et al., 2007; Tett et al., 2007). And compared to the original state, the degree of recovery is of alternative stability, resilience, or functionality (‘type II hysteresis’, Figure 1.1A, Elliott et al., 2007; Borja et al., 2010). Recovery is defined here as the ability of the ecosystem to progressively return to a level of functioning after a disturbance, eventually producing a system that is resilient to periodic stress and as self-sustaining as the reference system (Borja et al., 2010; Gladstone-Gallagher et al., 2019). But recovery is highly complex and in addition to the species interactions depends on the scale and intensity of the disturbance, abiotic properties, colonist supply, and the timing of the disturbance relative to recruitment (Pearson and Rosenberg, 1978; Norkko et al., 2006; Lohrer et al., 2010; Thrush et al., 2013b). While small-scale disturbances may see rapid recovery (days to weeks), larger or more severe events can result in protracted recovery periods of months to years, or even incomplete recovery (Beukema et al., 1999; Table 1 in Borja et al., 2010; Lohrer et al., 2010) if they are unaided. Re-establishing large bioturbators and the ecological functions they support is therefore essential for regaining the structural and biogeochemical integrity of soft sediment ecosystems while keeping hysteresis at a minimum.

1.1.3 Restoration of feedback loops through assisted recovery

Given the plethora of adverse ecological and economic consequences of accelerating environmental degradation (Ormerod, 2003), restoration ecology is becoming an important discipline in estuarine science (Elliott et al., 2007; Aronson and Van Andel, 2012; Bayraktarov et al., 2016). Primarily, a reduction of external stressors is essential, otherwise efforts along the restoration continuum such as remediation may be insufficient to guarantee success (Ormerod, 2003; Harris et al., 2015a, Gann et al., 2019). Subsequently, anthropogenic interventions such as rehabilitation, reallocation, or restoration (in coastal contexts, predominantly of oyster reefs, seagrass, kelp forests, saltmarshes) may assist the recovery of the sediment to maintain self-sustaining and resilient estuarine ecosystems (Aronson and Le Floc’h, 1996; Halpern et al., 2008a). Although an original state of the ecosystem may not be achieved, ecological functions can be recovered if restoration measures are implemented early enough or if appropriately applied and maintained (Hering et al., 2010). The challenge now lies in moving beyond passive recovery (via passive restoration such as rāhui/ no-take zones) toward active, scalable interventions that accelerate ecosystem recovery and ensure long-term resilience under ongoing environmental change.

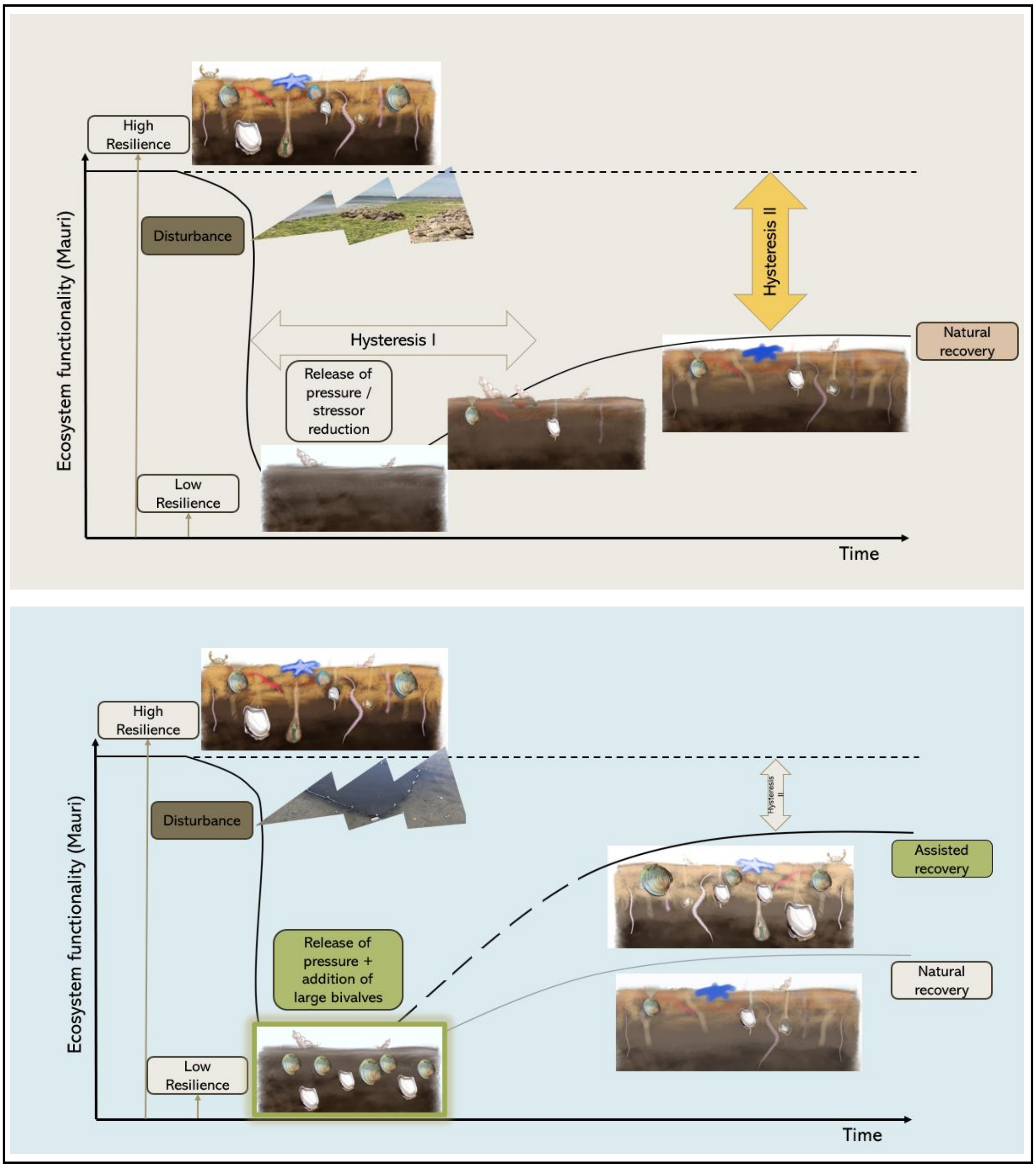


Figure 1.1 Conceptual model depicting the hypothesised effects of assisted recovery on hysteresis in soft sediment ecosystems. **(A)** Illustrates the decline of ecosystem functionality (Mauri = life force) on the example of a benthic ecosystem after a disturbance (algal bloom causing sediment anoxia and subsequent lethality of benthic organisms) and recovery remaining in a state of type II hysteresis over time (concepts from Elliott et al., 2007; Borja et al., 2010). **(B)** Recovery process altered with addition of ecosystem engineering bivalves as a bioremediation measure proposed here, potentially reducing hysteresis through assisted recovery.

The majority of manipulative disturbance-recovery experiments in temperate soft sediments have focused on the succession of species after a disturbance as a measure of recovery; showing minimal biodiversity in early successional stages and increasing biodiversity with subsequent recovery (Pearson and Rosenberg, 1978; Thrush et al., 2003; Guerra-García and García-Gómez, 2006; Norkko et al., 2006; Montserrat et al., 2008; van Colen et al., 2008). With higher abundance and diversity of infaunal species, the system is thought to have higher functional resilience (Lohrer et al., 2010; Norkko et al., 2019). However, recovery of biodiversity does not necessarily result in the recovery of function (Thrush et al., 2008b; Norkko et al., 2013; De Juan et al., 2014). While the focus of early restoration efforts has been predominantly on the recovery of biodiversity, it is the recovery of functions that is critical and not dependent on the full recovery of diversity. Recently, restoration efforts in estuaries have demonstrated measurable success in re-establishing ecosystem functioning (Borja et al., 2010; Fitzsimons et al., 2019; Lam-Gordillo et al., 2022a), which builds a foundation of knowledge on how to kickstart functional recovery. Particularly, species interactions and faciliatory networks show great potential to increase restoration success, yet, they have not been sufficiently leveraged for restoration purposes (Halpern et al., 2007).

As the loss of large functionally important species provides one of the main reasons for the loss of feedback loops, the re-introduction of large species early in the successional stages may be critical to ensure enhanced recovery of the ecosystem and facilitation of the establishment of other species therein. In New Zealand the *Tīmata Method* (tīmata = beginning, kickstart, Our Land and Water National Science Challenge, 2023) is described as a low-cost method to establish key species to kickstart the natural reversion process (in their case from farmland to native forest). The Tīmata Method has shown to be successful on land, and similar approaches have been tested in the marine realm to restore kelp forests and shellfish reefs, for example.

The interest in using key ecosystem engineering species like bivalves to restore habitats has grown in recent years (Dame, Zingmark and Haskin, 1984; Carmichael, Walton and Clark, 2012). Reef-forming mussels and oysters, have mainly been used to naturally reduce impacts of pollution and eutrophication as waste-reducing filter feeders (Petersen et al., 2015; Broszeit, Hattam and Beaumont, 2016), assimilators of land-derived nitrogen into tissue or for burial (Table 1 in Carmichael, Walton and Clark, 2012 for examples), and as mediators of benthic biodiversity (Benjamin et al., 2022; Sea, Hillman and Thrush, 2022). The potential for soft sediment dwelling animals to be used as nature-based solutions assisting recovery from eutrophication (sand prawn; Venter, Pillay and Prayag, 2020), organically polluted sediment (annelids; Ito et al., 2016), and even plastic pollution (mussels; Falkenberg et al., 2024) has also been increasingly explored (reviewed by Gonzalez et al., 2019).

Cockles and clams, being resistant to a range of temperature and salinity gradients, have been studied as potential species for bioremediation of aquaculture effluents (Nieves-Soto et al., 2011). Cockles bioremediate aquaculture wastewater through filtration of suspended solids (Miranda et al., 2009; Peña-Messina et al., 2009) and change the physical and chemical properties of aquaculture and human wastewater sediments (Zhao et al., 2019). Clams have a high potential to shape the archaeal (Deng et al., 2015) and bacterial communities in the sediment and affect biogeochemical fluxes due to their bioturbation activity (Ma et al., 2015; Shen et al., 2016; 2017; Nicholaus et al., 2019; Lukwambe et al., 2020). However, to date, bioremediation of impacted soft sediment ecosystems on a functional level has received less attention. This study seeks to include the Tīmata Method to experimentally test how to aid recovery following a disturbance in an estuarine soft-sediment context.

1.1.4 Study species

Here, I investigate two large bioturbating bivalves as potential bioremediators of degraded soft sediment. The wedge clam *Macomona liliana* (Māori name: *Hanikura*; hereafter referred to as *M. liliana*) and the New Zealand littleneck clam *Austrovenus stutchburyi* (Māori name: *Tuangi/Tuaki*; in New Zealand commonly called cockle, hereafter referred to as *A. stutchburyi*) are common, endemic, and important species in New Zealand's soft sediment estuarine ecosystems (Pridmore et al., 1990). Both species are recognised as key ecosystem engineers enhancing nutrient processing and oxygenation of the sediment (Thrush et al., 2006; 2014; Sandwell, Pilditch and Lohrer, 2009; Jones et al., 2011; Pratt et al., 2013; O'Meara et al., 2020). *Macomona liliana* and *A. stutchburyi* each exhibit several important traits which place them into different functional groups and render both species viable candidates for soft sediment remediation in terms of supporting recovery of biogeochemical gradients in the sediment as well as macrofaunal recolonisation and recruitment (Table 1.1).

Table 1.1 Summary of functional and life cycle differences between the two study species, *Macomona liliana* and *Austrovenus stutchburyi,* proposed for bioremediation species in this thesis. The two experiments were designed based on these traits and recruitment times.

Species, Order	**Feeding mode**	**Sediment depth**	**Mobility**	**Behaviour**	**Maturity**	**Spawning**	**Recruitment**	**Tīmata recovery mechanism (proposed here)**
Macomona liliana Tellinidae	deposit feeding at the surface via a long inhalant siphon (Morton and Miller, 1973; Powell, 1979)	~10 cm depth	limited (~ 10 cm in one tide cycle, (Thrush, Pridmore and Hewitt, 1994; Hewitt et al., 1996)	Porewater pressurizing	(> 22 mm shell length (Taylor, 1999)	austral summer (November - March) (Taylor, 1999)	between December – March (Taylor, 1999)	accelerate solute exchange, enhance primary production, increase macrofaunal diversity (Thrush et al., 1992; Volkenborn et al., 2012; Woodin et al., 2016)
Austrovenus stutchburyi Veneridae	suspension feeding on seston via short siphon (Powell, 1979; Williams and Pilditch, 1997)	upper 5 cm (Powell, 1979)	Mobile, vertical and horizontal movement (Hewitt et al., 1996; 1997; Jones et al., 2011)	Bioturbating	>18 mm (Larcombe, 1971)	austral summer (January – April) (Larcombe, 1971)	After 2-3 weeks of larval phase, they settle at a size of approx. 180 µm (Stephenson and Chanley, 1979)	Sediment aeration, enhance ammonium efflux influencing micro-phytobenthos production, increase species & functional diversity (Sandwell, Pilditch and Lohrer, 2009; Jones et al., 2011)

Macomona liliana, although not used for human consumption, serves as food for shorebirds, rays, and fish (Roper, Pridmore and Thrush, 1992; Thrush, 1999; Karlson et al., 2021). The feeding and burrowing behaviour of *M. liliana* draws organic material and microphytes from the surface and excretes waste directly into the sediment, enhancing the concentration of organic matter in the sediment (Wilcock et al., 1993). *M liliana* uses a long inhalant siphon to suck in deposits and microphytes from the sediment surface and induce pulses of oxygen-rich water into the subsurface sediment from the exhalant siphon, creating hydrostatic pressure gradients in the sediment profile (Pridmore et al., 1991; Volkenborn et al., 2012). This increases the oxic-anoxic interface, modulates the mineralisation rates of organic matter, accelerates solute exchange, and forces nutrient-rich anoxic water shallower in the sediment profile fuelling nitrification and enhancing primary production (Aller, 1994; Volkenborn et al., 2012; Woodin et al., 2012; Kristensen et al., 2014). This mechanism could support recovery from disturbed, eutrophic, anoxic sediments as the oxygenation and solute transport promoted by *M. liliana* are critical factors that enhance the coupling of nitrification and denitrification (Douglas et al., 2017), potentially relieving eutrophication pressures.

So far, translocations of *M. liliana* have focused on assessing density dependent biotic interactions with the macrofauna community and conspecifics (Thrush et al., 1992; 1996a; Hewitt et al., 1996) and sediment erodibility (Harris et al., 2015b). *Macomona liliana* additions to defaunated sediment significantly increased the total number of macroinvertebrates, taxa, deposit-feeders, and predators (Thrush et al., 1992). Adult *M. liliana* were found to influence conspecific and macroinvertebrate recruitment, with low adult densities aiding recruitment and high densities inhibiting it (Whitlatch and Zajac, 1985; Thrush et al., 1992; Thrush, Pridmore and Hewitt, 1994; Hewitt et al., 1997; Turner et al., 1997). I expect *M. liliana* to affect the recovery and functioning of soft sediments through their hydraulic behaviours and feeding that promote nutrient turnover, affect microphytobenthos and oxygen penetration. Despite their importance in benthic interaction networks (Thrush et al., 2014), the potential of *M. liliana* to restore benthic habitats via active translocations has not yet been assessed.

Austrovenus stutchburyi is valued as cultural keystone species (species with disproportionately large role in the environment relative to its abundance, Te reo Māori: *taonga*) and direct food source for animals and humans (Mccarthy et al., 2013). It is an important customary, recreational, and since 2002 also commercial fishery managed under the New Zealand Quota Management System (Lock and Leslie, 2007; Fisheries New Zealand, 2010; Hewitt and Cummings, 2013) High adult *A. stutchburyi* densities have been shown to increase ecosystem function as they enhance nutrient dynamics in particular ammonium efflux (via bioturbation and excretion), which boosts microphytobenthos productivity (Thrush et al., 2006; Sandwell, Pilditch and Lohrer, 2009; Jones et al., 2011; Norkko et al., 2013). Generally, higher average and total macrofaunal species and functional diversity is observed in *A. stutchburyi* beds relative to *M. liliana* beds, or to sandflats without large structuring organisms (De Juan et al., 2014; Karlson et al., 2016; Thomas et al., 2022).

Effects of transplanted *A. stutchburyi* on conspecific recruitment success has been variable; translocations had no strong effects on biodiversity and influences on the community composition in only one of two sites reported in Hewitt & Cummings (2013), suggest a more species-rich initial community composition is important to see effects. Unclear effects on community composition, plus the lack of investigation of the improvement of ecosystem function after disturbance and *A. stutchburyi* re-additions, leave some open questions which I target in this thesis. Furthermore, through their ability to modify the surface biochemistry of the sediment, *A. stutchburyi* may have the potential to affect the health and functionality of sediments along different gradients of environmental stress within an estuary.

Translocation trials using *A. stutchburyi* in New Zealand are emerging and *A. stutchburyi* is deemed a robust species for transplantation (Dobbinson, Barker and Jillett, 1989; Stewart, Creese and Lalwnitory, 2002; Marsden and Adkins, 2010 for a review; Hewitt and Cummings, 2013). These efforts aimed to restore biodiversity (Hewitt and Cummings, 2013), shellfish enhancement for human consumption, and to "bring the harbour back to life" by studying effects of translocations over the course of one year (Stewart, Creese and Lalwnitory, 2002; Cummings et al., 2007; 2010). Some translocation efforts involved community collaborations helping to "revive cockle populations" and to regenerate local shellfish stocks (Cummings and Hatton, 2003; Cummings, 2006; Cummings et al., 2007). However, their functional effect in supporting recovery after an acute disturbance and enabling recovery along different levels of multiple chronic stressors has yet to be explored. Given their robustness to survive more inhospitable sediment conditions, such as increased muddiness, eutrophication or increased contaminant concentrations, it makes this species an ideal candidate for field-based restoration trials. I expect *A. stutchburyi* to affect functional recovery from a disturbance (causing smothering, anoxia, species loss) by its bioturbating activity, primarily by stimulating oxygen and nutrient fluxes as well as providing improved sediments for macrofaunal recovery.

1.1.5 Knowledge gaps

Despite its undeniable potential for the active restoration of estuarine habitats, research on bioremediation as key support for benthic recovery after disturbance is scarce. Purposely adding large, engineering bivalves, fundamental to benthic interaction networks, as bioremediators into defaunated soft sediments to promote the recovery of ecosystem functions and benthic recolonisation has, to the best of my knowledge, not been tested. Based on the literature presented above, I have identified three specific knowledge gaps which are addressed in this thesis:

1) Evaluating effects of bivalve translocations on functional recovery to reduce hysteresis (Chapter 2). It is unclear whether introducing large bivalves early in the successional stage can enhance the functional recovery of the system by changing recovery trajectories (including the recovery rate and an altered end point of recovery). Such a “jump” in the successional sequence may significantly accelerate functional recovery. The fact that clams directly affect different biogeochemical processes, interlinked with modified macrofaunal community composition (Rossi et al., 2008), may be relevant for reducing hysteresis and aiding the holistic recovery of soft sediments (Figure 1.1B). Understanding these connections will provide important insights into feedback mechanisms that fuel recovery rates. Specifically, I ask: *when passive recovery is insufficient, which ecosystem engineers make the most difference in facilitating functional recovery?*

2) Testing for effects of large bivalves on the recovery of biodiversity in macrofaunal communities (Chapter 3). We need to increase our knowledge of combining different species in field-based bioremediation (Shen et al., 2016), as these key species can accelerate community-level recovery (Halpern et al., 2007; Gagnon et al., 2020). There is a gap of knowledge in using ecosystem engineers whose ecological traits are known to assist recovery in a targeted way, particularly in soft sediment systems. Previous work on the effects of both species on benthic interaction networks identified both study species as key players in feedback loops and nutrient processing (Thrush et al., 2014). However, we lack a detailed understanding of single species remediative effects on the macrofaunal community composition and recolonisation after disturbance in comparison to possibly synergistic effects of functionally complementary species. *Will a combined species approach help us support bioremediation actions within estuaries more efficiently?*

3) Understanding the applicability of sediment-dwelling clams for bioremediation across stressor gradients (Chapter 4). Despite the vast knowledge base on detrimental effects of stressors on clams and evidence of translocation survival rates, it has not been evaluated whether the addition of clams could be a viable tool for estuarine restoration along a chronic stress gradient. Given that survival rates may depend on certain factors that can be managed more easily than others, we need to know more about what limits translocation success. Furthermore, it is not known how "degraded" a soft sediment habitat can be before survival of translocated clams is compromised. Finally, there is no knowledge on whether translocated clams can improve ecosystem function across a stressor gradient which offers critical insights into different stages of degradation comparable to future levels of degradation. *If the reintroduction of ecosystem engineers is a feasible solution, what conditions limit translocation success and their performance under multiple stressors? And how high does retention need to be to affect functioning?*

1.2 Thesis overview, aims, and objectives

The aim of this thesis is to investigate whether the process of recovery can be aided and enhanced using large, endemic bivalves and to assess this application for the management and restoration of degraded estuaries. I aim to identify whether two functionally distinct ecosystem engineers can individually, and in combination, aid benthic recovery in situ after an acute disturbance and across a chronic environmental stressor gradient. Overall, I hypothesise that after acute stress the combined addition of wedge shells and clams will show increased ecosystem functions and facilitate species recovery differently compared to single additions. I furthermore expect that the success of clam additions along a chronic stress gradient will be context-dependent (stressor dependent) and that survival may directly affect the influence of bivalves on ecosystem function delivery across a stressor gradient. This research is relevant to both, local restoration efforts as well as the current state of knowledge in functional ecology. By weaving field ecology and management needs together, the results from this thesis may add to the field of restoration ecology with new evidence for a "function-first" approach. Moreover, it will inform management and restoration efforts elsewhere as accelerating recovery is of global interest across ecosystems. This thesis adds insights into novel restoration approaches including nature-based solutions to human-induced problems contributing to the United Nations' Decade on Ecosystem Restoration (2021 - 2030) (Waltham et al., 2020).

My thesis comprises three data-driven research chapters (Chapter 2-4, Figure 1.2) from two in-situ field experiments conducted inside the 200 km^2 Tauranga Harbour (Te Awanui). Tauranga Harbour is a semi-diurnal estuarine lagoon located at 37° 40'S and

176° 10’E, on the east coast of Aotearoa New Zealand's North Island. It is sheltered by a 24 km long barrier island (Matakana Island) on either side of which opens a tidal inlet, separating the estuary into a northern and a southern basin (Davies-Colley and Healy, 1978). It is a shallow harbour (average depth at low tide ~3 m) and comprised of approximately 60% intertidal sandflats (tidal range of 1.63 m; spring tide to 1.24 m; neap tide) (Heath, 1985; Park, 2004; Tay et al., 2012; Cussioli et al., 2015). Water temperature ranges from an average of 13.9°C in winter to 22.6°C in summer (Jones et al., 2011). Land use of the ~1300 km^2 wide catchment around the harbour is mainly agricultural, forestry, and native bush, with the urban centre (Tauranga city, international shipping port) to the southeast (Park, 2004; Ellis et al., 2013). Bay of Plenty Regional Council and iwi liaison ensured appropriate site selection and continuous engagement with the project. Ngāti Te Wai of Ngai te Rangi and Ngāti Ranginui (directly and via the Tauranga Moana Customary Fisheries Trust) were met with prior to commencement of the field work and appropriate customs were upheld to karakia (bless) the work (Ethics statement in Appendix I).

The consecutive chapters address the following objectives:

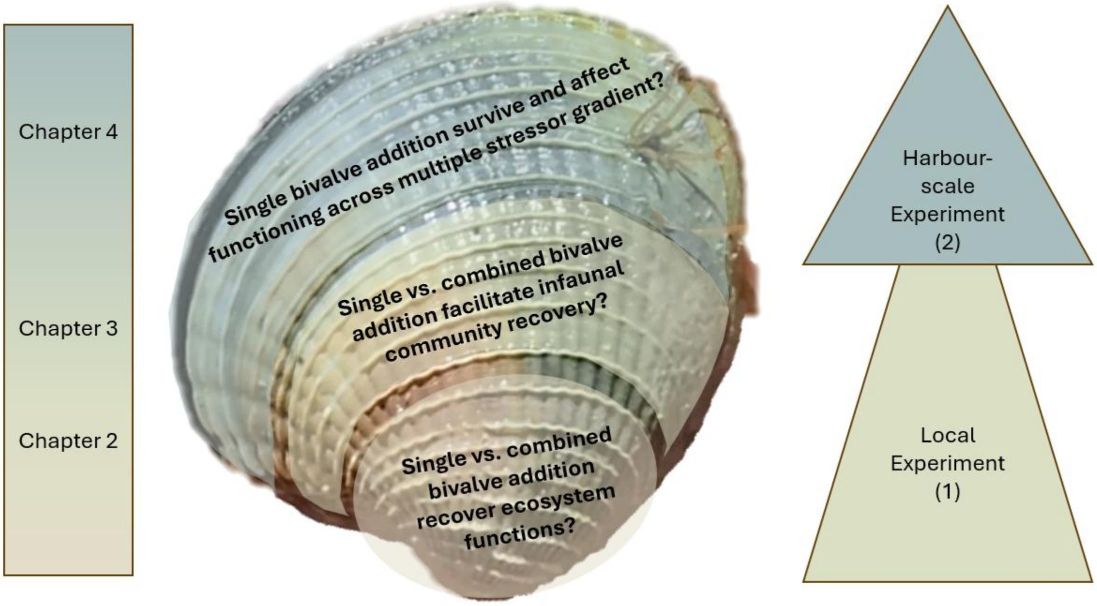


Figure 1.2 Schematic summarising the main research questions from the three research chapters of this thesis (2-4) from two experiments conducted (1) at one location and (2) multiple locations throughout the harbour.

1.2.1 Chapter 2 – Bioturbating bivalves show potential to bioremediate degraded soft sediments by restoring ecosystem function

Results from the first in-situ experiment are presented in Chapter 2 and 3. The aim of Chapter 2 was to evaluate how two large, functionally different bivalves (single species vs. combination) affect ecosystem functions at the sediment-water interface following an acute disturbance. The research plots were cleared of large fauna to imitate a disturbance event (physical defaunation) and subsequently large bivalves (either *M. liliana, A. stutchburyi*, or co-addition) were added, along with ambient and defaunation control plots. Samples from incubation chambers and the sediment were taken one month, three months and one year after the disturbance and subsequent re-addition of bivalves. I expected that the ecosystem functionality (measured via proxies of sediment parameters, carbon processing and nutrient fluxes) of the seafloor could be aided by the functionally complementing behaviour of the two species, accelerating recovery.

1.2.2 Chapter 3 - Differential ecosystem engineering of two bivalves may shape the recovery of benthic macroinvertebrate communities

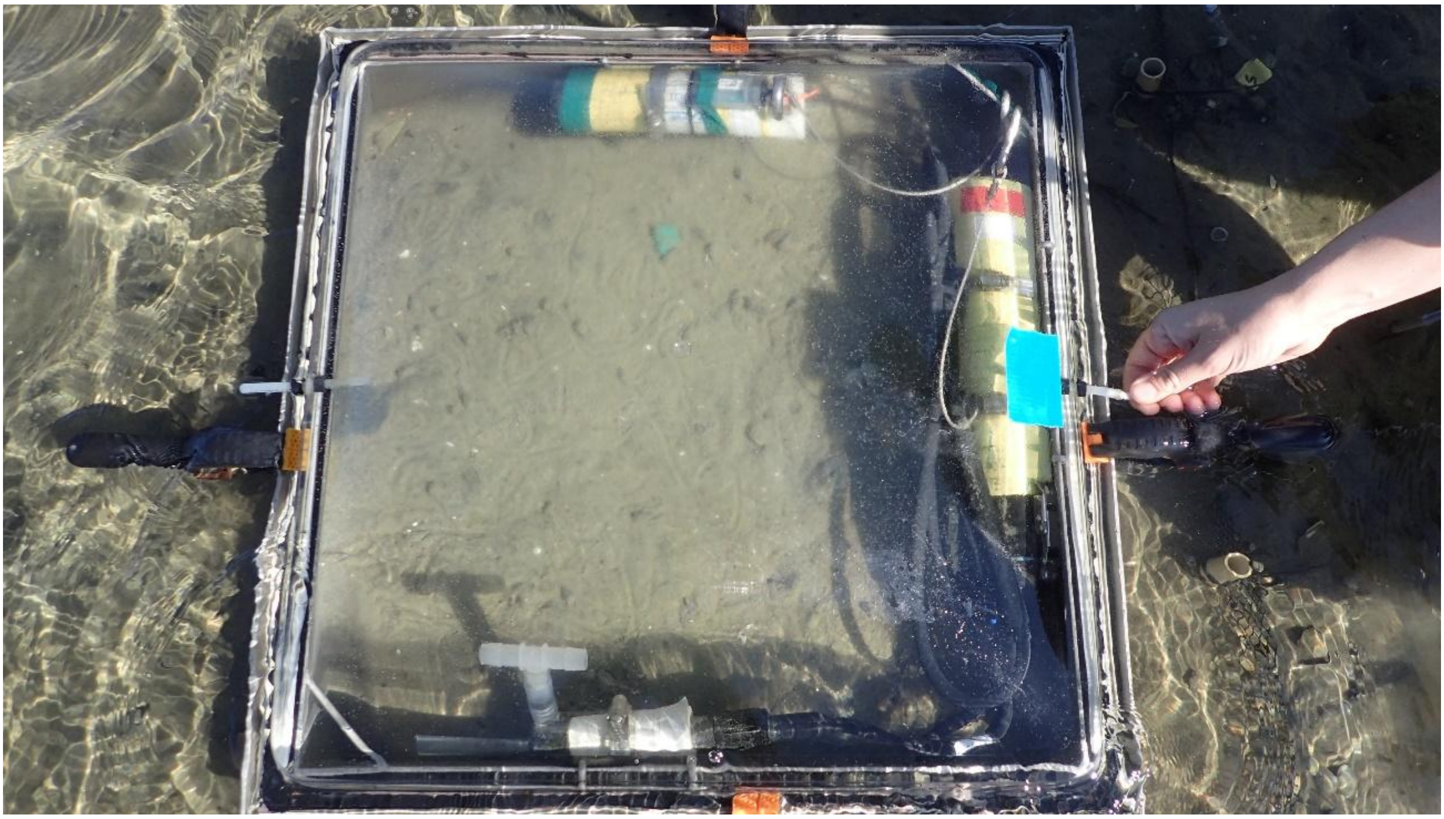
Chapter 3 focuses on the potential of bivalve additions (experiment described above) to facilitate recovery of the macrofaunal community and trait diversity over the course of one year, by investigating whether there is an individual or synergistic effect of bivalve additions on community recovery. The combination of key species may affect community recovery dynamics more than a single species addition. This was assessed by investigating the macrofaunal community composition recovery from the in-situ experiment across three sampling times. I aimed to evaluate whether the recovery process is accelerated and/or directed towards a different trajectory, quantifying the single species effect versus both species combined (synergistic bioremediation effect).

1.2.3 Chapter 4 – Translocating clams for estuarine restoration: Retention is key for enhancing ecosystem functioning across a stressor gradient

Chapter 4 shows results from the second experiment. The previous experiment (Chapter 2 & 3) informed the 4th chapter, to use the species which showed most potential to remediate degraded soft sediments (*A. stutchburyi*).

The final research chapter examines the retention (survival) of large *A. stutchburyi*, three months after transplantation, across a gradient of multiple cooccurring environmental stressors (sedimentation, nutrient, and heavy metal contamination) within the same estuary. Moreover, it aims to assess if translocation success affects ecosystem functions. The stress gradient offers a “space-for-time” approach (Habeeb et al., 2005; O’Brien, Dehling and Tylianakis, 2022) where muddier sites represent a more degraded estuary in the future, enabling me to assess worsening levels of ecosystem degradation and recovery potential through translocations. This chapter analyses whether the re-addition of the most promising species (*A. stutchburyi*) is feasible, can ensure survival (retention) across varying levels of stress, and compares ecosystem productivity (proxies for primary productivity, carbon degradation, microphytobenthos) between ambient seafloor and bivalve addition treatments.

Chapter 5 concludes this thesis with a summary and places my findings into the context of what is known, providing a synthesis of my findings and the broader literature on estuarine restoration using *A. stutchburyi*. Some considerations for future translocations for management are provided, distilling the key learnings into practical advice.



Top: Setting up chambers in the experimental plots in Tuapiro Estuary. Bottom: Close-up of an incubation chamber on an outgoing tide. February 2022.

Chapter 2

Bioturbating bivalves show potential to bioremediate degraded soft sediments by restoring ecosystem function

2.1 Introduction

Marine soft sediment ecosystems are of ecological and economic importance because of the biodiversity and fisheries they support and their roles in carbon storage, energy flow, and nutrient cycling (Snelgrove, 1997). Globally, coasts are impacted by anthropogenic disturbances (Halpern et al., 2008b) which leads to habitat degradation and the loss of valuable ecosystem functions and services (Lotze et al., 2006; Worm et al., 2006). Ecosystem restoration efforts are increasing; however, ensuring their successful, feasible, and scalable implementation is critical to revert degraded areas into functioning ecosystems. Manipulative disturbance-recovery experiments in temperate soft sediments have documented the succession of species after a defaunation disturbance event as measure of recovery (Thrush et al., 2003; Norkko and Thrush, 2006; van Colen et al., 2012). However, species richness may not directly reflect functional ecosystem recovery, given that ecosystem functions recover non-linearly and at different rates, often even after species are re-established (Loreau et al., 2001; Bolam, Fernandes and Huxham, 2002; Norling and Kautsky, 2007). The main goal for ecosystem restoration varies (see Gann et al. 2019 Recovery Wheel) but increasingly focuses on restoring lost functions and ecosystem services (Duarte et al., 2020). Therefore, the focus for successful restoration should be on the regeneration of functions, rather than on biodiversity alone (Macleod, Moltschaniwskyj and Crawford, 2008).

In coastal soft sediment ecosystems, increases in the density of key taxa can enhance ecosystem functioning (Sandwell, Pilditch and Lohrer, 2009; Karlson et al., 2016), as their behaviour is important for biogeochemical cycling (Lohrer, Thrush and Gibbs, 2004; Pratt et al., 2014). Infaunal bivalves have been recognised as critical in facilitating energy and matter fluxes, and concomitant functions such as sediment stabilisation, benthic production, and nutrient cycling (Borja et al., 2010; Byers and Grabowski, 2014; De Juan et al., 2014). Moreover, dense aggregations of large, adult bivalves, play a pivotal role in ecosystem functioning, being of higher importance, compared to juveniles and other infaunal species, due to their ability to disproportionally affect ecosystem functionality and facilitate recruitment (Thrush et al., 2006; Norling and Kautsky, 2007; Norkko et al., 2013). Bivalves at relevant sizes and densities, therefore, can improve physico-chemical properties of sediments through bioturbation, stimulation of nutrient cycling, and the addition of organic matter content through biodeposits (Sandwell, Pilditch and Lohrer, 2009; Woodin et al., 2016; Smaal et al., 2019). Although these long-lived species are critical for ecological functioning, they are generally slow to reach a sufficient size (adult sizes) to influence functioning in degraded areas (Norkko et al., 2002). In early succession, recovering soft sediments are usually first occupied by pioneer species (Pearson and Rosenberg, 1978), however, the early re-introduction of large keystone species after a disturbance, may stimulate important ecosystem functions, thereby accelerating recovery.

Disturbances in estuaries, such as through algal blooms causing anoxia, or physical seafloor disturbance, can alter the sediment biogeochemistry causing macrobenthic die-offs and organic enrichment, which results in habitat change and system-shifts to a degraded state (Thrush et al., 2008a). *Macomona liliana* (large wedge clam, a tellinid surface deposit-feeding bivalve) and *Austrovenus stutchburyi* (New Zealand little neck clam, a venerid suspension-feeding clam) are recognised as key species driving ecological functioning on intertidal sandflats in Aotearoa New Zealand (Pridmore et al., 1990). *Macomona liliana* is deep dwelling, around 10 cm below the sediment surface (Hewitt et al., 1997). Their feeding behaviour pressurises the sediment porewater, while forcing nutrient-rich anoxic water shallower in the sediment profile and into the oxic nitrification zone (bioadvection), thereby stimulating microphytobenthic activity through the provision of nitrogen in form of ammonium (NH_4^+-N, Volkenborn et al., 2012; Kristensen et al., 2014; Woodin et al., 2016). This process also exposes surrounding sediments to oxic-anoxic oscillations, which modulate the mineralisation rates of organic matter (Aller, 1994). *Austrovenus stutchburyi* bioturbates the upper 5 cm of the sediment through vertical and horizontal movement (Morton and Miller, 1973). Their position at the sediment-water interface supports benthic-pelagic coupling, transferring energy from microphytobenthos to higher trophic levels, enhancing primary production, and organic matter mineralisation by production of biodeposits (Lohrer et al., 2010). At high densities, *A. stutchburyi* also stabilises the sediment reducing sediment transport and resuspension (Jones et al., 2011; Yeoh et al., 2024). Adults of both bivalve species are known to enhance ecological processes associated with ecosystem resilience including increasing primary productivity and nutrient processing and the break-down of organic matter (Thrush et al., 2006; Pratt et al., 2013). These processes can be directly facilitated by the two species' functional traits (living position, feeding behaviour, bioadvection vs. excretion) which suggests that they may be good candidates for bioremediation. Furthermore, the addition of both species may have synergistic effects on the recovery dynamics through the combination and complementation of functional traits as suggested with other benthic species (Shen et al., 2016).

Despite growing evidence that suggests translocation of adult stock as the most promising technique for soft sediment habitat restoration (Thrush et al., 1992; Marsden and Adkins, 2010; Thomas et al., 2021), clams and more so, wedge shells have rarely been studied for the purpose of bioremediation of benthic estuarine function. To date, restoration efforts by infaunal suspension feeding clams focus on the improvement of water quality of aquaculture effluents, associated sediment, and the bacterial communities therein (Shen et al., 2016; Zhao et al., 2019; Lukwambe et al., 2020). In New Zealand, *A. stutchburyi* has been extensively studied, and although translocations of *A. stutchburyi* are recommended for restoring cockle beds (Stewart, Creese and Lalwnitory, 2002; Cummings et al., 2007; Marsden and Adkins, 2010), there is a lack of studies on the potential for bivalve additions for estuarine bioremediation. Translocating deeper-dwelling species, such as *M. liliana*, in addition to the surface bioturbator *A. stutchburyi* is a novel approach and yet untested. While the role of ecological theory in amplifying restoration outcomes has been suggested (Silliman et al., 2023), real world tests in marine soft sediments are limited, despite their promise to greatly advance the field of restoration ecology.

I conducted a manipulative disturbance-recovery field experiment to investigate the individual, and combined, effects of two functionally different infaunal bivalves as potential bioremediators of physically disturbed and defaunated estuarine soft sediment. My objective was to measure survival rates of translocated individuals through time and assess if, and how, the addition of these functionally different species would impact the recovery of relevant ecosystem functions. I hypothesised that disturbed plots with re-seeded adults of single species will regenerate functions in sediment properties, ecosystem productivity, and nutrient dynamics faster than plots without bivalve additions. *Macomona liliana* was expected to enhance oxygenation of subsurface sediments and expulsion of nutrient-rich porewater via bioadvection, while *A. stutchburyi* was hypothesised to influence oxygen-dependent processes in the upper sediment and increased nutrient flux via excretion (Woodin et al., 2016). Therefore, plots with both species were expected to synergistically restore soft sediment functionality faster compared to the plots with individual species.

2.2 Methods

2.2.1 Study area

The field experiment was conducted in Tuapiro estuary (37°29'30.7"S 175°57'05.3"E) in the northern part of Tauranga Harbour, a 200 km^2 large barrier-enclosed estuarine lagoon situated on the north-east coast of Aotearoa New Zealand's North Island (Figure 2.1A, B). The intertidal sandflats at the site are semi-diurnal with a mean inundation period of 8 h (tidal range of 1.24-1.62 m; Jones et al., 2011) and regularly exposed to wind waves that generate sediment transport. Water and air temperature range from a daily average of 13.9°C (winter) to 22.6°C (summer) and 12.0°C to 20.0°C, respectively (DataHub NIWA 2024). The macrofaunal community is dominated numerically by polychaetes, with bivalves (predominantly *M. liliana* and *A. stutchburyi*) as biomass dominants (Pratt et al., 2013).

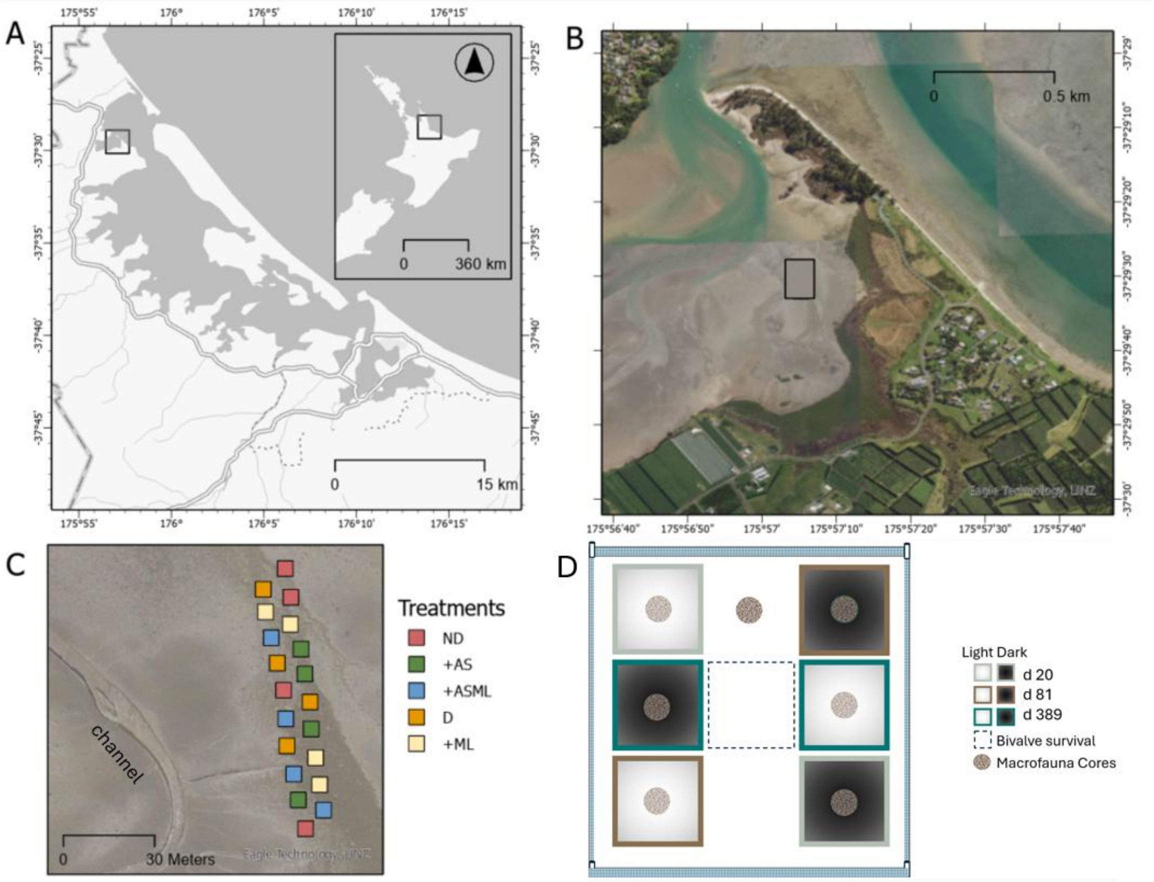


Figure 2.1 (A, B) Location of the study site at Tuapiro Estuary in the northern Tauranga Harbour, on the North Island of Aotearoa New Zealand. **(C)** The experimental treatment design; ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species. **(D)** Arrangement of light and dark incubation chambers within each plot, where measurements were taken in different parts of the plot during each sampling campaign (d 20, 81, 389 after bivalve additions). The central 0.5 x 0.5 m quadrat was excavated to assess bivalve survival at the end of the experiment. A core was taken 7 days after the defaunation to assess whether sediment had been defaunated.

2.2.2 Experimental Design

In late January 2021 (austral summer), a 90 x 10 m study area was established in the mid-intertidal, with the major axis oriented parallel to a tidal channel to minimize variation of inundation times (Figure 2.1C). Twenty 1.5 m x 1.5 m plots (2.25 m^2) were established 5 m apart and assigned randomly to one of five treatments (n=4); no disturbance ('ND': intact sediments, no manipulation), disturbance no addition ('D'; defaunation, no addition of bivalves), *M. liliana* addition ('+ML': defaunation + addition of *M. liliana*), *A. stutchburyi* addition ('+AS': defaunation + addition of *A. stutchburyi*), and addition of both species ('+ASML': defaunation + addition of both species). All plots, except ND, were defaunated by removing the sediment surface (5 cm) with a spade and systematically finger ploughing the remaining 10 cm of the sediment to remove remaining individuals. The sediment was then turned over to a depth of ~15 cm and homogenised with a spade. Following the disturbance, plot perimeters were fenced using plastic mesh (1 cm^2), buried 10 cm into the sediment and protruding 5 cm, to stop the migration of adult bivalves into/out of the plots, without restricting movement of smaller organisms (Jones et al., 2011). The large mesh size and short height above the sediment was chosen to minimise effects on water flow (Miller and Gaylord, 2007).

Seven days (d) after the disturbance, a macrofauna core (Ø 13 cm × 15 cm depth) was collected from each plot to confirm defaunation success. Thereafter bivalves were added to the +ML, +AS, +ASML plots. Adult *M. liliana* (>20 mm shell length) and *A. stutchburyi* (> 18 mm) were translocated from within 200 m of the experimental site. Approximately 450 *M. liliana* $plot^{-1}$ (200 m^{-2}) and 1800 *A. stutchburyi* $plot^{-1}$ (800 m^{-2}) were added to each single species and combined treatment plot. These densities were representative of medium density beds at healthy sites in many New Zealand estuaries (e.g., Sandwell et al. 2009; Ellis & et al. 2013; Berkenbusch & Neubauer 2016).

Plots were sampled on d 20, 81 and 389, representing 3 weeks, three months, and one year post addition of the bivalves, to capture the recovery trajectory over one year (as in Thrush et al., 2008a; Lohrer et al., 2010; De Juan et al., 2014). On each sampling date a different quadrant of the plot was sampled (Figure 2.1D). Samples of sediment properties (grain size, mud content, organic matter content, and microalgal pigment concentrations) were collected, and sediment – water column solute fluxes were measured as proxies for ecosystem functions using benthic incubation chambers. Finally, bivalve survival was assessed.

2.2.3 Sediment properties and bivalve survival

On each sampling date, benthic incubation chambers were placed (see below), and then five sediment cores (Ø 2.5 cm × 2 cm depth) were collected from beside each chamber, pooled and homogenised into one replicate, and stored in the dark at -20 °C for analysis of sediment grain size (GS) distribution, organic matter content (OM), and microalgal pigment concentrations (chlorophyll *a*, phaeophytin). After the chamber incubations, one large core (Ø 13 cm × 15 cm depth) was collected from the centre of each chamber for the assessment of large bivalve abundance. Cores were sieved in situ on a 0.5 mm mesh, preserved in 70% Isopropyl alcohol and stained with Rose-Bengal. Following the removal of the core, holes were immediately filled with defaunated fine sand to minimise disturbance to the plot (as in Lohrer et al. 2010). After the final sampling date (April 2022) the unsampled central 0.25 m^{-2} of each plot was excavated and sieved on a 4 mm mesh to capture all large bivalves. All adult *M. liliana* (> 20 mm) and *A. stutchburyi* (> 18 mm) were counted to estimate transplant survival and measured (maximum shell dimension).

Sediment grain size was measured using a Malvern Mastersizer-3000 (particle size range 0.05-2 mm) after removing organic matter content with 10% hydrogen peroxide over a minimum of 3 weeks. Sediment organic matter content was determined by loss on ignition comparing weights after drying at 60°C for 24 h at 550°C for 4 h. Sediment for chlorophyll *a* (chl *a*) and phaeophytin (phaeo) analysis was freeze-dried and then pigments extracted in 90% buffered acetone and measured on a Turner Designs 10-AU fluorometer before and after acidification (Arar and Collins, 1997). For this study, the adult transplanted bivalves collected in the macrofauna cores were separated from the smaller macrofauna using a 4 mm sieve, then counted and sized.

2.2.4 Sediment-water fluxes as proxies for ecosystem functions

I used in-situ light and dark benthic incubation chambers to measure solute fluxes across the sediment-water interface following established methodologies (e.g., Lohrer, Thrush and Gibbs, 2004; Sandwell, Pilditch and Lohrer, 2009; Jones et al., 2011). On each sampling event, flux measurements were made over two consecutive days (dark and light incubations occurring on alternate days) during midday high tides to maximise light conditions. Chambers were located in a different sector within the 2.25 m^2 plot on each sampling date (Figure 2.1D). In brief, the chambers consisted of 0.25 m^2 square metal bases (L50 cm x W50 cm x H15 cm; volume = 37 L) that were inserted ~ 5 cm into the sediment at low tide and fitted with a removable Perspex lid as the tide came in. Each chamber was equipped with a dissolved oxygen logger (miniDOT, PME, California, USA), a light and temperature logger (HOBO Pendant, HOBO, Massachusetts, USA), and a CTD pump (Seabird Scientific, Washington, USA) to intermittently stir the chamber water (for 5 s every 45 s). Dark chambers were shaded by a black plastic sheet to block photosynthetic activity, and the HOBO pendant light loggers were used to ensure darkness was achieved. Chambers were incubated for 3-4 h and water samples were taken from each chamber at the beginning and end of the incubation by filling Luer Lock syringes (60 mL) attached to a sampling port in the chamber lid via nylon tubing. To account for the contribution of water-column processes to solute fluxes, triplicate pairs of light and dark 1.5 L bottles were filled with ambient seawater, sealed, and fixed to the seafloor and similarly sampled after a 3-4 h incubation. As water column process accounted for < 5% of the benthic chamber fluxes no corrections to chamber measurements were made. Dissolved oxygen (DO) was measured from water samples with a YSI ProSolo ODO/CT in case of logger failure, and the remaining water samples were filtered through a Whatman GF/C filter and frozen for analysis of dissolved nutrients.

Seawater samples collected from the chambers were analysed for nutrient concentrations (ammonium (NH_4^+-N), nitrate (NO_3^--N) nitrite (NO_2^--N) and phosphorus in phosphate (PO_4^{3-}-P)) on a Lachat QuikChem 8500 Series 2 Flow Injection Analyser System (Zellweger Analytics Inc. Milwaukee, Wisconsin 53218, USA) using standard operating procedures. Solute fluxes (µmol m^{-2} h^{-1}) were calculated from light and dark chambers as (Eq. 2.1):

$$C_{\mathrm{final}} - C_{\mathrm{initial}} \times \frac{\mathrm{V}}{\mathrm{A} \times t} \qquad \text{Eq. (2.1)}$$

Where C represents the solute concentration in the initial (C_{initial}) and final (C_{final}) water samples (µmol L^{-1}), V is the total volume of seawater inside the chamber (L), A is the area of sediment enclosed by the chamber (m^{-2}), and t is the incubation period (h). A positive flux-value indicates an efflux from the sediment into the overlying water column and a negative value an uptake into the sediment. To calculate the DO flux, I used a 10 min average DO concentration measured at the start and end of the incubation by the oxygen loggers deployed in the chambers.

2.2.5 Data analysis

To investigate the effectiveness of large bivalve species in supporting recovery of ecosystem functionality after a physical disturbance, I used three groups of responses: 1) sediment parameters (median GS, mud content (% < 63 µm), OM) which give an indication of the recovery of physical sediment properties, 2) proxies for ecosystem functions associated with ecosystem productivity: net primary productivity (NPP), sediment oxygen consumption (SOC), gross primary productivity (GPP), microphytobenthic (MPB) biomass, and degradation of products (indicated by chl *a*, chl *a*:phaeo ratio, respectively), and 3) proxies for ecosystem functions associated with nutrient cycling: inorganic flux of nitrogen and phosphorus.

Responses for ecosystem productivity included: NPP (mmol O_2 m^{-2} h^{-1}), derived from the DO flux measured in the light chambers, with positive values indicating that primary production exceeded community respiration; SOC (mmol O_2 m^{-2} h^{-1}) as a measure of community respiration which was derived from the dark chamber DO fluxes in the absence of photosynthesis; the sum of NPP + SOC provided an estimate of GPP (i.e., primary production accounting for community respiration). Chl *a* (µg g dw^{-1}) was used as a proxy for MPB standing stock which accounts for up to 90% of total estuarine primary production (Jones et al., 2017). MPB alter nutrient recycling through oxygenation of the surface sediment and nutrient uptake (Miller, Geider and Macintyre, 1996). Surface sediment chl *a*:phaeo ratio was used as a proxy for processes linked to autotrophic organic matter turnover, or the 'freshness' of the autotrophic organic matter, which is affected by grazing and cell senescence (Bianchi et al., 1988; Ford and Honeywill, 2002). Inorganic nutrient fluxes (NO_3^-, NO_2^-, NH_4^+ (µmol N m^{-2} h^{-1}), PO_4^{3-} (µmol P m^{-2} hr^{-1})) represent a measure of net effect of physical, biogeochemical, and biotic processes on the key ecosystem functions associated with nutrient processing and regeneration. However, NO_3^- and NO_2^- fluxes were close to detection limits of 0.07 µmol m^{-2} h^{-1} (Eyre and Ferguson, 2002) so were not considered further. Preliminary analysis of NH_4^+-N and PO_4^{3-}-P fluxes showed no significant difference between the light and dark chambers on any sampling date (PERMANOVA, NH_4^+-N: df = 1, pseudo-F = 4.125, p(perm) = 0.081, and PO_4^{3-}-P: df = 1, pseudo-F = 2.631, p(perm)= 0.131), therefore each light/dark chamber pair was averaged prior to statistical analysis.

Repeated measures permutational analyses of variance (PERMANOVA) (Euclidean distance matrices) with 9999 permutations (Anderson, Gorley and Clarke, 2008) were used to determine treatment effects through time on each of the following univariate response variables: 1) sediment properties: median GS, mud content, OM, 2) ecosystem productivity: NPP, SOC, GPP, and MPB biomass:-chl *a*, chl *a*:phaeo ratio, and 3) nutrient cycling: NH_4^+, PO_4^{3-}). Each model included treatment (5 levels) and time (3 levels) as fixed factors, and plot (4 levels) as a random factor nested within treatment. As temporal succession in treatment effects was anticipated in my hypotheses, time was considered a fixed factor (Anderson, Gorley and Clarke, 2008). If recovery differed among treatments, I expected to detect this through the time × treatment interaction term. When the PERMANOVA was significant at a $p(\text{perm}) < 0.05$ in the absence of an interaction, multiple comparisons of means were performed with pairwise comparisons. I anticipated that bivalve mortality would lead to changes in seeded *A. stutchburyi* and *M. liliana* densities over time which may be important for interpretation of my results, I therefore used a PERMANOVA to detect differences between densities of each species across time and treatments using densities estimated from the cores taken from the centre of the benthic chambers. All graphs were created in R Studio with ggplot2 (R Core Team, 2024) and all PERMANOVA analyses were conducted in PRIMER-e version 7 with the PERMANOVA+ add on software (Anderson, Gorley and Clarke, 2008).

2.3 Results

Sea surface temperatures at the site in February 2021 (23.3°C) and 2022 (24.4°C) were similar at the beginning and the end of the experiment and representative of the austral summer season. The middle sampling date (April) was in autumn when sea temperature was lower (18.0°C). Similarly, the amount of photosynthetically active radiation (PAR) was variable seasonally and reflected summer (1025 – 219 µmol photons m^{-2} s^{-1}) versus autumn conditions (571 – 23 µmol photons m^{-2} s^{-1}, Table A2.1).

2.3.1 Survival of translocated bivalves

On d 20 adult densities of *M. liliana* and *A. stutchburyi* were reduced by 93% in D compared to ambient ND and one year later there was an increase in adult *M. liliana* densities but not *A. stutchburyi* (Figure 2.2A, B, Table 2.1). Overall, the bivalve addition treatments had higher bivalve densities compared to the D treatment, and this persisted throughout the year to varying extents. Densities of *M. liliana* in both +ML and +ASML treatments on d 20 were representative of the ambient ND densities, while *A. stutchburyi* densities in +AS and +ASML were 2.2-times higher than in the ambient sediments. Adult bivalve abundance in re-seeded plots (+ML, +AS, +ASML) decreased over time to resemble ambient levels (ND) after one year (Figure 2.2A, B, Table 2.1). At the end of the experiment the mean survival of transplanted adult *M. liliana* was 50% (range 38 - 56%) in +ML and 59% (38 - 80%) in +ASML. Adult *A. stutchburyi* survival was 15.5% (6.5 - 40%) in +AS and 17% (4 - 23%) in +ASML.

Table 2.1 Summary of repeated measures PERMANOVA results on adult bivalve density (*M. liliana*, *A. stutchburyi*), with fixed factors of time (20, 81, 389 d post bivalve addition), treatment (ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species), and the random factor plot nested within treatment to account for repeated sampling. Significant effects ($p < 0.05$) are highlighted in bold. In the instance of time × treatment interactions, p-values are not given for main effects, and PERMANOVA post-hoc pairwise tests show individual effects, separately.

Variable	Source	df	MS	Pseudo-F	p (perm)	Post-hoc pairwise tests
M. liliana	**Time x Treatment**	8	33.509	2.891	**0.018**	d 20: (ND = +ML = +ASML) > (D = +AS)
	Time	2	7.360	0.666		d 81: (ND = +ML = +ASML) > (D = +AS)
	Treatment	4	343.68	33.157		d 389: (ND = D = +ML = +ASML) > (+AS)
	Plot	15	10.365	0.894	0.573	
	Residual	30	11.589			
A. stutchburyi	**Time x Treatment**	8	1.616	1.535	**0.011**	d 20: ((+ASML > ND) = +AS) > (D = +ML)
	Time	2	251.96	9.358		d 81: (ND = +AS = +ASML) > (D = +ML)
	Treatment	4	1436.2	40.649		d 389: ((ND +ASML) > (D = +ML)) = +AS
	Plot	15	35.333	1.312	0.252	
	Residual	30	26.926			

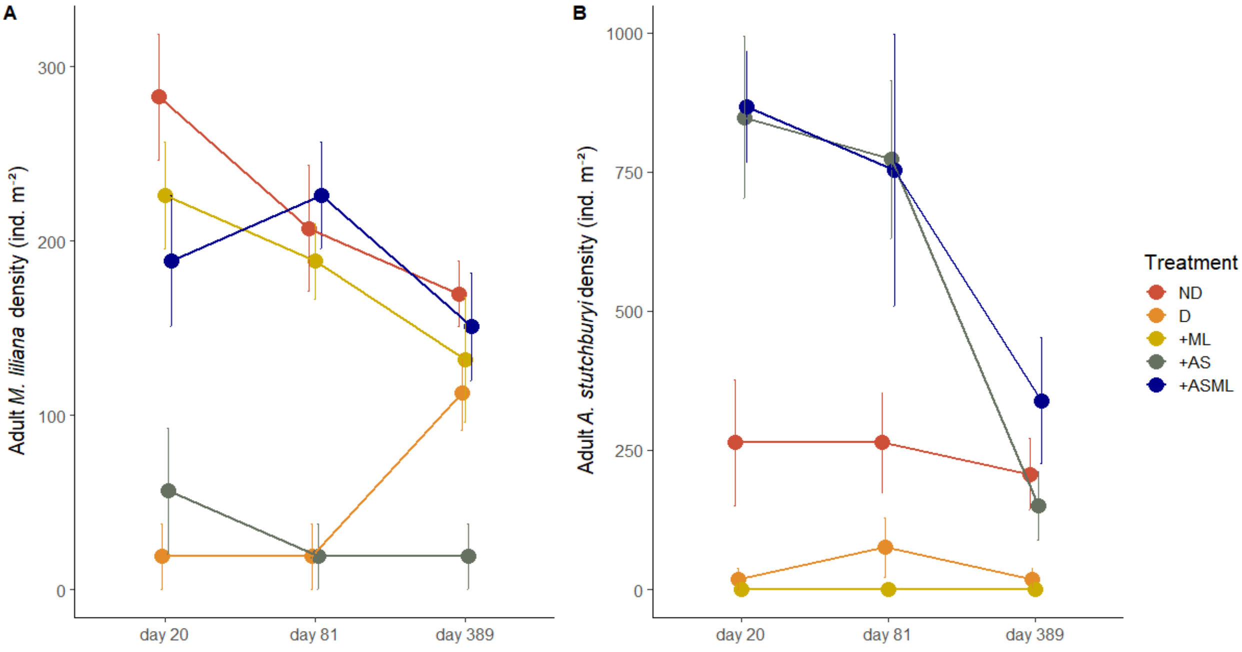


Figure 2.2 Mean adult bivalve density (± standard error) of **(A)** *M. liliana* (>20 mm) and **(B)** *A. stutchburyi* (>18 mm) across treatments over time (d 20, 81, 389 post bivalve addition) sampled from macrofauna cores. ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species.

2.3.2 Changes in sediment properties

Median grain size varied through time and was lower on d 81 than d 20 and largest on d 389. Mud content was significantly affected by treatment, but this effect varied among sampling dates (time x treatment interaction Figure 2.3, Table 2.2). Mud content in all defaunated treatments was elevated by 3.5 - 6% compared to ND treatments after 81 days. After one year (d 389) mud content remained elevated by 2 - 3% in defaunated treatments compared to ND, except +AS, in which mud content decreased significantly (relative to D) and was no longer significantly different from ND (ambient) levels. Organic matter in ND treatments was consistently lower than in D treatments and increased on d 81 (Figure 2.3, Table 2.2).

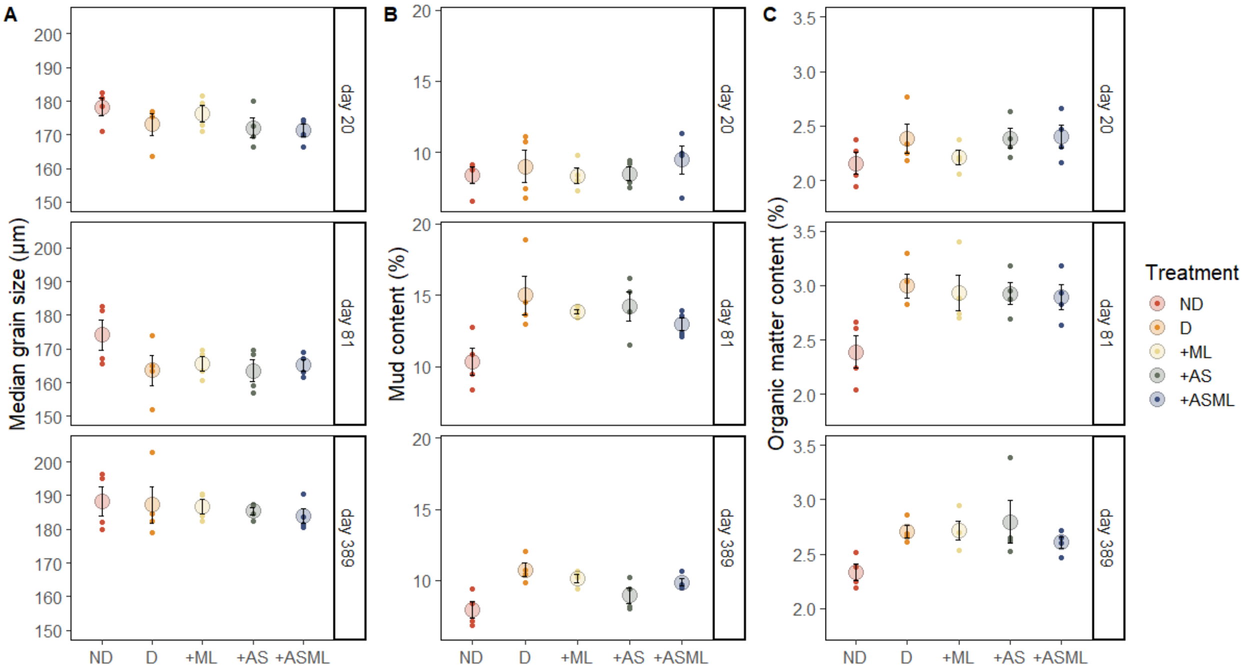


Figure 2.3 Selected sediment properties as a function of treatment and time (d 20, 81, 389 post bivalve addition). **(A)** median grain size, **(B)** mud content, **(C)** organic matter content. Large points represent mean values with error bars (± standard error) and small points show the underlying data values. ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species.

Table 2.2 Summary of repeated measures PERMANOVA results on univariate measures of ecosystem function. PERMANOVA tests (Euclidean distance) were performed on sediment variables, ecosystem productivity, and nutrient cycling as a function of time (20, 81, 389 d post bivalve addition) and treatment (ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species). To account for repeated measures, plot was assigned as random factor nested within treatment. Significant effects ($p < 0.05$) are indicated in bold. In the instance of time × treatment interactions, p-values are not given for main effects, and PERMANOVA post-hoc pairwise tests show individual effects, separately. GS = grain size; Mud = silt/clay (particles < 63 µm), OM = total organic matter content of sediment, NPP = net primary production; SOC = sediment oxygen consumption; GPP = gross primary production; Chl *a* = sediment chlorophyll *a* pigment content; Chl *a*: phaeo = ratio of chlorophyll *a* to phaeophytin pigment content; NH_4^+ = ammonium flux; PO_4^{3-} = phosphate flux.

Variable	Source	df	MS	Pseudo-F	p(perm)	Post-hoc pairwise tests
Sediment						
Median GS	Time × Treatment	8	27.645	2.112	0.065	
	Time	2	2001.8	152.94	**<0.001**	d81 < d20 < d389
	Treatment	4	116.67	1.216	0.344	
	Plot(Treat)	15	95.968	7.332	0.001	
	Residual	30	13.089			
Mud	**Time × Treatment**	8	4.26	2.501	**0.036**	d 20: ND = D = +ML = +AS = +ASML
	Time	2	134.35	78.884		d 81: ND < (D = +ML = +AS = +ASML)
	Treatment	4	12.581	3.202		d 389: (ND = +AS) < (D = +ML = +ASML)
	Plot(Treat)	15	3.93	2.307	0.023	
	Residual	30	1.703			
OM	Time × Treatment	8	0.042	0.817	0.592	
	Time	2	1.381	26.732	**<0.001**	d20 < d389 < d81
	Treatment	4	0.345	6.909	**0.003**	(ND < (D = +AS = +ASML)) = +ML
	Plot(Treat)	15	0.05	0.967	0.507	
	Residual	30	0.052			
Ecosystem productivity						
GPP	Time × Treatment	8	3.01E+05	1.199	0.365	
	Time	2	1.18E+07	47.176	**<0.001**	d 81 < (d 20 = d 389)
	Treatment	4	1.07E+06	8.843	**0.002**	((+ASML= +ML) < (ND = D)) = +AS
	Plot(Treat)	15	1.21E+05	0.483	0.864	
	Residual	30	2.51E+05			
NPP	**Time × Treatment**	8	4.40E+05	3.411	**0.011**	d20: (+ASML = +AS) < (ND =D = +ML)

	Time	2	2.66E+06	20.614		d81: (+ASML < (ND = D = +ML)) = +AS
	Treatment	4	3.65E+06	17.785		d389: (+ASML < D) = ND = +ML = +AS
	Plot(Treat)	15	2.05E+05	1.588	0.164	
SOC	Time × Treatment	8	3.58E+05	2.212	0.07	
	Time	2	3.12E+06	19.319	**0.001**	d81 < (d20 = 389)
	Treatment	4	1.54E+06	11.951	**0.001**	(+ASML = +AS) > (ND = D = +ML)
	Plot(Treat)	15	1.29E+05	0.798	0.662	
	Residual	30	1.62E+05			
	Residual	30	1.29E+05			
Chl *a*	**Time × Treatment**	8	6.319	6.723	**<0.001**	d20: ND > (D = +ML = +AS = +ASML)
	Time	2	239.46	254.78		d81: ND = D = +ML = +AS = +ASML
	Treatment	4	3.3	1.364		d 389: ND < (D = +ML= +AS = +ASML)
	Plot(Treat)	15	2.42	2.575	0.012	
	Residual	30	0.94			
Chl *a*:phaeo	Time × Treatment	8	1077.9	1.094	0.413	
	Time	2	3252.8	3.302	**0.043**	(d20 = d81) < d389
	Treatment	4	3119.6	4.108	**0.001**	(ND = +AS = +ASML) > (D = +ML)
	Plot(Treat)	15	759.43	0.771	0.865	
	Residual	30	985.19			
Nutrient cycling						
NH_4^+	**Time × Treatment**	8	4089.1	6.945	**0.010**	d20: (+ASML = +AS) > (ND = D = +ML)
	Time	2	35628	60.509		d81: (ND = +AS = +ASML) > (D = +ML)
	Treatment	4	26063	7.879		d389: ((ND = +AS = +ASML) > D) = +ML
	Plot(Treat)	15	3308.1	5.618	0.006	
	Residual	30	588.8			
PO_4^{3-}	Time × Treatment	8	0.198	0.333	0.880	
	Time	2	14.268	23.984	**<0.001**	d20 < d 81 < d389
	Treatment	4	3.073	3.607	0.052	((ND = +ASML) > D) = +AS, +ML
	Plot(Treat)	15	0.852	1.432	0.229	
	Residual	30	0.595			

2.3.3 Effects of *A. stutchburyi* on ecosystem functions

GPP changed through time, consistent with increases in summer (d 20 and 389) relative to autumn (d 81). Treatment effects were associated with *M. liliana* additions (+ASML and +ML) having less GPP than D and ND (Figure 2.4A, Table 2.2). The addition of bivalves reduced NPP relative to the ND and D treatments (Table 2.2). However, the relative magnitude and significance of these treatment effects varied with species and through time. NPP was lower in plots with added *A. stutchburyi,* relative to ND and D (+AS by 106%, +ASML by 110%), and this effect was greater than with the addition of *M. liliana* (+ML -35% lower than ND, Figure 2.4B). Concomitantly, SOC was higher in *A. stutchburyi* treatments, compared to ND, D, and +ML treatments. The highest SOC was measured in +AS and +ASML treatments on d 20 where SOC in these treatments was 113% - 116% higher compared to D, 71% - 74% higher compared to ND, and 92% - 95% higher than +ML. This effect was maintained, though to a lesser extent, on d 81. After one year (d 389), SOC remained 16% higher in +AS and +ASML treatments than D and 30 - 44% higher than +ML (Figure 2.4C, Table 2.2). Overall, the SOC in +ML treatments remained similar to that in D.

Initially (d 20), chl *a* was reduced in all disturbed treatments compared to ND, after which it increased over time (Figure 2.4D, Table 2.2). By d 81, chl *a* showed similar concentrations among all treatments, and on d 389, concentrations in all defaunated treatments exceeded those in ND treatments. The chl *a*:phaeo ratio increased through time in all treatments. However, after one year the chl *a*:phaeo ratio in +AS and +ASML treatments were similar to ND levels, while +ML and D treatments remained low (Figure 2.4E, Table 2.2).

All treatments, apart from D and +ML, were net sources of NH_4^+-N from the sediment to the water column (Figure 2.5A). *Austrovenus stutchburyi* treatments showed significantly increased NH_4^+-N efflux rates, compared with other disturbed treatments. This effect persisted for one year, despite a decrease over time (Table 2.2). The +ML treatment did not enhance NH_4^+-N efflux rates compared to D treatments. PO_4^{3-}-P fluxes marginally increased with time and were lower in D compared to +ASML and ND (Figure 2.5B, Table 2.2).

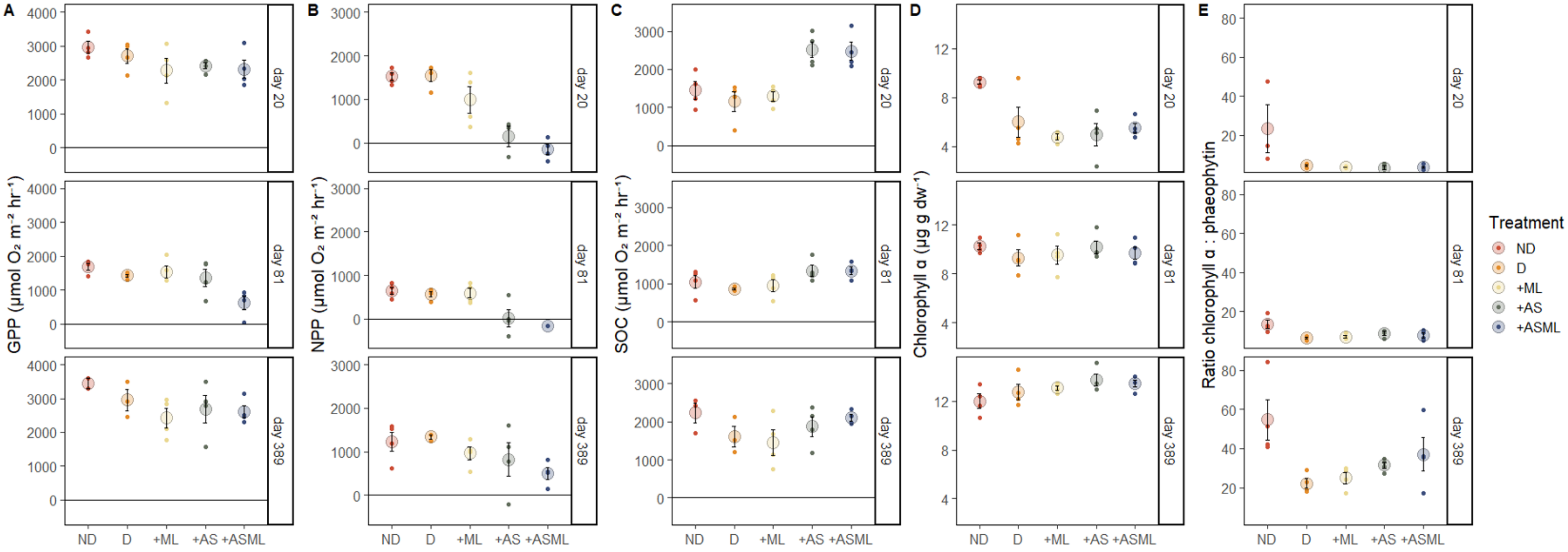


Figure 2.4 Several proxies of ecosystem productivity at the sediment-water interface as a function of treatment and time (d 20, 81, 389 post bivalve addition). **(A)** Gross primary productivity (GPP), **(B)** Net primary productivity (NPP), **(C)** sediment oxygen consumption (SOC) displayed as positive values, **(D)** chlorophyll *a*, **(E)** chl *a*:phaeophytin ratio. Large points represent mean values with error bars (± standard error) and small points show the underlying data values. ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species.

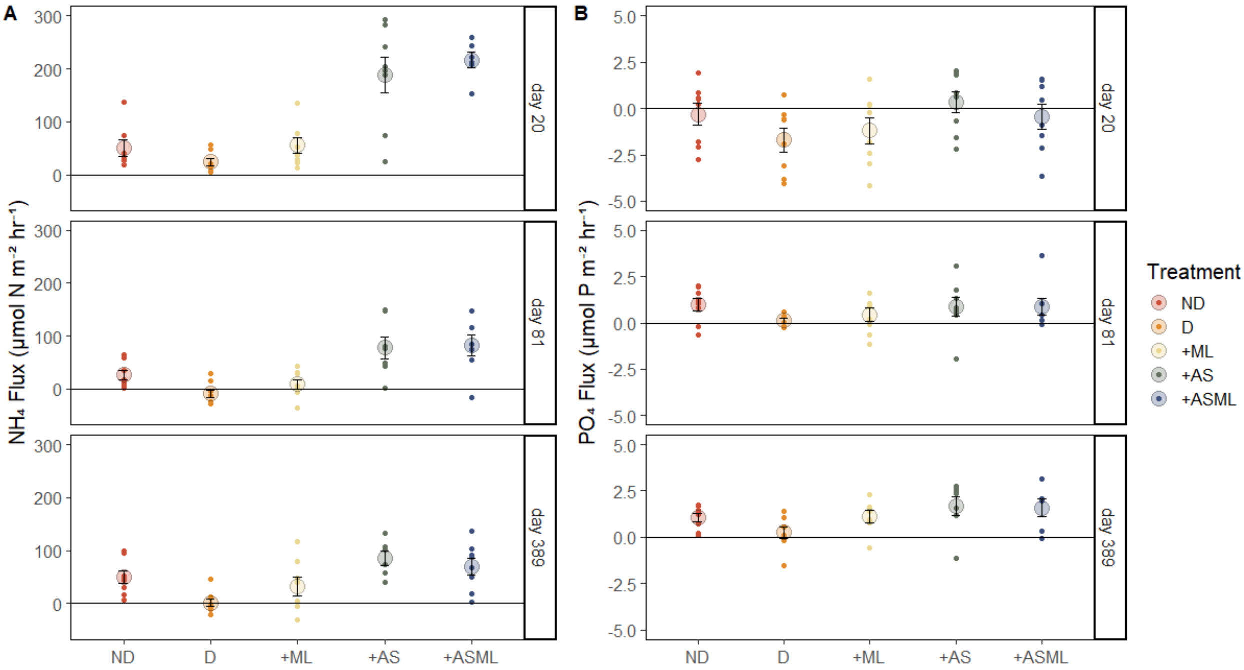


Figure 2.5 Nutrient flux at the sediment-water interface as a function of treatment and time (d 20, 81, 389 post bivalve addition). **(A)** nitrogen flux from ammonium (NH_4^+-N), and **(B)** phosphorus flux from phosphate (PO_4^{3-}-P). Positive flux resembles efflux into the water column; negative flux represents influx into the sediment. Large points represent mean values with error bars (± standard error) and small points show the underlying data values. ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species

2.4 Discussion

The re-introduction of *A. stutchburyi* to defaunated soft sediments affected the recovery of ecosystem functions via the decrease of mud content, change in ecosystem productivity, and increased ammonium exchange at the sediment-water interface. Furthermore, I showed that the survival of the translocated individuals is important for positive outcomes and should be a central aim of bioremediation efforts. This field manipulation experiment showcases the potential of adult bivalves, specifically the venerid clam *A. stutchburyi,* to facilitate the re-establishment of ecosystem functions in disturbed soft sediment habitats.

The defaunation process, resembling a physical disturbance event in the sediment, led to a higher mud content in all defaunated treatments. Added *A. stutchburyi* treatments exhibited decreased mud content after one year, suggesting that *A. stutchburyi* modifies the amount of mud retained in the sediment, likely by changing the erodibility of the seabed (Yeoh et al., 2024). Mud content has been shown to negatively affect *A. stutchburyi* densities and their effects on ecosystem function, whereas coarsening of sediment improved not only *A. stutchburyi* survival but also benthic biodiversity and productivity (Jones et al., 2011; Pratt et al., 2014). High densities of species functionally similar to *A. stutchburyi* have been found to increase particle resuspension of fine particles in muddy sediments, resulting in “sandification” of the sediment and lowered mud content (Soissons et al., 2019). Through sediment re-working, *A. stutchburyi* has the ability to manipulate their environment making them a critical player in shaping the physical conditions of an intertidal flat (Jones et al., 2011; Yeoh et al., 2024). Hence, my findings confirm the benefits of introducing large bioengineering clams early in the recovery process to influence ecosystem functions by the reworking of sediments (van Colen et al., 2012).

Additions of *A. stutchburyi* to defaunated sediments promoted the improvement of several ecosystem functions, while *M. liliana* additions did not affect the functions measured. I found significant increases in community metabolism (SOC) after *A. stutchburyi* addition, that were likely due to increased respiration by the higher clam number and biomass (Rossi et al., 2008; Sandwell, Pilditch and Lohrer, 2009). High SOC reduced NPP in the plots where *A. stutchburyi* were added, leading to a very low, to negative, net oxygen-efflux (NPP) from these sediments. After one year, SOC in *A. stutchburyi* addition treatments was still elevated relative to defaunated controls, reflecting survival of translocated *A. stutchburyi*. NPP was affected by lower light-levels in April (autumn) conditions reducing photosynthetic efficiency. *Austrovenus stutchburyi* effects on productivity were, however, masked when assessing GPP alone. Previous studies found a positive impact of *A. stutchburyi* density on GPP which has been attributed to enhanced nutrient provision and organic matter content of the sediment (Sandwell et al., 2009; Pratt et al., 2014, 2015), however, this was not reflected in the GPP of bivalve additions in this study.

The ratio of chl *a*:phaeo suggests a recovery in the *A. stutchburyi* addition treatments after one year to more high quality fresh primary production. This shows that *A. stutchburyi* facilitates autotrophic organic matter turnover and the regeneration of primary production. Although chl *a* concentrations in defaunated treatments increase over time back to, and above, non-disturbed levels, no significant differences in recovery among treatments were discerned. This stands in contrast to findings where increased numbers, or removal, of *A. stutchburyi* stimulated MPB activity (Thrush et al., 2006; Sandwell, Pilditch and Lohrer, 2009; Thomas et al., 2022). Nevertheless, the observed overall increase of chl *a* in defaunated treatments may be important in promoting recovery of macrofauna, as MPB has been shown to play an important part in the recovery of coastal food webs (Christianen et al., 2017).

Both treatments with *A. stutchburyi* enhanced nutrient fluxes compared to no addition treatments, supporting previous research that demonstrates them as key species for nutrient regeneration (Sandwell et al. 2009; Jones et al. 2011; Pratt et al. 2013). Ammonium levels in the disturbed, no addition treatments are significantly lower than ambient, even after one year. The addition of bivalves increased the ammonium efflux up to, and above, ambient levels, and this effect was more pronounced in *A. stutchburyi* addition treatments than in treatments with *M. liliana*. Higher numbers of *A. stutchburyi* have been shown to enhance water-column productivity as well as benthic productivity by increased ammonium efflux resulting from increased excretion volumes, bioturbation, and biodeposits (Thrush et al., 2006; Woodin et al., 2016; Thomas et al., 2022). Here, initially, ammonium efflux is substantially higher in the plots with the addition of *A. stutchburyi* compared to non-disturbed plots, a finding that was expected due to the higher density and the substantially larger size of translocated *A. stutchburyi* (24.5 ± 5.8 cm shell length, ~ 800 ind m^{-2}) compared to ambient individuals (15.0 ± 7.7 cm shell length, 250 - 650 ind m^{-2}). A similar observation was made from *Cerastoderma edule* additions (Rossi et al., 2008). Overall phosphate flux was low; yet the presence of large bivalves marginally enhanced PO_4^{3-}-P release from the sediment into the water column. Higher export of porewater phosphate to the overlaying water is linked to the species richness in benthic fauna, where species with complementary feeding modes enhance efflux (Karlson et al., 2005; Thomas et al., 2020; Lam-Gordillo et al., 2022), suggesting that benthic macrofauna community recovery with *A. stutchburyi* additions may be enhanced.

Although I found increased ammonium fluxes in *A. stutchburyi* additions, these did not equate to greater GPP. Increased efflux of ammonium through bioturbation and organically rich biodeposits from bivalves can stimulate bacterial activity and has likely fuelled some of the primary productivity in *A. stutchburyi* addition treatments (Newell, Cornwell and Owens, 2002; Giles and Pilditch, 2006; Thomas et al., 2021). However, there seems to be a disconnect between the higher availability of nutrients and productivity. Moreover, the higher biomass of *A. stutchburyi* may have prevented increased concentrations of chlorophyll *a* in the treatments where they were added compared no addition treatments due to higher grazing pressure of the added bivalves on MPB (Jones et al., 2017). This could also explain the higher chl *a*:phaeo ratio, suggesting comparably low primary productivity. Bioturbation by large bivalves may have also limited the establishment of MPB, as shown for large bioturbating infauna due to sediment resuspension (Pillay and Branch, 2011).

The additions of both species did not recover functionality faster (or more completely) compared to the plots with individual species, suggesting no effect of the dual addition. This may largely depend on the ecosystem functions measured, given the different functional roles of the species. Whilst *A. stutchburyi* influences productivity processes and excretion-based ammonium efflux (Woodin et al., 2016), effects of *M. liliana* may have been subtle, more variable, and the lack of porewater sampling may have left their contribution to recovery concealed. *Austrovenus stutchburyi* and *M. liliana* co-occur across a range of 0 - 80% sediment mud content in New Zealand estuaries and interactions between them may play a role in their distributions (Stephenson et al., 2022). Yet, the abundances of both species have been reported to be inversely correlated at extreme ends of the density spectrum (Stephenson et al., 2022). Here, the main differences are likely related to the increased *A. stutchburyi* density/biomass actively working the upper sediment intervals which shows to be crucial initially after disturbance (Sandwell, Pilditch and Lohrer, 2009).

This finding has important implications for multi-species restoration. From a practical perspective, handling only one species, such as *A. stutchburyi,* that is more robust and abundant in the Tauranga Harbour (Ellis et al., 2013), simplifies bioremediation efforts, making it more feasible and affordable. Nevertheless, the potential of multi-species restoration should be explored to evaluate further benefits of ecosystem functions that were beyond the scope of this study, for example rates of denitrification and organic matter breakdown (Schenone and Thrush, 2022).

Both species survived the translocation over the course of a year although with reduced numbers, decreasing significantly in the time between three months and one year. Similar survival patterns have been found in other bivalve transplant studies where survival is initially high but high mortality occurred in early winter (Cummings et al., 2007). I added *A. stutchburyi* densities similar to medium-high density beds in Aotearoa (Sandwell et al. 2009; Jones et al. 2011), and mortality during the experiment decreased densities to ambient levels at the site after one year. Natural *A. stutchburyi* mortality has been recorded as 17 - 30% (19 - 37% in individuals > 30mm, (Fisheries New Zealand, 2010). Yet, it may be critical for bivalve survival to adjust translocation densities to what the environment can support, which in this case was a relatively healthy but muddier site with less *A. stutchburyi* compared to the source population on the seaward side at Tuapiro Point. Cummings et al. (2007) conclude that higher density (832 ind. m $^{-2}$) may act as a stressor that renders *A. stutchburyi* less able to cope with extreme environmental conditions and propose that ~220 individuals per m^2 densities should be trialled to achieve higher survival. Further research is needed to generate a more generalisable understanding of seeding density and survival relationships across different locations. Notably, *A. stutchburyi* densities decreased slightly in ambient and no addition treatments between d 81 and d 389, suggesting that external influences (e.g., higher daily mean temperatures, larger temperature ranges, wind, warm periods during the Southern Oscillation Index, or high atmospheric temperatures coinciding with mid-afternoon spring low tides) may have played a role that year (Cummings et al., 2007; Tricklebank, Grace and Pilditch, 2021; Lam-Gordillo et al., 2024).

2.5 Conclusion

This study goes beyond re-establishing population densities to directly assess the recovery of key ecological processes that are important for ecosystem function and services. However, the observed mortality over time and the variability of environmental factors underscores the need for carefully assessing the habitat that individuals are transplanted into. A diversified and site-specific approach is needed as restoration is place-based. Testing the efficacy of reseeding bivalves across environmental gradients would help elucidate under which conditions the bioremediation of *A. stutchburyi* could be feasible, both from the standpoint of bivalve survival but also remediation of conditions. Further experiments should investigate the longer-term effects of bivalve addition on a broader set of ecosystem functions, and inter-species relationships such as dynamics associated with the recruitment of other species, to determine whether complementary or compensatory interactions between species can enhance ecosystem resilience.

Top: Treatment plots on a sunny day at Tuapiro Point. Bottom: Corner peg of an experimental plot with its inhabitants. February 2021.

Chapter 3

Differential ecosystem engineering of two bivalves may shape the recovery of benthic macroinvertebrate communities

---

3.1 Introduction

Estuarine soft sediment habitats are among the most productive and functionally diverse ecosystems globally providing valuable ecosystem services to humans (Barbier et al., 2011; Costanza et al., 2014; Snelgrove et al., 2014). Underpinning these services are ecosystem functions, many of which are performed by benthic macroinvertebrates, shaping biogeochemical dynamics at the sediment-water interface (Lohrer, Thrush and Gibbs, 2004; Thrush et al., 2006; Belley and Snelgrove, 2016). Species functional traits (e.g., size, feeding mode, mobility) influence estuarine function and the resilience through species networks and positive or facilitatory feedback loops (Snelgrove, 1997; Thrush et al., 2006; Reiss et al., 2009; Norkko et al., 2013; Karlson et al., 2016). However, human activities are causing widespread degradation of soft sediment habitats through eutrophication, sedimentation, physical disturbances from coastal development, aquaculture, and fishing activities (Levin et al., 2001; Lotze et al., 2006; Chariton et al., 2010). Such pressures lead to decreased native species richness and abundance, affecting essential benthic ecosystem functions and consequently impairing the services provided by these environments (Snelgrove et al., 2014; Thrush et al., 2017; Caswell, Paine and Frid, 2018; Wrede et al., 2019). Following a devastating disturbance and with the subsequent release of stressors the species community often has minimal diversity; but as biodiversity recovers over time, ecosystem functionality typically increases (Pearson and Rosenberg, 1978; Thrush et al., 2008a; van Colen et al., 2008; 2012). The re-establishment of ecosystem functions after disturbance is variable and often lags significantly behind taxonomic recovery (species abundance, richness, van Colen et al., 2008; 2012; Lohrer et al., 2010; De Juan et al., 2014).

Where there is a disconnect between taxonomic recovery and the regeneration of functionality can be attributed to the slow (sometimes incomplete) recovery of large, mobile individuals (Lohrer et al., 2010; van Colen et al., 2012; De Juan et al., 2014; Douglas et al., 2017), such as large bivalves, as their activities, in particular bioturbation (sediment mixing) and bioirrigation (burrow ventilation), disproportionately influence sediment biogeochemistry (Sandwell, Pilditch and Lohrer, 2009; Needham et al., 2011; Norkko et al., 2013; Pratt et al., 2014). In addition to facilitating the recovery of benthic biogeochemistry from disturbance, they can facilitate the recovery of other species (Halpern et al., 2007; Lohrer et al., 2013; Gagnon et al., 2020; Hewitt, Gladstone-Gallagher and Thrush, 2022; Searles et al., 2022). The introduction of large bivalves to degraded areas may, therefore, influence the abundance, and type of colonising species as well as the variability in assemblage structure (Thrush et al., 1992).

Past restoration has generally focused on removing stressors, generating habitat, creating protected no-take areas, or restocking lost species. Recently, the focus of restoration ecology has expanded to consider the maintenance of species interactions and faciliatory networks to support recovery dynamics and increase restoration success (Halpern et al., 2007 and the literature therein; Silliman et al., 2024). The importance of facilitation and the strategic re-establishment of key species can positively influence the environment and accelerate community-level recovery (Halpern et al., 2007; Gagnon et al., 2020; Silliman et al., 2024). Current soft sediment biogeochemical remediation focuses on improving hostile sediment conditions via the re-establishment of macrobenthic communities and their bioturbating activity (Deng et al., 2015; Harris et al., 2015a; Gonzalez et al., 2019; Lam-Gordillo et al., 2022a). The literature offers examples of positive interspecific interactions using dual species including species combinations of for example mangroves, saltmarsh, cord grass, mussels, and oysters, seagrass and clams (see Angelini et al., 2016; Renzi, He and Silliman, 2019; Reeves et al., 2020; Donaher et al., 2021), as well as the restoration of benthic communities through the translocation of single species to improve biogeochemical conditions (Thrush et al., 1992; Lam-Gordillo et al., 2022a). To date, however, many restoration projects lack the integration of interspecific interactions between key ecosystem engineering species (Zhang et al., 2018; Gagnon et al., 2020). Harnessing facilitative biological interactions between multiple species could provide a more robust nature-based remediation option

(Shen et al., 2016). Here I tested the role of two key bivalve species in the recovery of sandflat biodiversity following disturbance.

In New Zealand sandflats, two co-occurring key bivalve species *Macomona liliana* (large wedge clam) and *Austrovenus stutchburyi* (New Zealand littleneck clam) can dominate macrofaunal community biomass and have a strong influence on ecosystem functioning (Pridmore et al., 1990; Thrush et al., 2006; Sandwell, Pilditch and Lohrer, 2009; Pratt et al., 2013) and the types of other macroinvertebrate species present (Thrush et al., 2006) via their sediment engineering traits. *Macomona liliana* is a deep-burrowing facultative deposit feeding tellinid bivalve (Powell, 1979; Pridmore et al., 1990) that significantly contributes to bioirrigation through their feeding behaviour, influencing oxygen-dependent processes, organic matter degradation, and nutrient cycling in deeper sediment layers by excreting waste at depth (Wilcock et al., 1993; Volkenborn et al., 2012; Woodin et al., 2012; Kristensen et al., 2014). *Austrovenus stutchburyi*, a suspension-feeding venerid bivalve, is a surface-dwelling suspension feeder and bioturbator (Morton and Miller, 1973; Powell, 1979) that oxygenates the sediment surface layers, enhances nutrient regeneration, and influences primary production through their movement in the sediment (Woodin et al., 2016; Jones et al., 2017). This improves the physical conditions of the surface sediment to support higher abundance and diversity of benthic fauna (Whitlatch et al., 1997; De Juan and Hewitt, 2011; Karlson et al., 2016).

The two bivalve species are known to influence macrofaunal biodiversity through a range of synergistic but also antagonistic intra- and interspecific effects in systems where both species co-occur (Thrush et al., 2006; Stephenson et al., 2022). While their movement has been shown to destabilise the sediment, disturbing infauna and potentially decreasing diversity (Widdicombe et al., 2000; Norkko et al., 2006; Lohrer et al., 2008), their early introduction into defaunated sediments may be crucial to improve hostile sediment for later arrivals. The removal of *M. liliana* increased the density of small surface deposit feeders (*Aonides, Aquilaspio, Colurostylis*; Thrush et al., 2006), whilst additions of adult *M. liliana* to experimentally defaunated sediments have shown to facilitate juvenile recruitment of *A. stutchburyi* and *M. liliana* (Thrush et al., 1992). *Austrovenus stutchburyi* is known to promote recovery of subsurface deposit feeder densities (*Heteromastus*, *Nucula*) and juvenile bivalves (Hewitt et al., 1996; 1997; Thrush et al., 1996a; 2006; Whitlatch et al., 1997). When these species occur together, they may provide a beneficial habitat for other benthic macrofaunal species via the re-working of sediment at different depths at a faster rate than during natural recovery. This facilitation effect remains, however, largely untested.

Here, I examined whether the re-addition of these two key species alter recovery of biodiversity following a physical disturbance and consequent defaunation of the sediment. The novelty of a re-addition study using both *M. liliana and A. stutchburyi* lies in its explicit aim to leverage their distinct yet complementary ecosystem engineering traits. I expected that bioturbation of overturned defaunated sediment by bivalves may reestablish sediment biogeochemistry faster making it more suitable for other species. This study seeks to examine whether this approach is feasible, and whether the two species produce similar or different results. Specifically, I hypothesised that 1) bivalve additions would recover species taxonomic and functional diversity nearer to ambient communities faster compared to disturbed treatments without bivalve addition, and 2) that the combined re-addition of bivalves may yield a taxonomic and functional recovery most similar to the ambient community.

3.2 Methods

3.2.1 Study site and experimental manipulation

The experiment was performed in a fine-sand intertidal habitat near Tuapiro Point in the Tauranga Harbour, northeastern Aotearoa New Zealand (37°29'30.7"S 175°57'05.3"E, see Chapter 2, Figure 2.1). Site sediment properties are representative of many New Zealand sandflats (e.g., Clark et al., 2021; Gammal et al., 2023) and the macrofaunal community is dominated by polychaetes while bivalves (predominantly *A. stutchburyi* and *M. liliana*) make up for the largest biomass (Pratt et al., 2013; Karlson et al., 2016; Drylie et al., 2020). In January 2021 (austral summer), 20 experimental plots (1.5 x 1.5 m) were established 5 m apart, at mid-tide level, and parallel to the shoreline and a tidal channel. Five treatments were interspersed randomly among the 20 plots: ambient/no disturbance (ND), defaunated (D), defaunated + addition of *A. stutchburyi* (+AS), defaunated + addition of *M. liliana* (+ML), and defaunated + addition of both species

(+ASML) (4 replicates of each treatment). Treatment creation (all except ND) entailed removing the sediment surface (5 cm) with a spade and systematically finger ploughing the sediment to remove remaining bivalves. Finally, the sediment was manually homogenised to a depth of ~15 cm. Following the disturbance, all plots (including the ND) were fenced with plastic mesh (1 cm^2 openings) which was buried 10 cm beneath the sediment surface and protruded 5cm above to avoid the migration of adult bivalves into/out of the plots (Jones et al., 2011). The large mesh size allowed the migration of smaller fauna.

Seven days after the disturbance, a macrofauna core (Ø 13 cm × 15 cm depth) was extracted from each plot to ascertain the efficacy of defaunation, after which, adult bivalves were introduced into the addition (+ML, +AS, and +ASML) plots. Adult *M. liliana* (≥20 mm shell length) and *A. stutchburyi* (≥ 18 mm), were translocated from locations within 200 m of the experimental site. Approximately 450 individuals of *M. liliana* (200 m^{-2}) and 1800 individuals of *A. stutchburyi* (800 m^{-2}) were added to each single species and combined species treatment plots. These densities were indicative of medium density beds observed in Tauranga Harbour and New Zealand estuaries more broadly (Ellis et al., 2013; Berkenbusch and Neubauer, 2016).

The bivalve addition treatments were successful in elevating adult bivalves in +ML, +AS and +ASML treatments resulting in 91% elevation in abundance of *M. liliana* and 97% elevation of *A. stutchburyi* compared to the D plots after one month. The densities were similar to ND levels for *M. liliana* and 2.2x higher for *A. stutchburyi*. After one year adult bivalve densities in addition plots had reached ambient levels (see Chapter 2, Figure 2.2, Table A3.3).

3.2.2 Macrobenthic fauna community sampling

Since timing of disturbance in relation to seasonal recruitment events is an important factor for assemblage recovery (Kröger et al., 2006; De Juan et al., 2014), the experiment was conducted covering the macrobenthic peak recruitment period during late summer (Stephenson and Chanley, 1979; Taylor, 1999). To quantify the recovery of benthic macrofauna from the disturbance, sampling occurred on d 20 (end of summer, before settlement of recruits), d 81 (autumn, during recruitment), and d 389 (end of following summer, one year after recruitment period) after the addition of adult bivalves. On each sampling date, one macrofauna core (Ø 13 cm × 15 cm depth) was collected from a different quadrant of the experimental plot. Samples were sieved through 500 µm mesh screens and retained macrofauna preserved in 70% isopropyl alcohol. Core holes were filled with defaunated fine sand to minimise disturbance to the plot (Lohrer et al., 2010). In the laboratory, macrofauna were stained with rose Bengal, separated from the sediment, identified to the lowest practical taxonomic level (usually species, except some that were identified at higher taxonomic levels, e.g., genus or family) and counted. All *M. liliana* and *A. stutchburyi* > 5 mm were sized on the long shell axis with callipers while small juveniles (≤ 5mm) were sized using a microscope (Olympus) with a scaled eyepiece reticle.

3.2.3 Sediment properties

Sediment characteristics in each plot on each sampling date were assessed based on methods described in detail in Chapter 2. Briefly, five pooled syringe cores (Ø 2.5 cm × 2 cm depth) collected from around each macrofauna core were stored in the dark and frozen for later analysis of sediment grain size (GS) distribution, organic matter content (OM), and microalgal pigment concentrations (chlorophyll *a*, phaeophytin). Sediment grain size was measured using a Malvern Mastersizer-3000 after removing organic matter with 10% hydrogen peroxide for 3 weeks. Particles larger than 4 mm were removed with a sieve and sodium polymetaphosphate was added to disperse the particles (Singer et al., 1988). OM content (%) was calculated from the difference between sediment dry mass and combusted mass after subsamples were dried (at 60^{o}C for 24 h) and combusted (at 550^{o}C for 4 h) in a Thermo Scientific Type 6000 muffle furnace (Thermolyne Thermo Fisher). Sediment for chlorophyll *a* (chl *a*) and phaeopigment (phaeo) analysis was freeze-dried (Lyovapor L-200 from Büchi (Switzerland; pressure 2mbar, temperature -50^{o}C)), weighed then extracted in 90% buffered acetone. Extract fluorescence was measured fluorometrically before and after acidification with 1M hydrochloric acid on a Turner Designs 10-AU fluorometer (Arar and Collins, 1997).

3.2.4 Data analysis

3.2.4.1 Community recovery

I utilised multivariate and univariate measures to assess the interacting and independent effects of bivalve additions on measures of macroinvertebrate community recovery in experimental plots. *Macomona liliana* and *A. stutchburyi* were assigned to the categories: adult (>20 mm shell length for *M. liliana* and >18mm for *A. stutchburyi*), pre-adults (19.9 – 10 mm and 17.9 –10 mm) or juveniles (< 10mm shell length as in Hunt et al., 2020; Stephenson et al., 2022). Bivalve species abundance < 10mm remained in the macrofauna community dataset for statistical analyses, as they are an important part of the recovering community, whereas bivalves > 10mm, ambient and translocated adult bivalves, were not included in the macrofaunal community analyses to avoid translocated individuals being considered as part of the recovering community.

First, I explored how the multivariate community structure changed as a function of time and treatment. I created an nMDS ordination (non-metric multidimensional scaling) based on Bray-Curtis similarity of square root transformed community data (Field, Clarke and Warwick, 1982). A series of univariate response variables were also generated to describe the alpha diversity of the macrofauna community. These response variables included: total number of macrofauna individuals (abundance) and taxa (richness). The abundance of juveniles (< 10 mm) of *M. liliana* and *A. stutchburyi* was also considered as a univariate response variable separately to explore whether adult bivalve addition enhanced juvenile densities and supported the growth of a recruitment cohort throughout the year.

To assess how univariate and multivariate measures of community composition varied with treatments and time, I used permutational analyses of variance (PERMANOVA, Anderson, Gorley and Clarke, 2008) with time (3 levels) and treatment (5 levels) as fixed factors and plot as a random factor nested within treatment to account for repeated measures. Bray-Curtis similarity was used to generate the resemblance matrix for PERMANOVA with the multivariate community data, and Euclidean distance was used for the univariate response variables. All PERMANOVAs were run with 9999 permutations (Anderson, Gorley and Clarke, 2008). Main effects (time and treatment) were not considered in the event of a significant site × treatment interaction ($\alpha < 0.05$), instead post-hoc pair-wise tests were used to identify treatment effects at each time point separately. In the absence of a significant interaction term, multiple pair-wise tests were conducted on the significant fixed factor (time, treatment) to identify which groupings contributed to differences from the main tests. A SIMPER analysis was used to investigate the percentage contribution of species to the dissimilarity between treatments at each sampling time compared to ambient plots (ND) (Clarke and Warwick, 1994). Abundances of important taxa identified by the SIMPER analysis were plotted to help interpret the community shifts identified. NMDS, PERMANOVAs, and SIMPER were conducted in PRIMER-e version 7 with the PERMANOVA+ add-on software (Anderson, Gorley and Clarke, 2008).

3.2.4.2 Functional trait diversity

To assess the functional recovery of benthic macrofauna I chose a set of seven biological traits with 35 trait-modalities (Table A3.1). The selected functional traits included bioturbation, body size, feeding mode, living habit, morphology, sediment position, and sediment stabilisation and describe behavioural, morphological, and physiological attributes of the organisms closely related to ecosystem functioning, such as nutrient cycling and sediment transport (Lam-Gordillo, Baring and Dittmann, 2020; 2021). Trait information was obtained from the New Zealand Trait Database (NZTD) for shallow-water marine benthic invertebrates (Lam-Gordillo et al., 2023). The NZTD database applied a fuzzy coding procedure assigning scores from 0 to 1, with 0 being no affinity and 1 being high affinity to a trait.

To assess the influence of bivalve additions on the recovery of functional traits in the communities, community-level weighted means (CWM) of trait values were calculated and analysed using the FD package (Laliberté, Legendre and Shipley, 2014). CWMs allow comparisons of traits expressed per treatment community (Lam-Gordillo et al., 2022b). Statistical analyses were carried out in R (R Core Team, 2024) and PRIMER-e version 7.

3.3 Results

3.3.1 Sediment properties

Details on surficial sediment characteristics are reported in Chapter 2. These remained similar over the course of one year, with sediments comprising fine sands (median grain size 163-188 µm) with a mud content (% < 63 µm) of 8 - 15% and OM between 2 - 3% (Table A3.2). Sediment chl *a* concentrations varied between a minimum of 4.77 µg g dw^{-1} in defaunated (+ML) treatments on d 20 and a maximum of 13.74 µg g dw^{-1} in defaunated +AS treatments on d 389. Chl *a* concentrations in all defaunated treatments were 35 - 48% lower compared to ND on d 20, reached ND levels on d 81 and exceeded

ND levels by 6 - 14% on d 389. Phaeo concentrations ranged between 0.24-1.58 µg g dw^{-1} and were elevated 1.8 - 3.2x in defaunated treatments compared to ND with an overall decreasing trend on d 389.

3.3.2 Taxonomic recovery of benthic community

A total of 4011 macroinvertebrates (excluding *A. stutchburyi* and *M. liliana*) were counted. The macrofaunal community was dominated by polychaetes which comprised 72% of the total abundance and 18 of the 50 taxa identified. Bivalves contributed to 9% of the total abundance (3 taxa excluding *A. stutchburyi* and *M. liliana*), gastropods 8% (10 taxa), amphipods 2% (5 taxa), and other taxa in the classes Clitellate, Nemertea, Anthozoa, Crustacea (not including Amphipoda), Maxillopoda, Malacostraca, and Polyplacophora to ~ 10%. A total of 387 *M. liliana* and 541 *A. stutchburyi* individuals were found in the 60 macrofauna cores across 20 plots and three sampling occasions, including transplanted adult individuals. For the sampled *M. liliana,* 106 of them were classified as adults, 129 as pre-adults, and 152 as juveniles (< 10 mm). Juveniles accounted for 39.2% of all *M. liliana* sampled. *Austrovenus stutchburyi* had 243 adult individuals, 57 pre-adults, and 241 juveniles, the latter accounting for 44.5% of *A. stutchburyi* sampled over the three sampling times. Macrofaunal densities and species richness were similar to other studies conducted in this estuary (Sandwell et al., 2009; Jones et al., 2011).

Initially, the community composition in all disturbed plots was significantly different to ND. Disturbed plots recovered and became more similar to the ND through time (Figure 3.1, Table 3.1). However, the specific recovery trajectories differed slightly for each of the treatments and at the end of the experiment (d 389), the D and +ASML treatments were the most similar on average to the ND treatment.

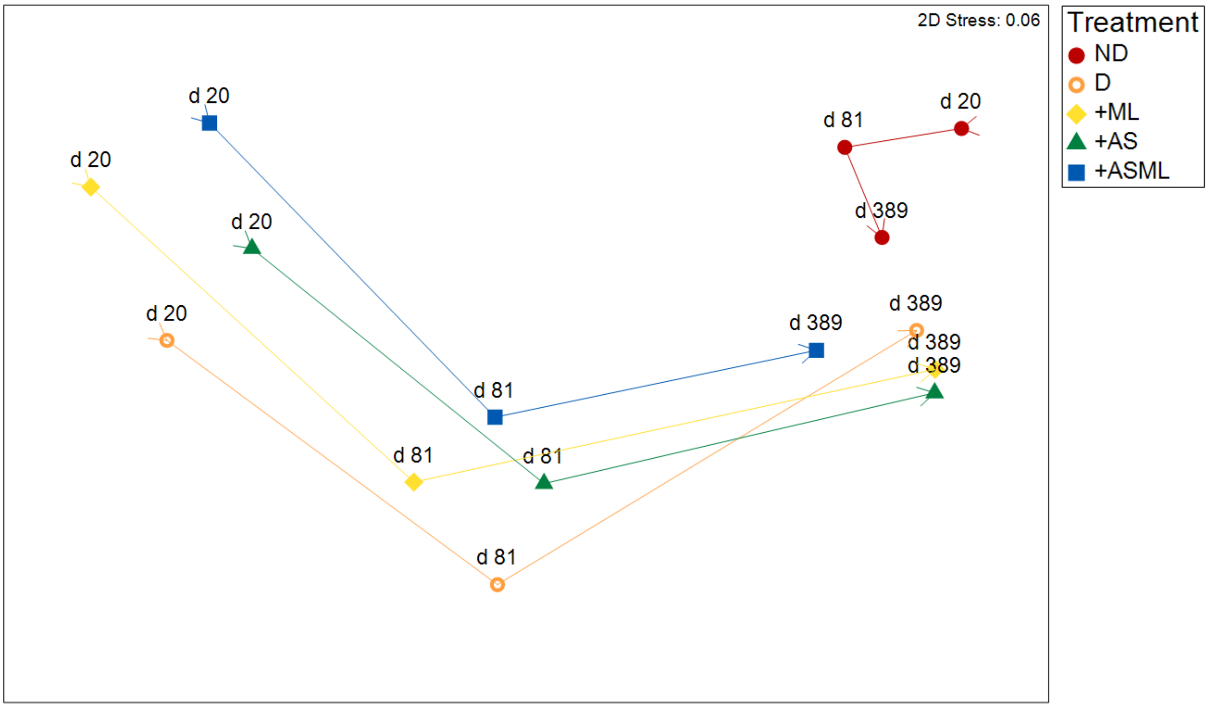


Figure 3.1 Non-metric multidimensional scaling plot (NMDS, Bray-Curtis similarity) of macrofaunal recovery trajectories. The centroids of each group (n=4) are shown to visualise how the macrofauna community composition varied with treatment and sampling date following disturbance/adult bivalve addition (d 20, 81, 389 post bivalve addition). Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi;* +ASML = defaunation + addition of both species. Figure A3.1 is provided to show the distribution of data points around the centroid including ten most important taxa identified by SIMPER analysis and *M. liliana* and *A. stutchburyi* as overlays.

Table 3.1 Results of repeated measures PERMANOVAs comparing multivariate (Bray-Curtis similarity, square root transformed) and univariate (Euclidean distance) indicators of macrofauna community composition as a function of time (fixed factor: 3 levels; day 20, 81, 389) and treatment (fixed factor: 5 levels; ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species), and plot (random factor: plots 1-20). Significant effects are highlighted in bold (α ≤ 0.05), and post-hoc pair-wise test results are given for significant interaction. Main effects are not considered in the case of a significant interaction term.

Variable	Source	df	MS	Pseudo-F	P(perm)	Post-hoc pairwise tests
Community recovery						
Multivariate community	Time x Treatment	8	1558.9	1.964	**<0.001**	d 20: ND ≠ (D = +ML = +AS = +ASML)
	Time	2	11923	15.02		d 81: ND ≠ ((+ML ≠ +AS) = +ASML = D)
	Treatment	4	3380.1	*6.882*		d 389: (ND ≠ (+ML = +AS)) = D = +ASML
	Plot (Treatment)	15	916.44	1.154	0.161	
	Res	30	793.85			
Total abundance	Time x Treatment	8	896.45	1.313	0.284	
	Time	2	19328	28.317	**0.001**	d 20 ≠ d 81≠ d 389
	Treatment	4	21686	29.141	**0.001**	ND ≠ (D = +ML = +AS = +ASML)
	Plot (Treatment)	15	744.18	1.090	0.393	
	Res	30	682.58			
Taxa richness	Time x Treatment	8	9.6917	1.138	0.257	
	Time	2	135.65	19.272	**0.001**	d 20 ≠ d 81≠ d 389
	Treatment	4	117.94	16.521	**0.002**	ND ≠ (D = +ML = +AS = +ASML)
	Plot (Treatment)	15	7.14	1.024	0.466	
	Res	30	7.04			
Bivalve recruitment						
Macomona liliana juveniles	Time x Treatment	8	71686	2.752	**0.024**	d 20: ND ≠ (D = +ML = +AS = +ASML)
	Time	2	5.15E+05	19.754		d 81: ND ≠ (D = (+ML ≠ +AS) = +ASML)
	Treatment	4	21507	0.776		d 389: (ND ≠ (+ML = +ASML)) = D = +AS
	Plot (Treatment)	15	2150	0.826	0.664	
	Res	30	26048			
Austrovenus stutchburyi juveniles	Time x Treatment	8	21759	0.350	0.943	
	Time	2	8.68E+05	13.979	**0.001**	d 20 ≠ (d 81= d 389)
	Treatment	4	1.74 E+05	4.84	**0.01**	(ND ≠ +ML) = D = +AS = +ASML
	Plot (Treatment)	15	21759	0.578	0.877	
	Res	30	62092			

The disturbance initially reduced total abundance and taxa richness in all defaunated treatments including bivalve addition treatments (Figure 3.2A, B, Table 3.1). Abundance and richness showed some recovery through time, however, both metrics remain significantly reduced in these treatments compared to ND after one year (abundance by 38 - 45%, richness by 25 - 30%, Figure 3.2A, B).

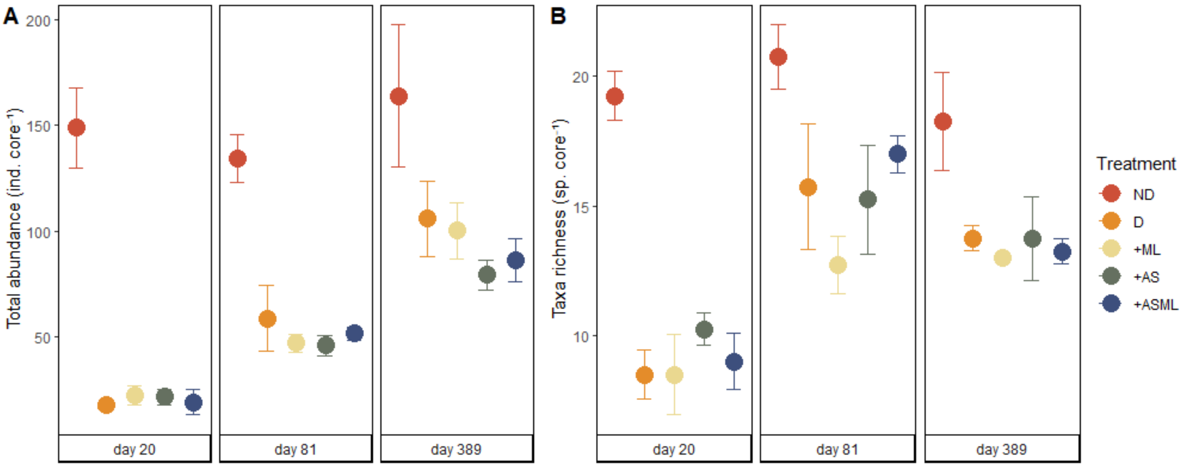


Figure 3.2 Selected alpha diversity metrics of community composition (mean ± 1SE, n=4) as a function of treatment and time (d 20, 81, 389 post bivalve addition). **(A)** Abundance, and **(B)** Species richness. Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species).

SIMPER analysis revealed that the same top contributing species are responsible for the dissimilarity between all disturbance treatments and ND for all sampling times (Table 3.2, Figure A3.1). This was due to higher mean abundances of *P. aucklandica, L. parengaensis, Nereididae, Oligochaeta, A. trifida, M. dakini, Anthopleura sp*. in the ND treatment. However, the abundance of the top 10 taxa as identified by SIMPER revealed contrasting responses. Most species showed lower abundances in the disturbed treatments relative to ND that persisted for the experiment (e.g., *P. aucklandica, L. parengaensis, A. trifida, M. dakini*, and *Anthopleura sp.;* Figure 3.3A, C, E, F, G). Other groups were initially reduced in all disturbed treatments but reached ND levels by the end of the experiment (*Nereididae, Oligocheata,* Figure 3.3B, D). However, some species peaked in disturbed treatments relative to the ND. For example, Polydorid spp. remained constant in ND and +AS, but peaked in abundance on d 81 in all other defaunated treatments (Figure 3.3H). *Z. lutulentus* also showed a peak in all abundance in disturbed treatments relative to ND on d 81 (Figure 3.3J). *P. aucklandica* abundances showed an overall increase in on d 389 across all treatments.

Macomona liliana juvenile density changed through time and peaked on d 81 for all defaunated treatments. The ND treatment was higher than defaunated treatments on d 20, lower than all defaunated treatments on d 81 and remained significantly lower than +ML and +ASML on d 389. The increase in juveniles on d 81 was greatest in +AS treatments which differed from the +ML treatment (Figure 3.4A, Table 3.1). Pre-adults of *M. liliana* remained lower than ND levels and similarly low across defaunated treatments except for an increase in density in +AS treatment to ND levels on d 389 (Table A3.3, Figure A3.3A).

Austrovenus stutchburyi juveniles increased in all treatments through time with a significant increase between d 20 and subsequent time points (Figure 3.4B, Table 3.1). *A. stutchburyi* juvenile densities in +ML treatment were significantly lower compared to ND. Pre-adult *A. stutchburyi* were reduced in all defaunated treatments compared to ND and did not show density changes across time (Table A3.3, Figure A3.3B).

Table 3.2 Results of SIMPER analysis comparing the taxa that contributed > 5% to the dissimilarity between treatments over time (d 20, 81, 389 post bivalve addition). Ratios of mean Bray-Curtis dissimilarity / standard deviation of dissimilarity (Diss/SD) describe taxa best discriminating between treatments, where a good discriminator ratio is >1.3 (Clarke and Warwick, 1994). Significant comparisons from PERMANOVA results are indicated by asterisks and the dissimilarities highlighted in bold. *Treatments:* ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species.

Day 20	**Species**	**Dissimilarity**	**Mean abundances**		**Diss/SD**	**Contribution (%)**
ND - D *		**71.65**	**ND**	**D**		
	Prionospio aucklandica		6.18	0	9.84	15.18
	Nereididae		4.66	0.85	3.87	9.27
	Lasaea parengaensis		4.26	1	2.39	8.10
	Oligochaeta		3.67	0.5	3.01	7.74
	Aonides trifida		3.41	0.85	3.50	6.26
	Magelona dakini		2.33	0	5.88	5.82
ND - +ML *		**68.39**	**ND**	**+ML**		
	Prionospio aucklandica		6.18	0.25	6.55	15.11
	Lasaea parengaensis		4.26	0.79	2.64	9.03
	Nereididae		4.66	1.14	2.75	9.00
	Oligochaeta		3.67	0.5	2.89	8.05
	Anthopleura sp.		2.48	0	3.75	6.25
	Austrovenus stutchburyi		2.26	0.25	2.82	5.23
ND – +AS *		**67.44**	**ND**	**+AS**		
	Prionospio aucklandica		6.18	1.06	4.22	12.96
	Lasaea parengaensis		4.26	0	5.15	10.79
	Nereididae		4.66	0.79	3.61	9.61
	Oligochaeta		3.67	1.16	1.97	6.24
	Aonides trifida		3.41	1.04	2.62	6.00
	Anthopleura sp.		2.48	0.25	2.75	5.55
ND – +ASML*		**68.93**	**ND**	**+ASML**		
	Prionospio aucklandica		6.18	0.25	5.94	15.15
	Nereididae		4.66	0.25	4.91	11.13
	Lasaea parengaensis		4.26	1.04	2.82	8.31
	Oligochaeta		3.67	0.97	1.98	7.72
	Magelona dakini		2.33	0.43	2.12	5.03
Day 81	**Species**	**Dissimilarity**	**Mean abundances**		**Diss/SD**	**Contribution (%)**
ND – D *		**49.74**	**ND**	**D**		
	Prionospio aucklandica		5.82	1.39	3.46	12.52
	Lasaea parengaensis		4.82	1.8	1.71	9.26
	Nereididae		3.67	0.93	2.16	7.98

	Magelona dakini		2.3	0	2.39	6.34
	Aonides trifida		3.35	1.24	1.69	6.13
	Oligochaeta		2.82	0.71	2.68	5.77
ND – +ML *		**51.14**	**ND**	**+ML**		
	Prionospio aucklandica		5.82	0.25	4.83	16.19
	Lasaea parengaensis		4.82	1.9	2.50	8.37
	Magelona dakini		2.3	0	2.53	6.54
	Nereididae		3.67	1.47	1.96	6.39
	Oligochaeta		2.82	1	1.93	5.37
	Polydorid *spp.*		1.04	2.88	1.54	5.37
ND – +AS *		**48.85**	**ND**	**+AS**		
	Prionospio aucklandica		5.82	0.68	3.54	15.12
	Lasaea parengaensis		4.82	1.18	6.06	10.61
	Nereididae		3.67	1.29	9.06	6.91
	Oligochaeta		2.82	0.68	2.09	6.39
	Magelona dakini		2.3	0.25	1.93	5.89
ND – +ASML *		**45.28**	**ND**	**+ASML**		
	Prionospio aucklandica		5.82	0.93	4.13	14.89
	Lasaea parengaensis		4.82	2.18	4.27	7.96
	Nereididae		3.67	1.1	8.99	7.83
	Magelona dakini		2.3	0.25	1.96	6.13
	Aonides trifida		3.35	1.6	2.19	5.25
+ML - D		41.49	**D**	**+ML**		
	Lasaea parengaensis		1.9	3.25	1.25	7.83
	Heteromastus filiformis		2.07	3.02	1.29	7.29
	Nereididae		1.47	2.58	1.16	6.23
	Prionospio aucklandica		0.25	2.28	2.25	5.49
	Polydorid *spp.*		2.88	2.2	1.25	5.31
	Cominella glandiformis		0	2.09	1.41	5.03
+AS – D		43.87	**D**	**+AS**		
	Polydorid *spp.*		2.27	0.5	1.47	8.4
	Heteromastus filiformis		1.27	1.71	1.43	6.23
	Aonides trifida		1.24	2.29	1.18	5.77
	Lasaea parengaensis		1.8	1.18	1.09	5.27
	Polydorid *spp.*					
+ML – +AS *		**42.43**	**+ML**	**+AS**		
	Polydorid *spp.*		2.88	0.5	1.80	11.74
	Cominella glandiformis		0	1.4	1.50	6.45

+ML- +ASML		34.54	**+ML**	**+ASML**		
	Lasaea parengaensis		1.90	2.18	1.73	6.19
	Polydorid *spp.*		2.88	2.12	1.11	6.07
	Nereididae		1.47	1.10	1.63	5.66
+ASML- +AS		36.58	**+ASML**	**+AS**		
	Polydorid *spp.*		2.12	0.5	1.82	9.04
	Cominella glandiformis		0.68	1.14	1.32	5.58
	Lasaea parengaensis		2.18	1.18	1.73	5.48
Day 389	**Species**	**Dissimilarity**	**Mean abundances**		**Diss/SD**	**Contribution (%)**
ND - D		34.89	**ND**	**D**		
	Prionospio aucklandica		9.59	8.09	1.58	9.03
	Lasaea parengaensis		3.34	1.47	2.48	7.71
	Aonides trifida		2.83	0.96	2.05	7.46
	Anthopleura sp.		2.38	0.68	1.89	7.32
	Oligochaeta		1.56	1.87	1.36	5.41
ND - +ML *		**35.33**	**ND**	**+ML**		
	Lasaea parengaensis		3.34	0.79	2.68	10.46
	Anthopleura sp.		2.38	0.25	2.95	8.71
	Prionospio aucklandica		9.59	7.95	1.69	8.61
	Aonides trifida		2.83	1.45	1.38	6.04
ND - +AS *		**38.81**	**ND**	**+AS**		
	Prionospio aucklandica		9.59	6.68	1.95	10.96
	Lasaea parengaensis		3.34	1.1	6.20	8.39
	Aonides trifida		2.83	0.6	2.34	8.29
	Anthopleura sp.		2.38	0.25	2.93	8.09
ND - +ASML		33.82	**ND**	**+ASML**		
	Lasaea parengaensis		3.34	0.5	2.85	12.38
	Prionospio aucklandica		9.59	7.07	1.67	11.68
	Anthopleura sp.		2.38	0.68	1.92	7.64
	Magelona dakini		1.35	0.25	1.61	5.13

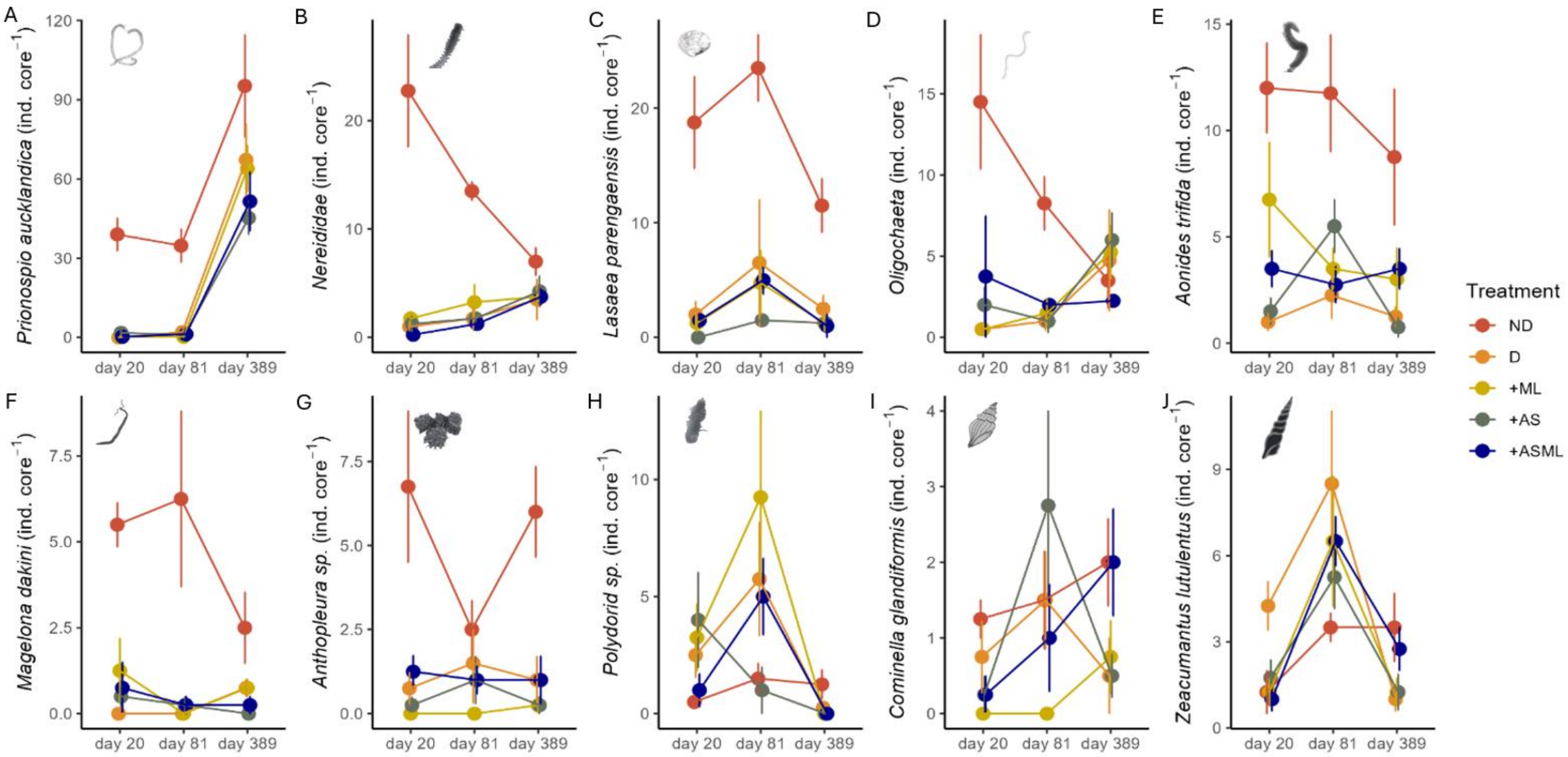


Figure 3.3 Mean (± standard error) taxa abundance per core of the 10 species (**A-J**) identified by SIMPER analysis as the top contributors to the dissimilarity in community composition as a function of treatment through time (d 20, 81, 389 post bivalve addition). Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species).

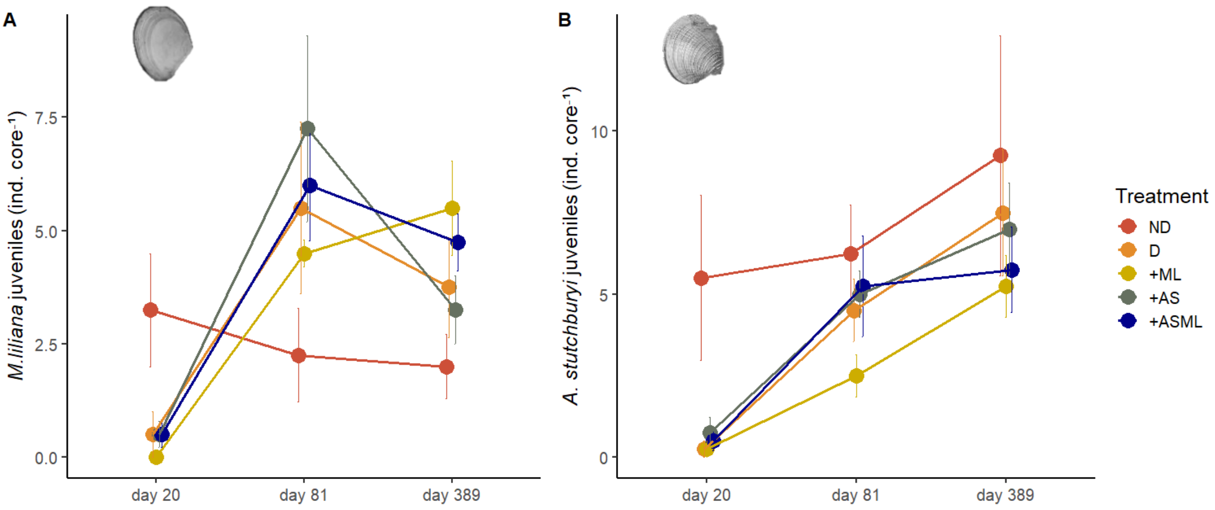


Figure 3.4 Mean (± standard error) densities of juvenile (< 10 mm) **(A)** *M. liliana*, and **(B)** *A. stutchburyi* per core across treatments through time (d 20, 81, 389 post bivalve addition). Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species.

3.3.3 Functional trait recovery

The CWMs of the functional traits and their modalities show the changes in functional composition that are driven by changes in abundance of taxa executing different functional roles. The disturbance initially selected for communities with less sediment stabilisers, small species, tube-dwelling, vermiform, and more surface modifiers, grazer/scraper and surface/shallow living trait compositions (Figure 3.5, Figure A3.2). The +ML and +ASML treatments enhanced the number of sediment stabilisers (Figure 3.5A), while +ML enhanced the proportion of small sized fauna, tube-dwelling living habitat, and vermiform morphologies (Figure 3.5B, C, D). Broadly, as shown in the species composition, there is a convergence with the ND plots over time.

Similarly, on d 81 +ML treatments show higher percentage of small individuals (Size, Figure 3.5B), tube-dwelling (Living habitat, Figure 3.5C) and vermiform (Morphology, Figure 3.5D) compared to D, +AS and +ASML. In contrast, *A. stutchburyi* addition treatments show higher levels of burrowers (Living habitat) and an almost all-encompassing percentage of species with round/globulose morphology. On d 389 most of these trends disappeared with the trait communities remaining very similar, including ND and D. Slight differences occur in the +AS treatment showing less stabilisers, more burrowers, and free-living surface crawlers, and increased ambient (ND) levels of round/globulose morphologies remained in +ASML. CWMs in the Feeding mode trait modality in +AS and +ASML treatments resemble those of ND (Figure A3.2B).

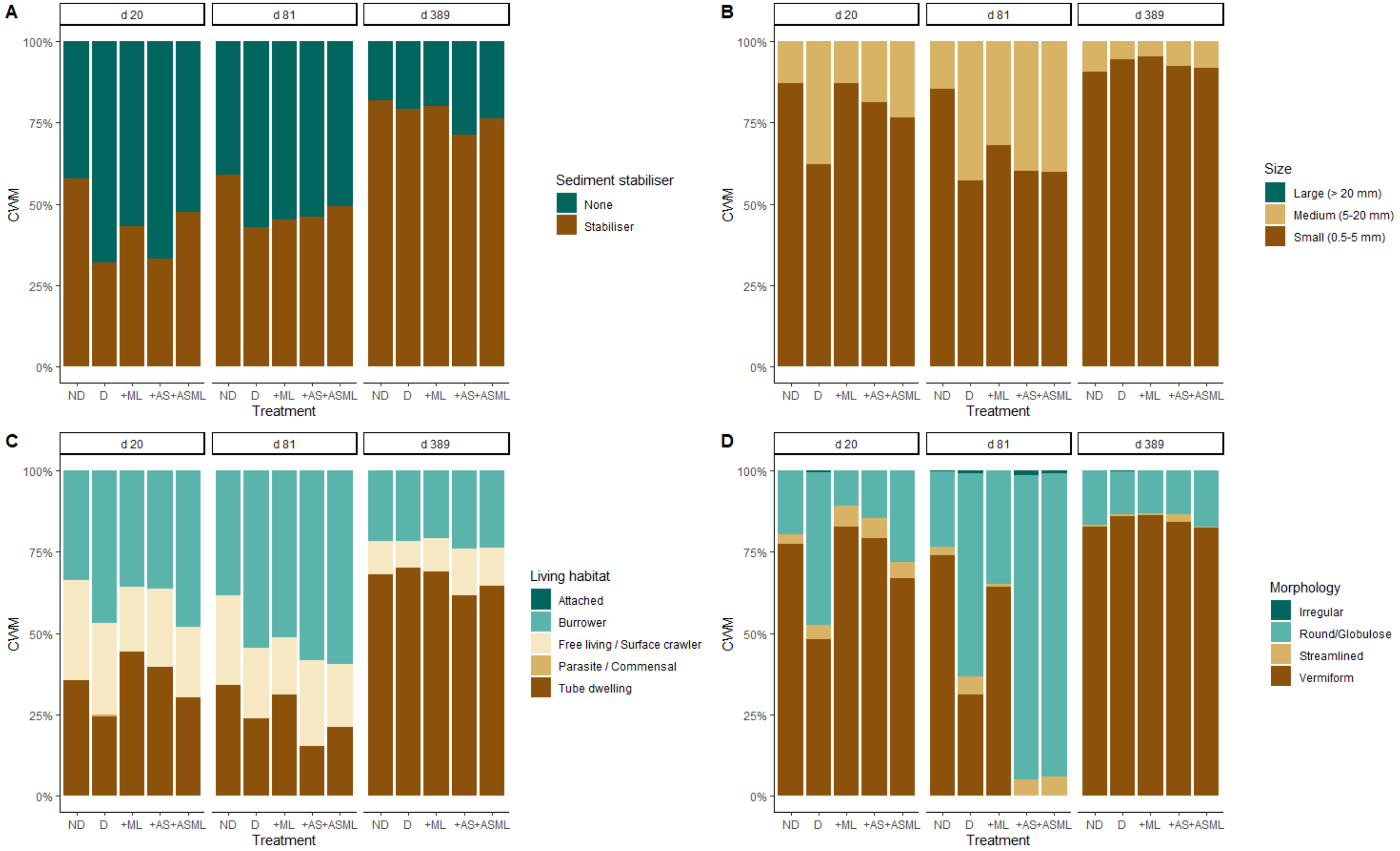


Figure 3.5 Community weighted means (CWM) of selected trait values and associated trait modalities across treatments and time (d 20, d81, d389 post bivalve addition). **(A)** Sediment stabilisation, **(B)** Size, **(C)** Living habitat, **(D)** Morphology. *Treatments:* ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species. See Suppl. Figure A3.2 for the additional three CWMs of traits.

3.4 Discussion

The taxonomic and functional response of a defaunated macrofaunal sandflat community to the reintroduction of adult bivalves was explored in situ and linked to assemblage recovery. I show that community changes over time were driven by changes in the relative and absolute abundances of species, rather than the species composition or richness. The experiment showed that adult bivalve additions were successful for both species initially with reduced but persisting numbers after one year (Chapter 2). This field manipulation experiment showcases the potential of adult bivalves to engineer the defaunated seafloor habitat, with subtle influences on colonists and early disturbance-recovery dynamics. For instance, the addition of the venerid clam *A. stutchburyi* appeared to circumvent an initial disturbance response of opportunist tube-forming spionid polychaetes after 81 d. While *M. liliana* juvenile recruits were enhanced in all defaunated treatments compared to ambient, and this was most pronounced in *M. liliana* addition treatments. However, after one year there were only subtle differences in the recovery measures of treatments suggesting that all treatments approached ambient communities; hence they recovered through time.

My results indicate that the addition of adult bivalves did not create shifts in benthic community composition or diversity as hypothesised but rather caused subtle changes in the relative abundances of a few taxa (as in Thrush et al., 2006; Bishop and Kelaher, 2007; Gladstone-Gallagher, Lundquist and Pilditch, 2014; Drylie et al., 2020). The magnitude of change in community composition between each time step was similar across treatments, suggesting that rates of recovery may be similar among treatments. Differences in relative abundances led to slightly varying pathways of recovery.

The experimental disturbance lastingly impacted the macrobenthic community composition by substantially reducing the abundance of most species. Whilst recovery was initiated, this effect persisted throughout the duration of the experiment. This concurs with similar disturbance-recovery studies describing that a physical disturbance can impact a community until >1 year post disturbance (Beukema et al., 1999; Dittmann, Gunther and Schleier, 1999; Kröger et al., 2006; Norkko et al., 2006; Thrush et al., 2008a; Lohrer et al., 2010; De Juan et al., 2014).

The sampling day in austral autumn (d 81), three months after the re-addition of bivalves, and directly after the seasonal recruitment period, yielded interesting results related to treatment differences in the early opportunist colonisers. All disturbed plots, except *A. stutchburyi* only addition treatments, showed increased abundances of Polydorid species, mucus-lined tube-building spionid opportunists (*Boccardia syrtis, Pseudopolydora*, *Polydora* spp.). Polydorid species are small, opportunistic, surface deposit or suspension feeders, with little bioturbating effects (Rhoads and Boyer, 1982). An 'overshoot' abundance of colonists relative to ambient conditions after disturbance (Beukema et al., 1999), followed by a decline are representative of opportunistic responses to disturbances (Thistle, 1981) and have been observed previously (van Colen et al., 2008; De Juan et al., 2014). Polydorid species have been recorded to rapidly colonise defaunated plots (Shull, 1997). The polydorid *B. syrtis* has been recorded as the most abundant species recolonising small scale, disturbed plots showing temporary establishment, restricted to the initial phase of the recolonisation process (Whitlatch et al., 1998).

In this study, this polydorid colonisation was inhibited by the presence of large *A. stutchburyi* which may be due to their continuous bioturbation activity (biogenic disturbance) changing the stability of the sediment (Woodin, 1976; Norkko et al., 2006; Thrush et al., 2006). *Austrovenus stutchburyi* mixes surficial sediments through its vertical and horizontal movements and at high densities, can exert an inhibitory impact on the soft sediment community, directly restricting the settlement of new species and juvenile bivalves (Turner et al., 1997; Whitlatch et al., 1997). My study may indicate that high densities of large bioturbating bivalves can particularly affect small surface-feeding infauna, reducing the presence of spionid pioneer species (Woodin and Jackson, 1979; Flach, 1996; Whitlatch et al., 1997). The replacement of the small-sized early colonisers by large-sized bioturbating organisms (increased bioturbation potential) has been shown to have a disproportionately stronger effect on sediment processes and properties (van Colen et al., 2012). *Austrovenus stutchburyi* may circumvent the initial successional stage dominated by opportunistic species through a combination of bioturbation, destabilising the surface sediment and thereby engineering the biogeochemical properties of the sediment.

Three months after the re-addition of bivalves, this study captured a recruitment event of both bivalve species. Bivalve recruitment in my treatments was expected to vary between species. As hypothesised, the addition of adult bivalves affected the recolonisation of juvenile *M. liliana* and *A. stutchburyi* differently.

Juvenile *M. liliana* successfully recolonised all defaunated treatments on d 81 and showed elevated juvenile densities in +*M. liliana* addition treatments (relative to ambient) at the end of the study period. The relationship between adults and juveniles is highly context and habitat-specific. Adult *M. liliana* in high densities are known to have strong faciliatory (Roper, Pridmore and Thrush, 1992; Douglas et al., 2023) or inhibitory (Thrush et al., 1992; 1996a; 2000; Thrush, Pridmore and Hewitt, 1994; Hewitt et al., 1997) influences on the composition of the surrounding benthic community and conspecific recruitment. Positive associations were observed under higher levels of ecosystem stress. the addition of adults to defaunated sediment has been shown to increase the number of juvenile conspecifics, possibly through biological cues that indicate habitat suitability (Roper, Pridmore and Thrush, 1992) and from Structural Equation Modeling (Douglas et al., 2023). At a muddy-sand site, highest juvenile densities were associated with high adult densities (Thrush et al., 1996a). Here, initially, juvenile *M. liliana* juveniles peaked in all disturbance plots, and this was most pronounced in the *A. stutchburyi* addition treatments. However, after one-year juvenile *M. liliana* were only elevated in treatments where adult *M. liliana* had been added. The peak in density on d 81 was mainly driven by *M. liliana* < 5mm, whilst the number of juveniles persisting in treatments after one year was attributed to densities of the slightly larger (5-10mm) individuals suggesting small recruiting juveniles in autumn survived until after one year (Figure A3.4). And some of these juveniles grew into ‘pre-adults’ (10-18 mm) over the course of a year (see size frequency plots in Figure A3.3). As *M. liliana* juveniles are restricted to the first 2 cm of the sediment and have been observed to actively avoid unfavourable sediment conditions for survival (Pridmore et al., 1990; Cummings et al., 1993; 1995; Hewitt et al., 1997; Turner et al., 1997), it could be suggested that the defaunation offered a favourable habitat for recruitment, especially after three months, compared to ambient.

I observed the growth of an *A. stutchburyi* cohort within the time of the experiment (summer to summer), as *A. stutchburyi* grows only up to ~10mm shell length within the first year as a juvenile (McKinnon, 1996) which matches the observations of gradually increasing juveniles across all plots. The consistently lower densities of *A. stutchburyi* juveniles in defaunated treatments compared to ambient shows that the disturbance seemed to have impacted the recruitment of this species, suggesting that ambient conditions are more favourable. Given that juvenile *A. stutchburyi* are highly mobile (Hewitt et al., 1996) they may have selected areas of established benthic communities for settlement. Recolonisation by *A. stutchburyi* juveniles occurred across all treatments, showing that the increase of conspecific juveniles was independent of the number of adults present in the plots (Hewitt and Cummings, 2013). Yet, lower densities in *M. liliana* only plots may have been triggered through surface deposit feeding activity of adult *M. liliana* which can hinder the settlement of juvenile *A. stutchburyi* at high densities (Thrush et al., 1996a; 2000). This may represent an antagonistic effect of dense aggregation of *M. liliana* feeding activities on *A. stutchburyi* larval settlement (Thrush et al., 1996a; 2000; Lelieveld, Pilditch and Green, 2004), in the absence of a protective *A. stutchburyi* shell layer (Thrush et al., 1996a).

Functional groups of species with shared biological traits are increasingly used as proxies for ecosystem function (Norkko et al., 2013, Lohrer et al., 2015), often explaining changes better than traditional taxonomic classifications alone (Bremner et al., 2006; Queirós et al., 2013, Cadotte et al., 2011). The CWMs are proportional to abundances and may therefore give a better representation of where shifts in the functional recovery occur, although the magnitude of change is unaccounted for. CWMs showed that differences between treatments in functional trait communities were most pronounced after one month of the disturbance having enhanced the proportional abundances of small to medium sized, epibenthic, free-living, shallow-dwelling and grazing/scraping surface crawlers and suspension feeders. The increase of small, tube dwelling, vermiform sediment stabilisers across all treatments coincides with the strong increase in *P. aucklandica* abundances, given that a site-wide peak occurs in this species on d 389. Nuances in trait space are hence most informative for the first two time points, shedding light on the effects either bivalve addition have on the early community recolonisation.

I found no evidence that the co-addition of bivalves improved the macrofaunal community recovery in the combined treatment after one year. This might be because there was good natural recruitment of the bivalves giving rise to the whether effects might be greater in environments with no/low recruitment of the bivalve species? It may also be because the presence of more than one key species can have higher potential of introducing confounding effects for the other to thrive (Angelini et al., 2011). Given that in practice, the co-addition of the two bivalves may prove logistically difficult, especially in sites where the two species are not naturally present as *M. liliana* are fragile and deeper dwelling, using only *A. stutchburyi* for restorative action may be the better option.

Subtle effects in the recovery between disturbed treatments were reflected in the proxies for ecosystem functions (see Chapter 2). Although the survival of translocated *A. stutchburyi* after one year was low (16%), measures of recovery (sediment parameters, ecosystem productivity, nutrient cycling) were enhanced in *A. stutchburyi* addition treatments. While *M. liliana* and co-addition had limited influence on the assessed functions, the treatment with *A. stutchburyi* additions showed reduced sediment mud content by 2 - 3%, enhanced sediment oxygen consumption by 16 - 30%, and increased ammonium flux by 40-fold compared to no addition treatments, even after one year. The decreased mud content in *A. stutchburyi* treatment may also be connected to the decreased amount of sediment stabiliser traits, and a decrease in tube-dwelling species compared to increased burrowers and surface crawlers, species with epibenthic sediment position, and streamlined morphologies in these treatments after one year. These epibenthic burrowers were mainly species in the class Malacostraca (Orders *Amphipoda, Isopoda,* and *Cumacea*) which modify the surface of the sediment during their feeding activities (Thomas et al., 2022). The effect of bioturbating macrofauna on sediment erosion is complex but it has been shown that an amphipod (*Corophium)* can seasonally reduce the sediment-erosion threshold (Grant and Daborn, 1994). This could be further investigated by including a measure of bioturbation potential in future studies (sensu Solan et al., 2004; van Colen et al., 2012). Enhanced SOC and NH_4^+ were a result of respiration and excretion of the increased *A. stutchburyi* biomass in the treatments (Chapter 2) but can be linked here to high macrofaunal metabolism and higher densities of borrowing traits, the lower densities of sediment stabilisers and higher densities of juvenile bivalves potentially acting as bioirrigators.

For future restoration trials I suggest 1) larger patch sizes of *A. stutchburyi* transplants (De Juan and Hewitt, 2011), 2) to investigate longer time scales (>1 year) after transplantation, 3) the simultaneous measurements of important environmental variables such as temperature, location on tidal height, and exposure to rainfall (Dobbinson, Barker and Jillett, 1989; Stewart, Creese and Lalwnitory, 2002; Cummings et al., 2007) and 4) test for different effects of the bivalve addition in different sites with varying grain sizes or stressor regimes. In addition to sites with different disturbance regimes, 5) adding these two species to sites with different colonist pools could show stronger effects of bivalve addition. Translocating adult bivalves could potentially be more useful when there are no extant populations close by. Therefore, the addition of both bivalves may provide a beneficial tool to support benthic recovery that should be considered in future studies.

3.5 Conclusion

My research highlights the importance of the early reinstatement of facilitatory feedback loops within a recovering community to inform management actions that promote functioning of estuarine benthic ecosystems. This research demonstrated that, although recovery was driven mainly by the variability of species abundance in the experimental site, and temporal dynamic shifts associated with treatments, the addition of sediment-engineering bivalves subtly modified the community composition differently, to the extent that recovery trajectories were slightly altered. This can be attributed to a change in taxonomic diversity, *M. liliana* and *A. stutchburyi* recruitment, and initial Polydorid species density over the course of the experiment. I cannot draw conclusions about the end points of recovery as they remain inconclusive. However, these results indicate that more research is needed for nature-based solutions to improve the health of these important ecosystems (Lam-Gordillo et al., 2022a) allowing managers to account for slow and unpredictable recovery in sand-flat systems (De Juan et al., 2014).

Top: Re-seeding of A. stutchburyi at Waimapu Tauranga Harbour, January 2023. Bottom: Large A. stutchburyi from the source population at Tuapiro Point.

Chapter 4

Translocating clams for estuarine restoration: Retention is key for enhancing ecosystem functioning across a stressor gradient

4.1 Introduction

Estuarine seafloor environments are highly productive ecosystems that provide a range of critical services to humans (Savage et al., 2012; Thrush et al., 2013a; Snelgrove et al., 2014). Yet worldwide these ecosystems have experienced rapid degradation in the last 150–300 years which is ongoing (Lotze et al., 2006; Halpern et al., 2008b). There is global concern about the degradation of coastal intertidal habitats and increasing interest to conserve, protect, and restore these environments to improve ecosystem function and the services they provide (French McCay et al., 2003; Bullock et al., 2011). A promising approach is to use locally available species to aid the restoration of such degraded habitats (McLeod et al., 2019; Gagnon et al., 2020). Bivalves are increasingly used for the restoration and bioremediation of degraded habitats and water quality (Arnold, 2001; Byrne and O'Halloran, 2001 for a review; Carmichael, Walton and Clark, 2012; Shen et al., 2016; Benjamin et al., 2022); however, to enhance the effectiveness of the restoration effort, an understanding of the ecology and survival requirements of the utilised species is essential (Damodaran, 2024). While bioturbating bivalves have been shown to bioremediate degraded sediments from specific contaminants (Gonzalez et al., 2019 for a review; Nicholaus et al., 2019, see Chapter 2), active restoration trials of sediment-dwelling bivalves for the improvement of overall benthic functioning for estuarine restoration are scarce (except see Rossi et al., 2008; Deb et al., 2025).

Common stressors threatening the health of estuaries are sedimentation, nutrient loading, and heavy metal contamination, which can individually, and cumulatively, impact estuarine ecosystems (Ellis, Norkko and Thrush, 2000; Crain, Kroeker and Halpern, 2008; Ellis et al., 2017). Human induced increases of sedimentation, which usually originate from clearance of native vegetation, urbanisation, forestry activity on erodible land, in addition to natural erosion processes, alter these habitats by increasing the mud content (Norkko et al., 2002; Ellis et al., 2015). This negatively impacts macrofaunal community diversity and abundance (Cummings et al., 2003; Thrush et al., 2003; Ellis et al., 2004; Lohrer et al., 2004). Nutrients (nitrogen and phosphorus) are increasingly delivered to estuarine ecosystems due to human activities such as intensified application of fertilizer to agricultural land, sewage discharge, and urban/industrial runoff, frequently resulting in eutrophication of shallow coastal waters causing low sediment oxygen with cascading negative effects on benthic macrofauna (Diaz and Rosenberg, 1995; Nixon, 1995; Morris and Keough, 2003; Byers and Grabowski, 2014). Increased rates of anthropogenic heavy metal contamination from urbanised and farmed coastlines further exacerbate the amount of stress an estuarine system is subjected to (Kennish, 1994; Robb, 2014; Jordan, Weller and Pelc, 2018). Prevalent estuarine contaminants, also in New Zealand, are predominantly copper, lead, and zinc delivered by polluted stormwater runoff (ARC, 2004; Karydis and Kitsiou, 2013; Aguirre et al., 2016). These three heavy metals can be absorbed into tissue and can negatively affect macrobenthic communities (Hewitt et al., 2009; Fukunaga et al., 2010; Thrush et al., 2013a). Moreover, these stressors often co-occur with a potential for synergism in their adverse effects, leading to the amplification of stressor impacts or unpredictability of consequences for the health of benthic fauna and the ecosystem (Crain, Kroeker and Halpern, 2008; Rynkowski et al., 2025 for a review). Long sediment and water retention in estuarine systems which are subject to slow tidal movement lead to heightened vulnerability to a combination of stressors of past and present pollution (Aguirre et al., 2016). Multiple stressors can disrupt estuarine processes and harm macrofauna, causing shifts in benthic communities, ecosystem resilience, and functioning (Lenihan et al., 2003; Lohrer et al., 2011; 2012).

In Chapter 2 I found that the addition of large *Austrovenus stutchburyi* (New Zealand littleneck clam) can influence key ecosystem functions at the sediment-water interface, if translocations were implemented at an early stage in the recovery of a disturbed soft sediment system. This experiment provided evidence that the re-introduction of *A. stutchburyi* may be effective for bioremediation of degraded estuaries (Chapter 2). However, the success of using bivalves for bioremediation may be limited by their tolerance to multiple stressors, and restoration efforts may be negated if bivalves remain exposed to the pressures that instigated the degradation in the first place (zu Ermgassen et al., 2020; Benthotage et al., 2022). Thus, it is essential to understand the effects of interacting stressors on translocation species and translocation success before undertaking large-scale bioremediation or restoration management actions.

In New Zealand, the suspension-feeding venerid clam *A. stutchburyi* plays a key role in the functioning of healthy estuarine soft sediment habitats. It bioturbates the top layer of the sediment (Powell, 1979; Hewitt et al., 1996; 1997), thereby mediating all oxygen-dependent processes, such as carbon cycling, primary productivity, and nutrient exchange (Sandwell, Pilditch and Lohrer, 2009; Jones et al., 2011). *Austrovenus stutchburyi* is a robust species for translocation (Stewart, Creese and Lalwnitory, 2002; Hewitt and Norkko, 2007). It has been used for biomarker studies undertaken to assess the survival and health of animals which were transplanted from clean sites to sites with increased sedimentation/contamination (De Luca-Abbott, 2000; 2001; Norkko et al., 2005). Past studies in the U.S. suggest using adult clams (*Merceneria merceneria)* for translocations due to higher survival (Peterson, Summerson and Huber, 1995; Marelli and Arnold, 1996). In New Zealand, experimental studies further investigated the optimal densities, sizes, growth, and survival in transplanted *A. stutchburyi* (see Dobbinson, Barker and Jillett, 1989; De Luca-Abbott, 2001). Suitable densities for *A. stutchburyi* were recorded as 200 individuals per 0.25m^2 (~800 ind. m^2) due to denser patches of individuals. Denser patches potentially supported retention, and recovery rates varied from low to 90% after one year (Stewart, Creese and Lalwnitory, 2002), whereas similar densities were considered too high as only 30% retention was recorded elsewhere likely due to a combination of outmigration from plots and mortality from extreme environmental conditions and caging (Cummings et al., 2007). In some studies, low mortality of transplanted adult *A. stutchburyi* within the first 29 weeks (~7 months) after transplantation has been recorded (Cummings et al., 2007). Stewart, Creese and Lalwnitory (2002) even found recovery rates of up to 90% after one year. In other studies, the survival of transplanted *A. stutchburyi* in contaminated sites was poor (Stewart, 2005), yet *A. stutchburyi* has been shown to survive sublethal effects in contaminated sites (De Luca-Abbott, 2000). These transplant studies directed towards restoration were mainly driven by the aim to increase *A. stutchburyi* populations (Cummings et al., 2007; Marsden & Adkins, 2010 for a review; Stewart et al., 2002). However, studies evaluating how multiple sublethal stressors can affect the transplant survival and helping to identify where and when restoration is likely successful are lacking.

The primary aim of this study was to assess translocation success “retention” (measured as survival of translocated individuals) of *A. stutchburyi* across a gradient of environmental stress within a large estuary. As a secondary outcome, it aimed to assess if translocations led to improved functioning of the soft sediment. Specifically, I asked 1) in what densities are transplanted *A. stutchburyi* retained and is this related to the site-level environmental gradient and/or ambient *A. stutchburyi* density? 2) can we measure differences in benthic productivity, and carbon and nutrient cycling after successful *A. stutchburyi* additions? I hypothesised that survival of transplanted *A. stutchburyi* will be higher in less impacted areas compared to more degraded sites and that the recovery of ecosystem functioning is context dependent, mainly on the level of mud stress and ambient *A. stutchburyi* health and lesson the relative contaminant loading. This is expected because the contaminant loading of nutrients and heavy metals is expected to be low compared to global standards (ANZECC, 2000), proportionally enhancing the level of mud stress in this context. This work will advance our understanding of the role of sedimentary stressors on translocation success providing an improved understanding of how management can use *A. stutchburyi* for estuary-wide improvement of sedimentary conditions and functions (bioremediation) to yield the best results for restoration (Ravit et al., 2014).

4.2 Methods

4.2.1 Study area and experimental design

A translocation experiment was conducted within the Tauranga Harbour situated on the northeast coast of Aotearoa New Zealand's North Island (Figure 4.1A). It is a 200 km^2 semi-enclosed harbour that receives terrestrial input from a catchment of about 1300 km^2. The catchment is dominated by urban, and agricultural development (Park, 2004; Ellis et al., 2013). Pastural and forestry land use contribute to 90% of total terrestrial sediment load into the harbour (Sinner et al., 2011). Site selection was based on data from Ellis et al., (2013; 2015). Ellis et al. (2013) surveyed the harbour and proposed a site-specific benthic health index based on the physical (site characteristics and three stressors: sediment grain size, nutrient concentrations, heavy metal burden) and biological data (macrofauna and *A. stutchburyi* abundance). The benthic health categories ranged from 1 ('healthier') to 5 ('more impacted') reflecting varying levels of contamination. I selected nine sites along this gradient of benthic health for this experiment to establish a 'stress' gradient and assess whether this correlated with ambient *A. stutchburyi* health parameters (Figure 4.1B, Table A4.1). Individual stressors varied between selected sites, which provided a way to investigate if and where transplanted adult *A. stutchburyi* can be retained and the impacts of specific stressors on their ability to improve ecosystem productivity. Sites with increased stressors represent degradation in a space-for-time approach. Sites were pre-assessed in a pilot study to ensure the presence of *A. stutchburyi*.

The translocation experiments took place over the austral summer season between January and April 2023 (duration of three months, or 85 d). Adult *A. stutchburyi* were sourced from three locations, one in the northern harbour (ATH), one in the centre (TUAP), and one in the south (REA, Figure 4.1A, Table A4.1). Source populations were selected based on high background densities (> 1000 ind. m $^{-2}$) of large *A. stutchburyi* (minimum shell length > 18 mm) with overall high condition index (CI >2, Table 4.1). High background densities of *A. stutchburyi* at these sites were critical to ensure collections would not deplete the source populations. In January 2023, large *A. stutchburyi* (> 18 mm) were translocated from the closest source populations to experimental sites to minimise travelling time and maintain the *whakapapa* (heritage) of the animals. Two sites received *A. stutchburyi* from ATH, four sites from TUAP, and three from REA (Table 4.3). At each site eight 1 m^2 plots were randomly distributed 5 m apart in a ~100 m^2 area and marked with corner pegs. They were then classified as ambient plots (no treatment) and translocation plots (translocated + *A. stutchburyi* treatment, hereafter +AS) yielding four replicates each.

Approximately 800 *A. stutchburyi* individuals (representing healthy densities in the harbour, Ellis et al., (2013; 2015), as in Chapter 2 & 3) were added to the translocation plots (inserted in the correct orientation with their siphons upward into the sediment on an incoming tide to maximise settlement success). One temperature logger (sampling frequency 1 h, sampling resolution 0.1°C; EnvLogger T2.4, electricblue, Portugal) was deployed at each site at ~ 5cm depth for the duration of the experiment. Plots were uncaged given that caging does not improve retention of adult *A. stutchburyi* (Cummings et al., 2007). After 85 d (April 2023), sampling occurred during two consecutive weeks. In the first week, sediment to water-column oxygen fluxes were measured using benthic incubation chambers, and rapid organic matter assays (ROMA) were deployed. In the second week ROMA plates were retrieved, *A. stutchburyi* specimen and sediment samples collected.

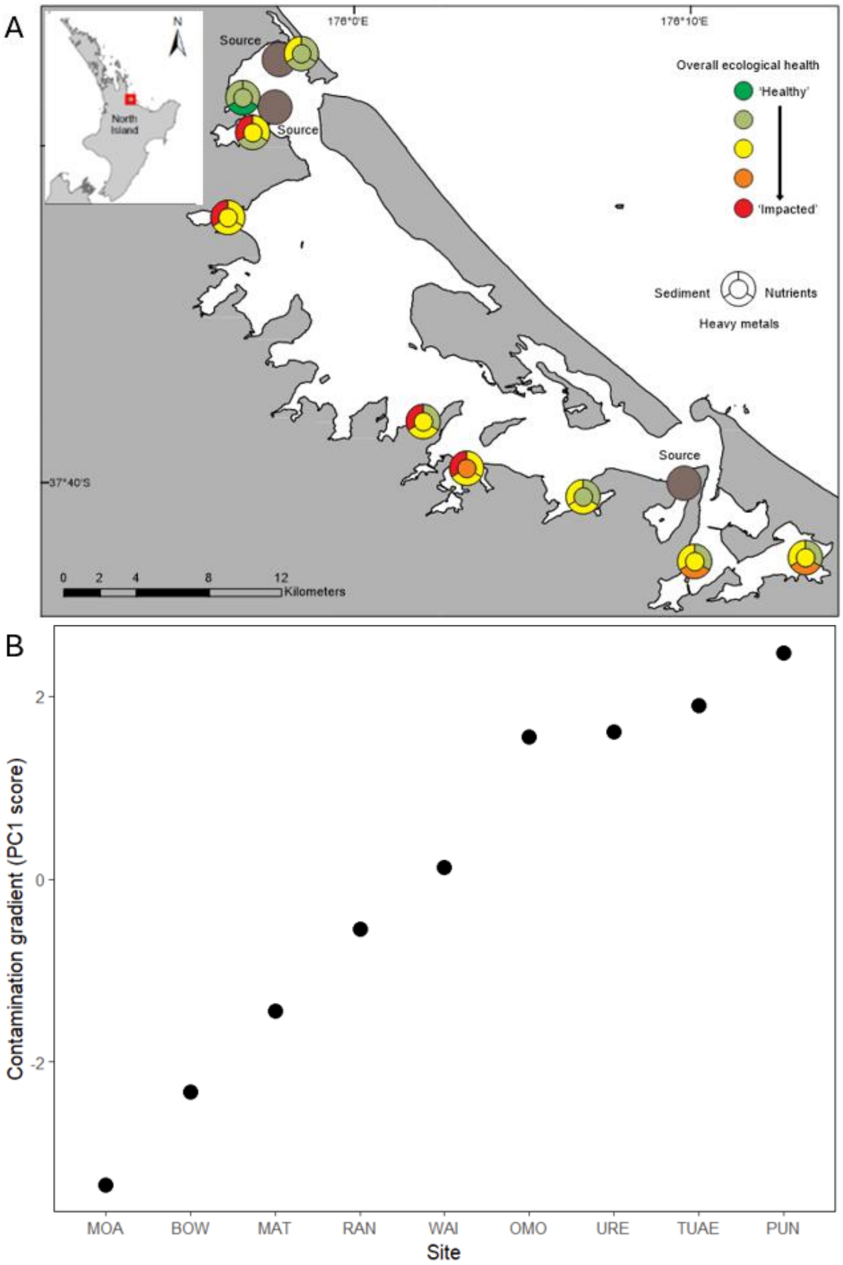


Figure 4.1 (A) Map of the Tauranga Harbour showing source populations (brown) and translocation sites displayed to represent their level of overall health (centre of circle; PC1 score) and individual stressor intensity (in thirds of the outside circle; sediment, nutrients, and heavy metal contamination), based on results from this study. **(B)** Multiple stressor health gradient (PC1 score) calculated from levels of sediment mud content, nutrients and heavy metals in the sediment. Sites are ordered from least to most contaminated.

Table 4.1 Indicators of site health including multiple stressor variables, calculated gradients, and ambient *A. stutchburyi* metrics. Mean (range) sediment mud content, total nitrogen (TN), total phosphorus (TP), lead (Pb), copper (Cu), and zinc (Zn) levels are shown. The gradient represents a PC1 score with individual gradients calculated by the transformed and normalised value multiplied by the Eigenvalue of the PC used.

Site	**Raw stressor measurements**							**Gradients**				**Ambient *A. stutchburyi***			
Source	**Mud (%)**	**TN (mg kg^{-1})**	**TP (mg kg^{-1})**	**Pb (mg kg^{-1})**	**Cu (mg kg^{-1})**	**Zn (mg kg^{-1})**						**Mean shell length (mm)**	**Mean CI**	**Density (ind. m^{-2})**	**Biomass (g m^{-2})**
ATH	6.21 (4.20-8.20)	250 (200-300)	80.86 (80.10-81.61)	1.62 (1.54-1.68)	0.32 (0.14-0.50)	11.63 (8.51-14.27)						22.45	2.45	2136	179.21
TUAP	5.66 (4.62-7.24)	300 (300-300)	126.88 (123.10-130.65)	1.81 (1.76-1.89)	0.34 (0.19-0.47)	9.20 (7.79-11.42)						24.35	2.47	1140	127.79
REA	5.77 (5.25-6.51)	400 (400-400)	129.64 (126.55-132.73)	2.02 (1.84-2.09)	0.60 (0.40-0.82)	13.39 (8.71-20.43)						22.32	2.33	1744	137.08
Translocation							**Salinity**	**Overall gradient (PC1)**	**Sediment gradient**	**Nutrient gradient**	**Heavy Metal gradient**				
BOW	7.52 (6.05-8.28)	335 (300-370)	84.23 (82.99-85.47)	1.53 (1.40-1.60)	0.42 (0.26-0.62)	8.08 (7.60-8.80)	20.7	-2.33	-0.20	-1.05	-1.09	15.86	1.71	1104	23.68
MOA	4.67 (3.56-6.89)	305 (250-360)	101.91 (87.11-116.72)	1.25 (1.20-1.30)	0.08 (0-0.17)	6.18 (4.90-7.00)	32.0	-3.35	-0.54	-0.83	-1.98	17.34	1.88	744	21.29
TUAE	17.69 (14.93-18.71)	575 (560-590)	155.57 (154.21-156.92)	2.53 (2.30-2.70)	0.99 (0.87-1.09)	12.70 (10.60-14.40)	33.7	1.90	0.43	0.93	0.53	12.42	1.77	627	7.32
URE	12.83 (7.61-17-27)	505 (500-510)	154.58 (145.42-163.75)	3.18 (2.40-3.90)	1.00 (0.64-1.45)	11.68 (10.50-14.40)	n.d.	1.61	0.16	0.67	0.78	17.29	1.98	13	0.40
OMO	23.09 (19.33-24.14)	435 (410-460)	134.13 (131.70-136.55)	2.65 (2.40-2.80)	0.80 (0.58-1.15)	18.88 (16.00-22.20)	29.9	1.55	0.63	0.16	0.77	14.51	1.28	65	0.82
PUN	16.82 (13.91-22.14)	595 (550-640)	163.86 (162.18-165.55)	3.45 (3.00-3.90)	0.70 (0.46-0.94)	17.48 (14.10-24.40)	29.9	2.48	0.38	1.11	1.00	13.95	1.23	1792	21.79
MAT	5.08 (3.68-5.70)	440 (380-480)	92.79 (87.94-97.63)	1.95 (1.80-2.10)	0.37 (0.28-0.46)	13.00 (9.00-18.30)	17.9	-1.44	-0.47	-0.52	-0.45	15.14	1.48	348	5.34
WAI	7.76 (6.00-9.47)	330 (290-370)	129.11 (137.34-130.87)	1.93 (1.70-2.10)	1.14 (0.86-1.45)	19.33 (15.00-27.30)	20.6	0.13	-0.18	-0.30	0.61	13.18	1.99	310	4.21
RAN	7.74 (5.56-11.51)	410 (390-430)	116.79 (116.43-117.15)	2.05 (1.70-2.50)	0.77 (0.42-1.06)	10.88 (5.60-17.30)	23.5	-0.54	-0.20	-0.18	-0.16	22.52	2.20	5	0.23

4.2.2 Environmental gradient and sediment parameters

Sediment samples were taken at all sites to reassess the level of health at each site ten years after the report by (Ellis et al., 2013) had been published, and to estimate the effect of added *A. stutchburyi* on proxies for sediment functioning (e.g., net primary productivity, benthic metabolism, carbon degradation). These included sediment samples for the assessment of stressors (to verify the stressor gradient), including mud content (particles < 63 µm), sediment nutrient content (NUT, total nitrogen (TN) and phosphorus (TP) loading), and sediment heavy metal contamination (HM, copper, Cu; lead, Pb; zinc, Zn).

Three sets of sediment cores were collected. Each set consisted of five sediment cores (Ø 2.5 cm x 2 cm depth) that were pooled to account for spatial heterogeneity and homogenised into one composite replicate. One set was collected from each ambient and translocation plot and stored in the dark at -20 °C for analysis of sediment grain size distribution, organic matter content (OM), and microalgal pigment concentrations (chlorophyll *a*, phaeophytin, four replicates). The second set of samples (four replicates) were taken within each ambient plot and kept cool to analyse sediment heavy metal concentrations. The third set of samples (two replicates) were collected from the area around the plots for sediment nutrient content analysis (TN, TP).

Analysis for sediment parameters have been explained in detail in Chapter 2 & 3. Briefly, to determine sediment grain size, samples underwent pretreatment with 10% hydrogen peroxide over a period of three weeks to remove organic matter. Particles larger than 4 mm were removed using a sieve and Calgon (sodium polymetaphosphate) was added as a dispersing agent (Singer et al., 1988). Grain size distribution was then measured using a Malvern Mastersizer 3000 laser diffraction particle size analyser (Malvern Panalytical). For organic matter (OM) analysis, samples were dried at 60°C for 24 h and subsequently combusted at 550°C for 4 h in a Thermo Scientific Type 6000 muffle furnace (Thermolyne, Thermo Fisher). The percentage of organic matter was calculated using the loss-on-ignition method, based on the difference in mass before and after combustion. Analysis for chlorophyll *a* (chl *a*) and phaeophytin (phaeo) involved freeze-drying the sediment using a Lyovapor L-200 freeze dryer (Büchi, Switzerland; operating at 2 mbar pressure and −50°C), followed by weighing and extraction in 90% buffered acetone (for 20 - 23 h). Fluorescence of the extracts was measured using a Turner Designs 10-AU fluorometer, both before and after acidification with 1 M hydrochloric acid (Arar and Collins, 1997).

Sediment nutrient samples were dried at 35°C, sieved to obtain the < 2 mm fraction and digested with nitric/hydrochloric acid. TN was assessed after catalytic combustion (900°C, O_2) separation and a Thermal Conductivity Detector (Elemantal Analyser, Hill Laboratories). Total recoverable phosphorous was retrieved from an Inductively Coupled Plasma Mass Spectrometry, (ICP-MS, Martin, Creed and Brockhoff, 1994), Hill Laboratories). For further gradient calculations, raw nutrient values were used even though the values were close to detection limits (TN: 500 mg kg^{-1} dry wright, TP: 40 mg kg^{-1} dry weight). Sediment heavy metal concentrations were determined via reverse Aqua Regia digestion after being dried at 50 °C and run on an ICP-MS (Quantitation Limit: Cu = 0.1 µg L^{-1}, Pb = 0.1 µg L^{-1} and Zn=1 µg L^{-1}). Heavy metal concentrations were expressed in parts per million (mg kg^{-1}).

4.2.3 Tissue heavy metal burdens

Heavy metal accumulation in translocation (collected at d 0, and on d 85) and ambient (collected on d 85) *A. stutchburyi* tissue was analysed via digestions. Approximately 2 g (randomly chosen individuals) of wet weight tissue per replicate was weighed into 50 mL tubes. Samples were freeze-dried with liquid nitrogen in a Buchi Lyovapor L200 at -57 °C for four days and re-weighed to obtain dry weight. Each sample received 2 mL of tetramethylammonium hydroxide (TMAH) and was heated in a 60 °C water bath until tissue was dissociated. After cooling, 0.5mL of > 30% H_2O_2 was added for oxidisation in the fridge overnight. Subsequently, 2 mL of 70% HNO_3 was added to each sample under heated conditions, then re-cooled and diluted to full volume (50 mL) with 0.2% cysteine solution. 10 mL of the solution was filtered through a 0.45 µm Sartorius Minisart filter of which 1 mL was extracted and added to a 15 mL centrifuge tube diluted with 0.2% cysteine solution. Quality control was ensured via two method blanks (no tissue added), two samples of TORT-3 Lobster Hepatopancreas (National Research Council Canada, Willie *et al.*, 2013) certified reference material, and two water blanks (Milli-Q ultrapure water). All samples were processed with an ICP-MS and tissue heavy metal concentrations were expressed as µg g^{-1} dry weight.

4.2.4 Retention (translocation survival)

Austrovenus stutchburyi were hand-collected from each source population during low tide (water height 0 – 20cm above seafloor) into large tubs which were filled with ambient seawater and regularly re-filled to ensure oxygenation of the water. To check that the source population animals had similar levels of health and would not account for differences in retention 100 individuals were randomly picked out of the water bath from each source population on the day of translocations and frozen to subsequently calculate overall ambient density (ind. m^{-2}), and ambient biomass (g m^{-2}).

On d 85, at the end of the experiment, sediment from the centre of each ambient plot (0.25 x 0.25 m^2 or 0.5 x 0.5 m^2 depending on *A. stutchburyi* densities) was extracted to about 8 cm depth and sieved on a 4 mm mesh for collection to estimate ambient *A. stutchburyi* densities. To quantify the overall retention of translocated *A. stutchburyi,* all four replicates of 1 m^2 +AS plots were thoroughly finger-ploughed for live and dead shells. Size and colouration of translocated individuals were markedly different than ambient individuals at all sites and could be easily differentiated (Table 4.1, Figure A4.1). Densities of +AS plots were checked against ambient to avoid misclassification. Live translocated *A. stutchburyi* were photographed on trays in situ to assess retention. Counts and sizing were done on ImageJ (Schneider, Rasband and Eliceiri, 2012). All translocated dead *A. stutchburyi* shells (but intact on the hinge) were counted in situ to calculate the overall number of *A. stutchburyi* accounted for from the translocations. All live *A. stutchburyi* were then released. I further refer to this response variable as *A. stutchburyi* retention rather than survival because survival and out-migration cannot be differentiated.

The condition index (CI) for ambient individuals was calculated to see whether the environmental gradient was correlated with *A. stutchburyi* population health parameters (CI, density, shell length). Ash-free dry weight (AFDW) from all individuals collected from source (d 0) and ambient (d 85) plots was calculated (dried at 60°C and combusted for 4h at 550 °C). The CI (Boscolo, Cornello and Giovanardi, 2003; Zeng and

Yang, 2021) was calculated by the ratio of AFDW to total estimated shell volume (Eq. 4.1):

$$CI = \frac{AFDW}{\left(\frac{\pi\,\mathrm{SL\,W\,H}}{6}\right)} \times 100 \qquad \text{Eq. 4.1}$$

where SL is the shell length (mm), W is the shell width (mm), H is the shell height (mm), (estimating the total volume of *A. stutchburyi*, assuming the shape of an ellipsoid, (Davenport and Chen, 1987), and AFDW (in mg).

Biomass (g m^{-2}) was calculated for ambient samples by multiplying the mean AFDW of sampled *A. stutchburyi* from each ambient plot with the abundance per unit of area. There were no differences in the initial mean CI between source populations before transplanting (Kruskal-Wallis chi-squared = 4.7844, df = 2, p-value = 0.091) indicating source populations were similarly healthy. Shell length was 8% larger (~ 2 mm) in TUAP compared to REA and ATH (Kruskal-Wallis chi-squared = 71.197, df = 2, p-value <0.001), but all were larger (and clearly identifiable due to colour) than ambient individuals from translocation sites (Table 4.1).

4.2.5 Proxies for ecosystem function

4.2.5.1 Benthic incubation chambers

To estimate rates of ecosystem productivity and carbon flux, benthic incubation chambers were used to measure sediment-water oxygen fluxes during a mid-day high tide. One transparent (light) and one darkened dome-shaped plexiglass chamber (0.0016 m^2, containing 0.85 L of seawater above the sediment surface) were inserted approximately 10 mm into the sediment underwater on an incoming tide in each plot, ensuring that no air bubbles remained in the chamber (Bulmer et al., 2017). Dissolved oxygen (DO) flux was measured in light and dark chambers representing the presence and absence of photosynthetic activity by microphytobenthos, respectively. Light chambers represent net primary production (NPP, photosynthesis and community respiration, µmol O_2 m^{-2} h^{-1}), whereas dark chambers represent total community respiration as sediment oxygen consumption (SOC, oxygen utilisation only, µmol O_2 m^{-2} h^{-1}, (Pratt et al., 2014). The incubations commenced when the tidal height reached ~30 cm and the initial (C_{initial}) sample was taken with a 60 mL syringe via plastic tubing attached to each chamber after rinsing the tube to access chamber water. After an incubation period of approximately 5 h the final water sample (C_{end}) was collected. All chambers were sampled within 5 min of each other. Three 1 L light and darkened bottles were also filled with ambient seawater during initial sampling and anchored to the sediment surface to assess the influence of water column processes on the production of oxygen by water column phytoplankton. However, bentho-pelagic exchange rates were negligible and therefore not included in the analysis. DO measurements were conducted directly after collection using a calibrated optical dissolved oxygen and temperature meter (YSI ProSolo ODO/CT, YSI Xylem, Yellow Springs, OH, USA). Oxygen fluxes were calculated as (Eq. 4.2):

$$Oxygen\ flux = \frac{(C_{final} - C_{initial}) \times V}{A \times \Delta \mathrm{t}} \qquad \text{Eq. 4.2}$$

Where C represents the oxygen concentration (µmol/l) at the beginning ($_{initial}$) and end ($_{final}$) of the chamber enclosure, V = volume of seawater inside the chamber (L), A = area of sediment enclosed by the chamber (m^2), Δ t = Time between initial and final sampling (h).

Benthic incubations were not successful in translocation plots at two sites (BOW, PUN only dark chambers affected), likely due to *A. stutchburyi* preventing chambers from sealing at the base, and were hence excluded from analysis for NPP (included for PUN), and SOC. The site URE yielded only two replicate +AS measurements which were included in the analysis.

Photosynthetically active radiation (PAR) was recorded on land and on the seafloor for the duration of each incubation with individual PAR loggers (Odyssey PAR sensor) to account for differences in light attenuation on each sampling day. Only one replicate value of salinity was recorded during sampling in April from the first syringe collected (Table 4.1).

4.2.5.2 Rapid organic matter assays (carbon degradation)

To assess rates of carbon degradation I measured rates of organic matter degradation at different sediment depths, using rapid organic matter assays (ROMA, O'Meara, Gibbs and Thrush, 2018). The acrylic plates (180 x 90 mm) have 18 wells of 0.9 mL volume each arranged in three columns and are separated along the vertical profile at 1, 3, 5, 7, 10, and 15 cm from the top of the plate. A mixture of food grade agar, microcrystalline cellulose (CAS 9004-34-6; Thermofisher), and powdered bran flakes (Edmonds) was filled into each well representing approximately 0.026 g C mL^{-1} (O'Meara, Gibbs and Thrush, 2018). A 25 µm nylon mesh screen was used to exclude macro- and meiofauna from accessing the wells. In the field, once the incubation chambers were removed, one ROMA plate was inserted into each ambient and transplant plot (n=4). ROMA plates were retrieved during sediment sampling one week later after being incubated for 7 d (PUN only 6 d).

As an integrated proxy of carbon consumption by both infauna and microbially driven mineralisation processes, I calculated the mean carbon degradation rate (g C m^{-2} day^{-1}) from the volume of substrate lost from each well during a seven-day incubation within the upper 0–5 cm of surface sediment (hereafter referred to as CD, (O'Meara, Gibbs and Thrush, 2018). This depth range was selected because the top 5 cm of sediment typically exhibit the highest rates of mineralisation, contain most of the labile carbon still present in the system, and represent the most biologically active layer (Thomson et al., 2024). This zone also supports high densities of benthic macrofauna and corresponds to the sediment layer bioturbated by *A. stutchburyi* (Morton and Miller, 1973; Powell, 1979).

4.2.6 Data analysis

4.2.6.1 Multiple stressor gradient

To assess the effect of the stress level of the nine sites on translocated *A. stutchburyi*, a principal component analysis (PCA) was used to generate a single variable that would characterise an overall gradient corresponding to increases in the concentrations of combined stressors in the field, similar to the approach used by Hewitt, Anderson and Thrush, (2005), Hewitt et al., (2009), and Rodil et al., (2013). The PCA was performed on the log-transformed mud, nutrients (TN, TP), and heavy metal concentrations (Cu, Pb, Zn), where the first orthogonal axis (PC1 axis) explained 69.4% of the variance (Figure A4.2). This overall contamination gradient was used to calculate a mean value for each site where healthier sites were closer to -4 and less healthy sites closer to +4 (Figure 4.1B, Table 4.1). This gradient was subsequently used in the univariate analyses.

4.2.6.2 Statistical analysis

To assess the correlation between the stress gradient and ambient *A. stutchburyi* health parameters (CI, SL, density), and to evaluate the influence of the stressor gradient on *A. stutchburyi* retention, and the effect of the +AS treatment on benthic ecosystem functioning, I applied univariate and multivariate statistical analyses.

Using Spearman's rank correlation tests (appropriate for data with low replication), correlations were fitted between 1) the combined stressor gradient, individual stressor gradients, and ambient *A. stutchburyi* health, as well as sediment heavy metals and tissue burdens, and 2) retention densities and the stressor gradient. Correlations between sediment contamination (TN, TP, Cu, Pb, Zn) and sediment variables (mud, median grain size, organic matter content) were plotted using the *corrplot* function in R (Figure A4.3, Friendly, 2002). TN and TP were combined for the multivariate analysis (distance-based linear models, DistLM) into a "Nutrient" gradient (based on a PC1 score explaining 89.2% of the variance) due to their high correlation (0.79, see Figure A4.3, approach used by Hewitt et al., 2009; Rodil et al., 2013; Tremblay et al., 2017 with heavy metals).

Permutational analyses of variance (PERMANOVA) (Euclidean distance) with 9999 permutations (Anderson, Gorley and Clarke, 2008) were used to test sediment variables and proxies for ecosystem productivity for a +AS treatment effect across sites. Each model included site (9 levels) and treatment (2 levels) as fixed factors. If functions differed among treatments and sites of varying health, I expected to detect this through the time × treatment interaction term (significance at a p(perm) < 0.05). Main effects were not considered in the event of a significant site × treatment interaction ($\alpha < 0.05$) and a post-hoc pair-wise test was performed to identify treatment effects at each site. Pairwise comparisons were not performed on a significant site term due to the interest in only the treatment effect across the gradient.

Proxies for ecosystem functions related to carbon cycling and ecosystem productivity were evaluated using directly measured proxies NPP, SOC, degradation of photosynthetic products (chl *a*:phaeo ratio), and sediment organic matter degradation CD. The ratio of chlorophyll *a* to phaeophytin in surface sediments was used as an indicator of autotrophic organic matter turnover, or the relative 'freshness' of the organic material, an attribute influenced by processes such as grazing and cell degradation (Bianchi et al. 1988; Ford and Honeywill, 2002).

Lastly, in order to assess how high the level of retention needs to be to affect proxies for ecosystem functions, the top four sites (> 44% Retention) were used to test the effects of translocations on functional responses using a PERMANOVA (as above). Each model included treatment (2 levels) and site (4 levels) as fixed factors. No interaction terms were detected, hence no pair-wise post-hoc tests were performed.

The map (Figure 4.1) was created with ArcGIS Pro (ESRI, 2025) and CorelDRAW (CorelDRAW Graphics Suite RRID:SCR_014235), all other figures (except Fig. A4.2) were generated in R Studio using ggplot2 (R Core Team, 2024), and Figure A4.2, PERMANOVA and DistLM (dbRDA) analyses were conducted in PRIMER-e version 7 with the PERMANOVA+ add on software (Anderson, Gorley and Clarke, 2008).

4.3 Results

4.3.1 Environmental gradient, ambient *A. stutchburyi* health, and temperature

Sediment mud content, TN, TP, Pb, Cu, and Zn content varied across sites (Table 4.1). Although concentrations of heavy metals were well below the Australian and New Zealand Environment and Conservation Council Interim Sediment Quality Guidelines (Pb = 50 mg/kg, Cu = 65 mg/kg, Zn = 200 mg/kg, (ANZECC, 2000)), differences in stress could be discerned and a gradient was established (Figure 4.1B). Mean mud content of sites ranged from 4.67 (MOA) – 23.09% (OMO), TN did not exceed 600 mg kg^{-1}, TP ranged between 84.23 (BOW) – 163.86 mg kg^{-1} (PUN), Cu did not exceed 1.14 mg kg^{-1}, Pb ranged between 1.53 (BOW) – 3.45 mg kg^{-1} (PUN), and Zn ranged between 6.18 (MOA) – 19.33 mg kg^{-1} (WAI).

Ambient *A. stutchburyi* densities were neither influenced by the overall gradient nor individual stressor levels, whereas biomass decreased with increasing mud (21.29 g m^{-2} in low mud MOA to 0.82 g m^{-2} in high mud OMO), with increasing nutrients (low NUT 23.69 g m^{-2} BOW – high NUT 7.32 g m^{-2} TUAE), and with increasing HM (low HM MOA - 0.40 g m^{-2} URE). Ambient CI decreased with increasing mud gradient (1.9 MOA – 1.3 OMO), whereas the shell length decreased with the overall contaminant gradient (MOA

17.34 mm – PUN 13.95 mm) and each individual gradient (NUT: low 15.86 mm BOW – high 13.95 mm PUN, HM: MOA - PUN, Table 4.1, 4.2).

Sediment temperature (mean, median, max., min.) was similar across sites with minimal variation throughout the 85 d period (Table A4.2).

Table 4.2 Summary of Spearman's Rank Test results showing the relationship between ambient *A. stutchburyi* health metrics and overall stressor gradient and individual stressor gradients. S = sum of squared differences, assessment of monotonic relationship using Spearman's rho (ρ) indicating the strength of the relationship (0 = no difference, 1 strong positive, -1 = strong negative relationship), significant terms are indicated in bold. Nut = nutrient, HM =heavy metal.

Variable	Predictor Variable	S	rho	p
Ambient Density	Gradient	62389	-0.003	0.979
	Mud	68401	-0.1	0.404
	Nut gradient	66321	-0.066	0.580
	HM gradient	72701	-0.169	0.156
Ambient Biomass	Gradient	74242	-0.194	0.103
	Mud	77659	-0.249	**0.035**
	Nut gradient	77656	-0.249	**0.035**
	HM gradient	82487	-0.326	**0.005**
Ambient CI	Gradient	9765.6	-0.257	0.131
	Mud	10706	-0.378	**0.024**
	Nut gradient	9443.7	-0.215	0.207
	HM gradient	9733.4	-0.253	0.137
Ambient shell length	**Gradient**	11544	-0.486	**0.003**
	Mud	10992	-0.415	**0.013**
	Nut gradient	10353	-0.332	**0.048**
	HM gradient	10409	-0.340	**0.043**

4.3.2 *A. stutchburyi* tissue heavy metal burden

HM tissue burdens were recorded in ambient (d 85) and translocation (d 0, d 85) *A. stutchburyi*. On average translocated *A. stutchburyi* had lower heavy metal burdens than ambient animals (Table A4.4). Cu burdens in tissue were between 7 - 52% lower in translocation compared to ambient individuals, with the exception of Cu concentrations at PUN that were 32% higher in translocated individuals. Pb concentrations were between 51 – 100% lower compared to ambient individuals. Zn concentrations were between 0 - 35% lower in translocated compared to ambient tissue burdens. There was no correlation between sediment metal loading and translocated *A. stutchburyi* for Cu (p = 0.444), nor Zn (p = 0.60) and lead showed a significant decrease in tissue concentration with increasing sediment Pb concentrations ($p < 0.001$) likely due to the high variability in very low tissue burdens (< 0.2 µg g $^{-1}$ DW).

4.3.3 Translocation Retention

I successfully translocated and observed partial retention of *A. stutchburyi* in all 9 sites across the Tauranga Harbour. Retention rates varied from 28 - 75% with levels of retention fluctuating across healthier and less healthy sites (Table 4.3). The maximum increase of *A. stutchburyi* densities was observed in sites RAN, URE, OMO (>500% increase compared to ambient) and TUAE and MAT (~95% increase). One site showed high numbers of dead shells within plots (OMO, 52% of initially transplanted *A. stutchbury*i numbers), whereas at all other sites dead shells accounted for only 1-9% of initial numbers. Sites with the highest retention were MOA, TUAE (north), URE (central), and RAN (south). Lowest retention was detected at sites BOW, PUN, and WAI (northern, central, and southern harbour respectively).

Translocation retention density was not affected by the overall contaminant gradient, mud, nutrients, or ambient *A. stutchburyi* densities (Table 4.4). Only the heavy metal gradient was negatively correlated with retention densities (S = 10647, rho = -0.37, p = 0.026), which may have been driven by the stronger negative correlation of retention with Zn concentrations (S = 11608, rho = -0.49, p = 0.002) compared to Pb (marginal influence, S = 9475.3, rho = -0.22, p = 0.19) and Cu (S = 9038.5, rho = -0.16, p = 0.34, Figure 4.2, Table 4.4).

Table 4.3 Summary of *A. stutchburyi* translocation survival metrics across sites showing mean values and ranges in brackets for individual and shell counts.

Site	**Source population**	**Stressor gradient value (PC1)**	**Live *A. stutchburyi* retained after 3 months (ind. m^{-2})**	**Percentage retention (%)**	**Translocation successful for ecosystem productivity analysis**	**Dead shell within plot (ind. m^{-2})**	**Mean percentage of dead shell (%)**	**Mean accounted for from 800 individuals translocated (%)**	**Post-addition density (ind. m^{-2})**	**Mean % increase from ambient density (%)**
MOA	ATH	-3.35	550 (490-609)	69%	x	72 (58-93)	9%	78%	1294	77
BOW	ATH	-2.33	301 (202-353)	28%		27 (20-35)	4%	41%	1405	30
MAT	REA	-1.44	294 (278-312)	37%		20 (12-33)	3%	39%	642	95
RAN	REA	-0.54	392 (325-439)	49%	x	42 (14-75)	9%	54%	397	>1000
WAI	REA	0.13	231 (216-241)	29%		15 (12-16)	2%	31%	541	77
URE	TUAP	1.61	352 (298-406)	44%	x	12 (10-17)	1%	46%	365	>1000
OMO	TUAP	1.55	345 (326-374)	42%		332 (251-413)	52%	85%	410	561
TUAE	TUAP	1.90	601 (546-678)	75%	x	69 (46-84)	6%	84%	1228	97
PUN	TUAP	2.48	226 (182-298)	28%		11 (5-19)	1%	30%	2018	13

Table 4.4 Summary of Spearman's Rank Test results showing the relationship between *A. stutchburyi* retention metrics and overall health gradient and individual stressor gradients and ambient population metrics. S = sum of squared differences, assessment of monotonic relationship using Spearman's rho (ρ) indicating the strength of the relationship (0 = no difference, 1 strong positive, -1 = strong negative relationship), significant terms are indicated in bold. Nut = nutrient, HM =heavy metal.

Variable	**Predictor Variable**	**S**	**rho**	**p**
Retention Density	Gradient	8904.7	-0.146	0.395
	Mud	7397	0.048	0.781
	Nut gradient	7778	-0.001	0.995
	HM gradient	10647	-0.370	**0.026**
	Copper	9038.5	-0.163	0.341
	Lead	9475.3	-0.220	0.198
	Zinc	11608	-0.494	**0.002**
	Ambient Density	8737.2	-0.125	0.47

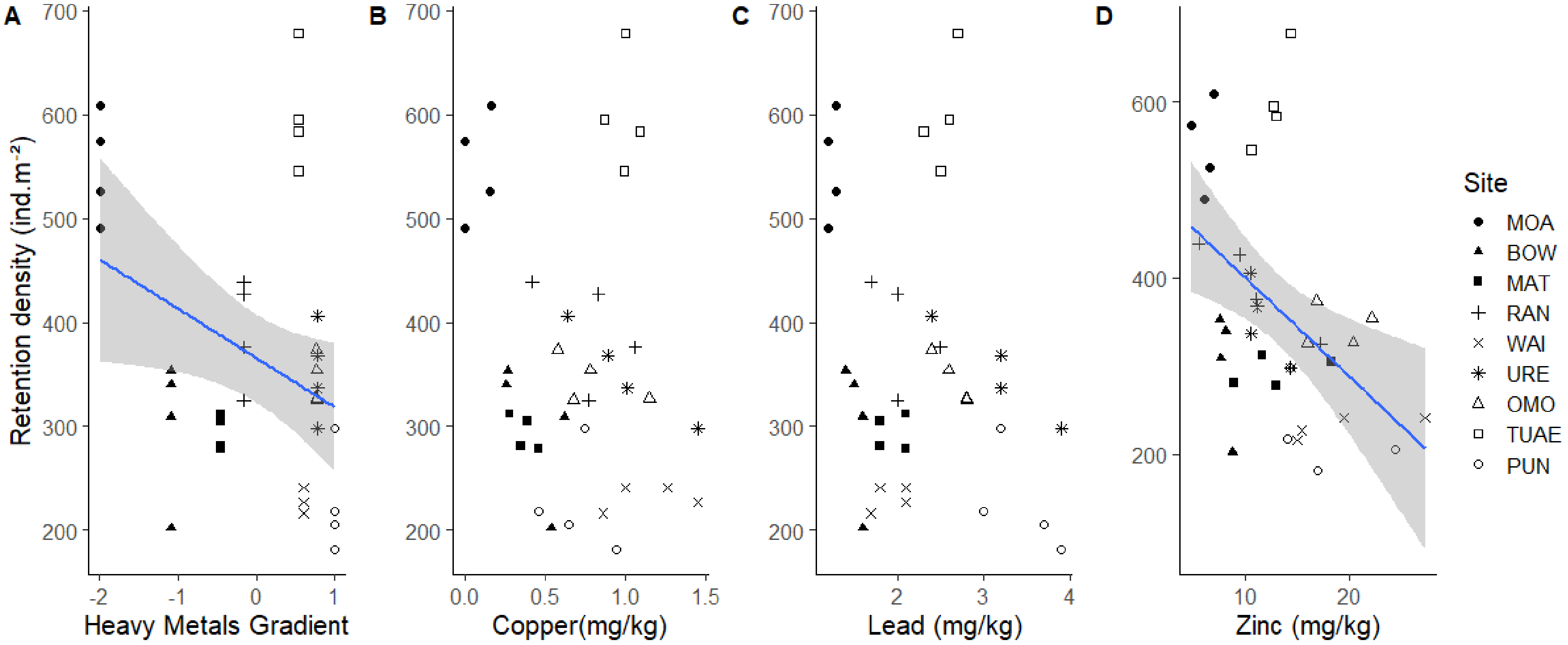


Figure 4.2 Relationship between retention density of translocated *A. stutchburyi* and **(A)** the heavy metals gradient, raw values of **(B)** copper (Cu), **(C)** lead (Pb), and **(D)** zinc (Zn), individually. Relationships that show a best-fit line were returned significant from the linear model.

4.3.4 Effects of treatment on sediment and proxies for ecosystem functions

4.3.4.1 Sediment properties

Sediment properties varied between sites but did not differ between +AS treatments and ambient plots (Table A4.5). Median grain size ranged from a mean of 143 µm (fine sand at TUAE) - 411 µm (medium sand at MAT, (Wentworth, 1922)) and organic matter content ranged between 1.66% (BOW) - 3.95% (URE). Chl *a* and phaeo content ranged between 9.98 (BOW) - 28.61 µg g dw^{-1} (MAT) and 0.87 (RAN) - 4.16 µg g dw^{-1} (TUAE), respectively, contributing to a chl *a*:phaeo ratio ranging between a mean of 4.53 (TUAE) - 35.17 (MAT).

4.3.4.2 Ecosystem productivity

While there were differences between sites for all proxies for ecosystem productivity, there was no treatment effect of +AS on the measured functions (Table A4.6), except for NPP. However, the interaction effect for NPP was driven by only one site (RAN). As low *A. stutchburyi* retention may have masked a potential treatment effect, a subsequent test included only the top four sites in which retention was highest (> 44%). In these four sites I detected moderate evidence of a +AS treatment effect on NPP, SOC, and CD. Mean NPP was decreased by 62% (PERMANOVA, df = 1, Pseudo-F = 7.7835, p-value = 0.016), whereas mean benthic metabolism (SOC, PERMANOVA df = 1, Pseudo-F = 5.2315, p-value = 0.04) and mean organic matter degradation (CD, PERMANOVA, df = 1, Pseudo-F = 6.0725, p-value = 0.021) were enhanced by 24%, and 23% in +AS treatments compared to ambient, respectively (Figure 4.3). The chl *a*:phaeo ratio was not affected by the treatment (PERMANOVA, df = 1, Pseudo-F = 0.8112, p-value = 0.347).

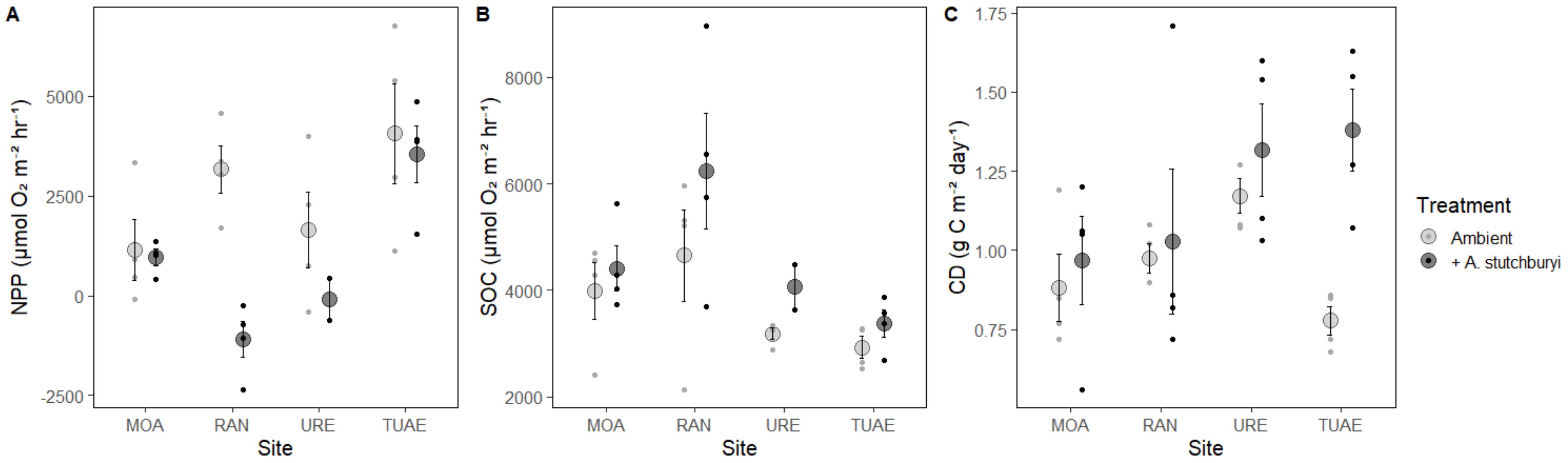


Figure 4.3 Selected proxies of ecosystem productivity **(A)** net primary productivity, **(B)** sediment oxygen consumption, and **(C)** carbon degradation across four sites in which translocations were > 44% and treatment (ambient, +*A. stutchburyi* additions). Large points represent mean values with error bars (± standard error) and small points show the underlying data values

4.4 Discussion

Translocations of bivalves across a gradient of stress within the Tauranga Harbour were successful. Although well below health guideline thresholds, mainly the level of heavy metal contamination was correlated with decreased retention. Interestingly, sites with low ambient densities of *A. stutchburyi* showed high potential for successful translocations. Although I detected no treatment effect of translocations on ecosystem productivity measures overall, in four sites that supported high retention of translocated clams, the intervention moderately affected benthic productivity. This may show promise for future soft sediment restoration to improve ecosystem functioning.

4.4.1 Ambient *A. stutchburyi* health across the environmental gradient

Along the gradient, smaller *A. stutchburyi* were found at sites with higher stress. Individual stressors were negatively correlated with biomass and CI but were not correlated with density. Variable bivalve density and health parameters for New Zealand species in response to environmental stressors, like increased mud or hypoxia, have been discussed previously (Norkko et al., 2005; Hewitt and Norkko, 2007; Salmond and Wing, 2022; Lam-Gordillo et al., 2024). Here I show that *A. stutchburyi* densities persist at sites of overall higher chronic stress which provide important opportunities for future restoration efforts in degraded parts of the estuary. At the same time moderately stressed sites showed reduced numbers of *A. stutchburyi* where translocations may effectively boost populations.

4.4.2 Retention success and its drivers

Austrovenus stutchburyi density in translocation plots was enhanced across all sites (as in Cummings et al., 2007) after three months, with the biggest change in medium to more degraded sites with minimal to low (< 100 ind m^{-2}) ambient *A. stutchburyi* densities. Sites with low (< 30%) retention were present in the northern, central, and southern part of the harbour ruling out a wider spatial effect. Given that medium health sites retained the most clams, such sites may provide the conditions for clams to have the highest impact in terms of kickstarting ecosystem function and may prove best for restoration. Effects of high conspecific density on the health (growth) of bivalves are well known, reduced growth being caused by food limitation, space, and interference (Smaal and Haas, 1997; Azouzi, Bourget and Borcard, 2002; Beal, 2006; Gagné et al., 2008). Here, ambient densities had no effect on retention rates. However, ecological feedbacks may play an important role in addition to the environmental gradient effect. It has been suggested previously that the number of species present at the transplant site has variable effects in the retention of transplants; a naturally lower number of ambient species may give more scope for increases to occur, or to be detected (Hewitt and Cummings, 2013).

In line with my hypothesis, healthier sites showed higher survival; however, retention of *A. stutchburyi* during the first three months after translocation appeared to depend on the level of heavy metal contamination, in particular Zn (and to a lesser extent Pb), rather than mud (moderate positive correlation of Zn and mud, 54%) and ambient *A. stutchburyi* health metrics.

Many heavy metals bind to fine sediment particles (Thrush et al., 2013a). Also here, Pb was highly correlated with mud, nutrients and organic matter (Figure A4.3), due to its high rate of precipitation/adsorption in the presence of clay suspensions (CCREM, 1987). The sources of heavy metals differ. Street runoff and industrial and municipal wastewater discharges are main sources of Pb (USEPA, 1976; Jaques, 1985). Zn originates from tyre wear and runoff from galvanised iron roofs, and discharges from municipal wastewater treatment plants (Malle, 1992; Landner and Reuther, 2004). The lower correlation between Zn and mud may explain the higher variability of this element. Contaminated sediments have been shown to cause mortality of large, mobile, bioturbating organisms (Hewitt et al., 2009). Dead shell counts did not correlate with any of the stressors, as only one site showed high dead shell counts (OMO, mean of 332 individuals) compared to the other eight sites (overall mean of 34 individuals counted as dead). This was likely due to OMO's very sheltered location and slow current movement. Zinc toxicity in macrofauna increases with higher temperatures and lower salinity, conditions that enhance Zn bioavailability (Jones, 1975; Bryant et al., 1985; Luoma and Rainbow, 2008). Sites with the highest Zn concentrations (WAI, PUN, OMO) may be affected by increased freshwater runoff which may influence bivalve vulnerability to Zn. This can however not be investigated in this study due to low sample size of salinity measurements. Ambient shell length and biomass were negatively correlated with increasing heavy metal stressors, suggesting that even low-level chronic exposure may reduce *A. stutchburyi* health. Decreased *A. stutchburyi* abundance has been recorded previously in the Tauranga Harbour along an increasing heavy metal gradient (Tremblay et al., 2017). While field observations have linked higher sediment Cu concentrations to lower *A. stutchburyi* abundance (De Luca-Abbott, 2001; Thrush et al., 2008b), a manipulative field experiment found no change in abundance in treatments spiked with Cu, Zn, or a mixture of Cu, Zn, and Pb after 20 days (Fukunaga et al., 2010), possibly due to the limited duration of the study.

Interestingly, I found that translocated individuals after 3 months had lower heavy metal tissue burdens compared to ambient *A. stutchburyi* at all sites except one, which is likely due to shorter exposure time. In contrast, Fukunaga and Anderson (2011) observed that over a 10-day exposure to various treatments of spiked sediments (40-60 mg/kg Cu, 30-95 mg/kg Pb and 133-200 mg/kg Zn) *A. stutchburyi* accumulated Pb and Zn in their body tissues even though no mortality occurred. Their treatments showed however, almost 10-fold higher contamination levels than ambient sediments recorded here. Tissue heavy metal burdens are expected to reflect runoff sources and metal bioavailability (Peake, Marsden and Bryan, 2006), which are influenced by salinity affecting the kinetics of heavy metal accumulation in the tissues (Bryan, Langston and Langston, 1992; Marsden and Rainbow, 2004). Concurrently, a positive relationship between surface sediment Pb and Zn concentrations and *A. stutchburyi* tissues has been previously documented (Marsden, Smith and Rainbow, 2014). Assuming sediment heavy metal loading remained constant over the course of the experiment, findings suggest that tissue burdens of translocated *A. stutchburyi* did not reach ambient levels of heavy metal contamination within three months and were not correlated to ambient sediment metal loading. This warrants further field trials to assess the role of bivalve additions in bioaccumulating/desorbing heavy metals at very low concentrations and their role in potentially altering sediment metal dynamics. Although bivalves and other bioturbating organisms showed no evidence of influencing the heavy metal release from sediments in a broad-scale review (Gonzalez et al., 2019), large, bioturbating species may alter sediment redox conditions (Lenihan et al., 2018), thereby altering metal bioavailability (Amato et al., 2016; Remaili, Simpson and Jolley, 2017).

Heavy metal contamination across the nine Tauranga Harbour sites was within the lower 10% of the Australian and New Zealand Environment and Conservation Council interim sediment quality guidelines thresholds (Cu 1.8%, Pb 6.9%, and Zn 9.7%, ANZECC (2000)) and significantly lower than the Effect Range Low guidelines (Long et al., 1995). Overall, heavy metal concentrations have improved compared to measurements made within the past decade (Ellis et al., 2015; 2017; Tremblay et al., 2017). However, changes in benthic community composition and function have been shown to occur at levels below these thresholds (Hewitt et al., 2009; Lohrer et al., 2012). Field-based species sensitivity distributions, at which 5% of taxa are affected (adjusted for the relative proportion of species that were not sensitive to each metal), predict biological effects at concentrations of 6.5-9.3, 18.8-19.4, and 114-118 mg kg^{-1} for Cu, Pb, and Zn, respectively (Hewitt et al., 2009). My recorded values fall below 20% of these effect concentrations (17.5%, 18.4%, 17.0% for Cu, Pb, and Zn, respectively, Table 4.1). I therefore conclude that, while Zn concentrations emerged as an important variable affecting *A. stutchburyi* retention, other unmeasured factors likely also contribute to reduced bivalve survival after translocation as the harbour can be categorised as a slightly to moderately disturbed system (ANZECC, 2000).

Further research is needed to generate a more generalisable understanding of seeding density and survival relationships across different locations. Notably, *A. stutchburyi* densities decreased slightly in ambient and no addition treatments between 3 months and 1 year in Chapter 2. This may also be a cause in this study, likely due to the varying tolerance of individuals which are adapted to different site conditions and external influences (e.g. predation, limited food supply, heat waves affecting shallower areas, Cummings et al. 2007; Tricklebank et al. 2021; Lam-Gordillo et al. 2024).

4.4.3 Translocation effects on ecosystem function

Across all study sites, no clear relationship emerged between bivalve retention and ecosystem function measures. This is unsurprising, since the retention success was highly variable between sites, three sites being below 30% retention.

However, after isolating the four sites in which translocations were most successful (based on retention rate; Table 4.3), several measures reflecting ecosystem productivity differed in translocation plots compared to ambient conditions. Specifically, net primary productivity was reduced, while sediment oxygen consumption increased, both aligning with findings from Chapter 2. The observed decrease in net primary productivity is mainly attributable to increased SOC in the +AS plots (higher respiration, Chapter 2). Concurrently, higher densities and generally larger *A. stutchburyi,* compared to naturally occurring populations, may have stimulated microbial activity through increased bioturbation and oxygen availability, resulting in enhanced sediment oxygen consumption where clams were added (Chapter 2). Lower net primary productivity may further be attributed to higher grazing pressure of the added bivalves on microphytobenthos (Jones et al., 2017) as well as the limited establishment of MPB due to sediment resuspension by large bioturbating infauna and physical disturbance through the translocation activity (Pillay & Branch 2011). The translocations also facilitated accelerated carbon remineralisation, likely by stimulating microbial activity through increased oxygen availability via bioturbation (Lohrer, Thrush and Gibbs, 2004; Rossi et al., 2008; Gonzalez et al., 2019). While this suggests a loss of organic carbon from these sediments via the remineralisation of detritus, it also reflects the active cycling of carbon and associated nutrients within the ecosystem which is an important aspect of secondary biomass production which (at least partly) retains the carbon within the system (Middelburg, 2018; Zhu et al., 2024). Such microbial stimulation has been shown to be particularly effective in sediment bioremediation, especially in contexts like aquaculture wastewater management (Zhao et al., 2019; Lukwambe et al., 2020). Yet, the very small sample size on which these conclusions are based make further research imperative to provide sufficient evidence for the applicability of *A. stutchburyi* translocations on their effect on fuelling ecosystem productivity.

I want to acknowledge that this study considered retention success on a relatively small spatial (9 sites, 1m^2 plot size) and temporal (three months) scale. Additionally, inundation time, or tidal shore height, has been shown to affect translocation success (Dobbinson, Barker and Jillett, 1989; Stewart, Creese and Lalwnitory, 2002; Cummings et al., 2007). Although this species is found in locations with inundation times of only 3.5 hours, translocations lower on the shore provided better conditions for growth than those higher on the shore, likely due to poorer conditions for food availability and increasing exposure time limiting growth (Larcombe, 1971; Dobbinson, Barker and Jillett, 1989). Even just small differences in tidal height (such as 5 cm out of a tidal range of 2-4 m, meaning 30 minutes less submergence time) showed differences in survival

(Hewitt and Cummings, 2013). I suggest that future retention trials across stressor gradients monitor retention for longer and include measurements of tidal inundation (or time exposed), salinity ranges, physical water velocity and wave regime, and sediment hypoxia into their predictor models. Using markers for the identification of translocated *A. stutchburyi* may have improved my study but was not feasible as translocations occurred as promptly after collection as possible to reduce stress on the individuals.

4.5 Conclusion

These findings underscore the ecological potential of successful bivalve translocation, particularly in enhancing sediment function through bioturbation and microbial stimulation. Improvements in benthic metabolism and carbon degradation suggest that translocated *Austrovenus stutchburyi* could play a valuable role in restoring ecosystem function, especially in degraded or nutrient-enriched soft sediment habitats. At the same time, increasing levels of anthropogenic contaminants present complex challenges for environmental managers (Van Der Oost, Beyer and Vermeulen, 2003). This harbour-wide experiment, conducted along a gradient of moderate environmental stress, contributes to our understanding of the factors influencing retention of adult *A. stutchburyi* following translocation such as zinc, even if present in relatively low sediment concentrations. However, the success of such restoration efforts hinges on whether environmental stressors such as heavy metal concentrations have been sufficiently mitigated to support survival and integration of translocated individuals.

Austrovenus stutchburyi *collections at Waikareao Entrance (Tauranga Harbour), January 2023.*

Chapter 5

Thesis summary and conclusion

5.1 Significance, summary and key findings

The degradation of the natural world is accelerating due to anthropogenic causes. Hence, restoration action is increasingly required to mitigate, halt, or reverse some of the negative effects on coastal ecosystems. The growing need to improve and adjust active restoration requires fine-tuned understanding as to how we can do it in specific sites and with specific species. This thesis contributes to a more comprehensive understanding of how the combination or single addition of endemic bivalve species affect recovery processes after acute (Chapter 2 & 3) and chronic (Chapter 4) stress and how feasible and effective it is, giving valuable insights into which factors to account for in future. It adds to the growing knowledge of ecosystem restoration that will be useful for managers and conservationists.

5.1.1 Thesis summary and key findings

The three complementary research chapters of this thesis provide empirical insights from two manipulative field experiments, into the applicability and feasibility of using *A. stutchburyi* and *M. liliana* as bioremediation species of their surrounding soft sediment habitat (Figure 1.2).

The ability of benthic bivalves, such as clams, to affect ecosystem function of their soft sediment habitat has been extensively documented (Rossi et al., 2008; Sandwell, Pilditch and Lohrer, 2009; Jones et al., 2011; Shen et al., 2017). This knowledge of the ecology of two important local species (*A. stutchburyi* and *M. liliana*) led to the hypothesis that they may be suitable for the functional restoration of degraded soft sediment communities. Moreover, the combination of these two species was thought to improve physicochemical and biological recovery dynamics due to their important, yet contrasting, roles in benthic interaction networks (Thrush et al., 2014).

Chapter 2 was designed to assess the potential of translocated *A. stutchburyi* and *M. liliana* to affect processes of ecosystem function within a disturbed soft sediment environment. I demonstrated that *A. stutchburyi* individually, rather than a combination of both species, can affect recovery of ecosystem functions and that these effects remain detectable after one year despite relatively low survival rates. In accordance with previous studies, *A. stutchburyi* additions enhanced benthic metabolism, ammonium efflux, and reduced the amount of mud present in the surface layer of the plots. These findings provide valuable insights into a key aspect of restoration ecology; the functionality of benthic systems (at least in parts) can be stimulated by bioturbating clams, which is transferable to other species with similar traits to *A. stutchburyi* elsewhere (such as the European cockle *Cerastoderma edule*, Rossi et al., 2008). Ensuring higher survival would likely result in further increased ecosystem productivity and nutrient exchange at the sediment-water interface making *A. stutchburyi* a potential bioremediation species for New Zealand's estuaries after disturbance. Although my findings show how survival trended towards ambient levels and recruitment was observed from the surrounding area, translocations might be more successful if there are recruitment or substrate limitations.

In Chapter 3, I focussed on the role of these two keystone species in facilitating the enhanced recovery of the macrofaunal community from the same disturbance experiment. Moreover, I investigated how the recovery of the community composition represented a recovery of functional traits. I found that the observed variation in the community over time was mainly driven by changes in the relative and absolute abundances of species, rather than species composition or richness. I further found differing effects of the two functionally distinct ecosystem engineers on the recovery of the macrofaunal community with a particular influence on temporary post-disturbance spionid recruitment and bivalve recruitment. The individual species engineered the seafloor system differently after three months; *M. liliana* additions showed higher opportunist spionid tube worm abundances, whereas *A. stutchburyi* only additions circumvented this classic disturbance response. However, interestingly, again no synergistic or additive effects of the combined species treatment on the community recovery were discernible, and after one year the communities were similar across treatments (including the defaunation no addition control). While all defaunated plots compared to ambient showed increased recruitment of *M. liliana* juveniles after three months (with persisting high numbers of juveniles after one year), *A. stutchburyi* juveniles were consistently lower in defaunated plots, and most notably in the *M. liliana* addition treatment. After a year, juvenile abundances approached ambient levels for both species, which indicates successful development of recruitment cohorts. This chapter highlights that *A. stutchburyi* may have the potential for effective short-circuiting of a hysteretic community composition that undergo slow recolonisation with early succession species. It also offers insights into the initial shifts in functional groups after three months and how these may influence recovery, yet, after one year, variations in species compositions across the entire study site were responsible for the overall similar trend in recovery.

In Chapter 4, I assessed the survival of the translocated individuals (translocation success) and their impact on ecosystem functions after three months. I was able to demonstrate that *A. stutchburyi* translocations across a gradient of multiple stressors within a moderately healthy estuary can be successful, albeit retention was variable across sites (between 28% and 75%). Survival was not dependent on the overall (cumulative) stressor gradient, but mainly on the levels of heavy metal contamination (predominantly zinc concentrations) in the sediment. I furthermore showed that successful translocations (if retention > 44%) can affect ecosystem productivity, which was a result of sufficient densities affecting some proxies measured for ecosystem productivity (benthic metabolism, net primary productivity and carbon degradation), but not all. These findings add valuable insight to apply this species as a bioremediation option to degraded parts of the estuary for active restoration trials.

5.1.2 Tīmata whakaora – kickstarting recovery

From a Māori perspective mauri (life force, vital principle) is a concentration of life itself within an entity, of which one component is similar to ecosystem health or a concept of ecosystem functionality which can diminish (Hēnare, 2001; Mead, 2003). Diminished mauri of an ecosystem can be restored through rituals of conservation to ensure that for example depleted food supplies can be abundant again (Hēnare, 2015). Hepburn et al., (2010) summarise that the mauri of the ocean is enhanced or decreased by the actions of people. The mauri of an ecosystem is critical for its wellbeing and hence, its restoration should be of utmost focus.

The restoration of marine ecosystem mauri is increasingly valued and included into western research (Morgan, 2006; Freilich, 2018) and acknowledged in this thesis through restoration of ecosystem function. The overarching aim of this thesis was to answer to hysteresis, an undesirable state of decreased ecosystem mauri, and I conclude that the answer lies in the presence of a taonga species, one that bioturbates the sediment and is simultaneously valuable for the seafloor and the people (Mccarthy et al., 2013). Using large clams for restoration offers not only an opportunity for the soft sediment environment to receive otherwise slow growing adults early on the stages of recovery, where early recolonisation may be altered from slow succession, but using this species may also contribute for inhabitants of the New Zealand coast to directly see changes in population structures over the longer term (see section 5.2.4). The Tīmata Method (kickstart) seems plausible and from what I can conclude here, feasible for restoring parts of the intertidal sand flats (in which the clam *Austrovenus stutchburyi* occur). I suggest taking this investigation further and assess how *A. stutchburyi* affect recovery dynamics in the long run (> 1 year), which may provide local stakeholders (iwi, hapū, councils, community) with more exact data on survival, recruitment and growth rates over time (see sections 5.2.4, 5.3.1).

5.2 Synthesis and future research

With restoration and bioremediation of degraded habitats increasingly becoming a focal point for environmental managers, this thesis identifies several key aspects to be considered for the successful implementation of bivalve translocations for soft sediment rehabilitation. While I could not demonstrate a method for the fast-tracked recovery of the degraded area, my research provides valuable considerations, critical for the successful translocation of live bivalves and provides consistent results regarding their effect on the degraded ecosystem for future trials and estuarine management.

5.2.1 Discrepancies between expectation and observation

The innovative idea behind this thesis was to investigate whether the known functional traits of keystone species can be used to short-circuit succession, thereby kickstarting the otherwise slow recovery process. I specifically chose the bioturbating clam *A. stutchburyi* and the porewater-pressurising wedge-shell *M. liliana* for their contrasting, yet complimentary, traits. Based on our ecological understanding of the species' roles in the ecosystem, I hypothesised *A. stutchburyi* to alleviate oxic depletion in the disturbed sediments, thereby facilitating recolonisation of more oxygen-sensitive species as well as the accelerated turnover of organic material and enhancement of nutrient cycling (Thrush et al., 2006; 2014; Sandwell, Pilditch and Lohrer, 2009; Jones et al., 2011). While I recorded an increase in sediment metabolism after the addition of *A. stutchburyi* (Chapter 2), it is impossible to determine to what extent this was due to the increased number or larger size of translocated clams or the recovering benthic ecosystem. Furthermore, instead of providing a strong faciliatory effect for other species, *A. stutchburyi* presence seemed to inhibit the establishment of early colonising *Spionids* (Chapter 3). If this led to an acceleration of the successional stages was not clear since the communities of all disturbed plots were very similar after one year. However, *A. stutchburyi* consistently altered the nutrient fluxes (Chapter 2) and carbon degradation (Chapter 4), net primary productivity, sediment oxygen consumption (Chapters 2 & 4) where they survived the translocation, highlighting their potential to affect benthic processes in degraded soft sediments.

Similarly, when conceiving the experiment, I expected *M. liliana* to provide accelerated solute exchange, enhance primary production and increase the total number of macroinvertebrate abundance, and taxa (Thrush et al., 1992; Volkenborn et al., 2012; Woodin et al., 2012). However, no distinct effects of *M. liliana* were measures in Chapter 2 and subtle engineering could only be discerned in Chapter 3 (see section 5.2.2).

5.2.2 Community recovery versus functional recovery

Linking ecosystem processes and macrofaunal recovery dynamics is complex, providing a major challenge for assessing restoration efficacy and success. When connecting findings from Chapter 2 and 3, it becomes clear that although large *A. stutchburyi* did affect ecosystem functions through their effect on the sediment biogeochemistry, this may also have been supported by the effect that the community had on the functions. As in a European study, complex processes rather than species function modified the magnitude and direction of observed effects of increased bivalve abundance on sediment biogeochemistry (*Cerastoderma edule*, Rossi et al., 2008). They found that differences in the functional response to the European cockle addition were mediated by the resident fauna composition via indirect effects on other species densities. Therefore, the deliberate addition of bioturbating bivalves will modify not only species composition and abundance but also the relationships between the biogeochemistry and densities of resident species (Rossi et al., 2008).

While I could not clearly delineate how the recovery rate and end point changes after the addition of each individual species to the community recovery in Chapter 3, I found that recovery trajectories are subtly altered in the early stages (3 months) after disturbance. It remains unclear, however, if successional recovery via the recruitment of opportunists will lead to the best succession for complete recovery, or the one where opportunists are circumvented. Polydorid species (as enhanced initially in *M. liliana* addition plots) are known to have facilitative effects in defaunated plots (van Colen et al., 2008), as in high numbers the densely packed tube mats can stabilise and bind the surface sediment (Thrush et al., 1996b), and tube-builders can facilitate recruitment (Gallagher, Jumars and Trueblood, 1983). It would therefore be interesting to further investigate how exactly the addition of *A. stutchburyi* affects the recovery speed and end point to draw a clearer conclusion.

Interestingly though, despite the convergence of macrofaunal community profiles across the disturbed treatments after one year (Chapter 3), the functional profiles remained distinct between treatments (especially the *A. stutchburyi* addition treatments, Chapter 2), suggesting a disconnect between species and functional recoveries in response to bivalve additions. This provides support for my hypothesis that functional recovery may be enhanced by the addition of certain species without it being visible in species diversity. This supports one of the main lines of thought for this thesis, that the functional recovery of soft sediment may be supported by the addition of *A. stutchburyi*. Reintroducing bivalves make a difference to the recovery of ecosystem function, which is an important finding for more research to be based on.

5.2.3 No observed synergism between the two keystone species

Species interactions and faciliatory networks have been demonstrated to increase restoration success, however their role has yet to be effectively integrated into restoration and conservation practices (Halpern et al., 2007; Silliman et al., 2024). I expected successful restoration to hinge on kickstarting facilitatory biological feedback loops by the interacting activities of both species. Contrary to my expectations the additions of both bivalves did not show any additional effects compared to individual additions (Chapter 2 & 3), a finding that leaves a gap for further investigations to fill. Although no combined effects were discerned, both species individually influenced recovery of the community composition in their own way, while only *A. stutchburyi* showed an effect on functional recovery from the variables I recorded (Chapter 2). Clear conclusions about the benefits of multi-species restoration could however not be drawn from my findings, especially because only site-scale changes in abundance drove recovery patters (certain taxa increased or decreased across all treatments), rather than treatment specific bivalve addition effects on different parts of the trait-based community (Chapter 3). It will be particularly interesting to zoom in on other multi-species facilitatory dynamics for ecosystem restoration, such as bivalve - microbe - microalgae dynamics (Ma et al., 2015; Shen et al., 2017; Liang et al., 2024), as this would provide a clearer picture on smaller-scale feedbacks in soft sediments, that may be more important in underpinning functional recovery in early recovery stages.

5.2.4 The important consideration of scale

Small-scale experiments in time and space, like experiment 1 (Chapter 2 & 3), are attempts to understand processes in nature by controlling as many environmental variables as possible (Hewitt et al., 2007). In contrast, Chapter 4 was an attempt at scaling up to approach estuary-scale dynamics in restoration. Given these differences, the nature of these experiments needs to be discussed in context of the naturally complex and scale-dependent ecosystems in which they were conducted (Hewitt et al., 2007). Field studies of benthic communities show that the rates and patterns of recovery are often non-linear, environmentally variable and scale-dependent (Norkko et al., 2006; O'Meara, Hillman and Thrush, 2017) and influenced by site-specific environmental factors (Zajac, Whitlatch and Thrush, 1998; Thrush et al., 2003). I need to acknowledge that ecosystem functioning experiments are difficult to perform as they involve measuring interactions between various bio-geo-physico-chemical process and different elements of biodiversity (Shen et al., 2016). Therefore, variability in ecosystem dynamics is to be expected, as they are natural phenomenon derived from interactions between environmental factors, natural-history characteristics and relative mobility of different taxa (Norkko et al., 2010). Soft sediment recovery can in many cases be observed on time scales feasible for scientific projects to capture (Thrush et al., 2008b; van Colen et al., 2009), which shows promise for this practice to be sufficiently tested before large-scale applications were to be realised (Fitzsimons et al., 2020). Although I detected significant effects within my experiments that are relevant for our understanding of restoring soft sediments, their low statistical power should be addressed, and future trials would benefit from increased sample size. Drawing from conclusions of this thesis, I suggest for a longer experimental time frame (> 1 year, monitoring of retention, functioning, and changes in the environment) as well as the application of larger spatial patches (16 m^2 as in Montserrat et al., 2008; Jones et al., 2011), to test ideal translocation patch sizes. The size of experimental plots may have influenced recovery by determining the extent to which species could recolonise from adjacent sediment versus recovery being dependent on recruitment and might therefore influence the applicability of my results for larger-scale management interventions. The above will help gain a real understanding of how to revive parts of the harbour, to see effects over time, and evaluate how long it takes before functional / harvestable populations reestablish.

5.2.5 Confounding observations and limitations

Although findings from the two experiments were enlightening, I can identify shortcomings, in particular one primary missing piece; physical processes were not measured sufficiently in experiment 2 (Chapter 4) to extract further causes for retention success. Future research should include measurements of inundation time (tidal height) of each translocation plot, water movement of the site, and individual salinity measurements into their retention analysis. Parameters such as tidal height with inundation times and concomitant food availability (Dobbinson, Barker and Jillett, 1989; Stewart, Creese and Lalwnitory, 2002; Cummings et al., 2007) are important factors to consider when designing restorative actions. Wave action and tidal flow parameters may yield insights into the amount of physical force the transplant have to withstand, compared what they were used to.

A site-specific, adaptive approach is needed to go forward as I increase our understanding of the limiting factors within differences in hydrology, sediment and nutrient dynamics, or predator pressure of each estuary ("Know the system you are working in" Fitzsimons et al. (2019)). For example, I show that *A. stutchburyi* additions to defaunated sediments enhance nutrient flux (in particular nitrogen in the form of ammonium, Chapter 2) and can be successfully used for translocations across an environmental stress gradient (Chapter 4). However, it is important to consider the level of nutrient input into the system that is targeted for restoration. In nutrient-rich (eutrophic) systems, additional ammonium release could further fuel phytoplankton blooms or nuisance macroalgae. Therefore, adding ammonium-enhancing bivalves to these areas might be counterproductive unless carefully managed and combined with nutrient input reduction strategies. In eutrophied estuaries, bivalve translocations may need to focus on filter-feeding species or those supporting denitrification. However, translocation of ammonium-enhancing bioturbators like *A. stutchburyi* into oligotrophic environments may be beneficial thanks to their ability to indirectly support denitrification by stimulating coupled nitrification/denitrification processes in oxygenated sediment layers, thereby enhancing the benthic nitrogen cycle (Douglas et al., 2017). Denitrification was measured for Chapter 2, however, only the last sampling time (d 389) returned viable results (denitrification values above zero, and no negative numbers). There were no differences between treatments after one year. As this attempt at connecting the dots between the ability of bivalves to affect the critical ecosystem function denitrification after disturbance was unsuccessful here, it should be re-attempted in future translocation field trials.

5.3 Considerations for future *A. stutchburyi* translocations

My findings, corroborated by the literature, indicate that translocations of local bivalves represent a suitable option for estuarine restoration, as long as their prolonged survival is ensured (Cummings et al., 2007; Fitzsimons et al., 2019; Overton et al., 2024). Therefore, based on the knowledge that clams and cockles are useful for bioremediation, are robust, large-growing, long-lived *(A. stutchburyi* reach a size of ~ 30 mm after only 6 - 8 years, and live up to 20 years, McKinnon, 1996), and provide enhanced ecosystem productivity (Chapter 2 & 3, Rossi et al., 2008). I propose that further trials are conducted with this species.

Austrovenus stutchburyi used in translocations can be sourced from existing populations or from hatchery stocks (Peterson, Summerson and Huber, 1995 with *Mercenaria mercenaria*; Stewart, Creese and Lalwnitory, 2002; Cummings et al., 2007). The first option is viable (this thesis). Source populations need to be carefully selected to ensure that sufficient numbers and sizes of *A. stutchburyi* are available to avoid depleting existing stocks as translocation of large numbers of adult bivalves for restorative purposes can impact the environment from where they are sourced. Moreover, site disturbance and subtle adverse effects on the established benthic source community need to be avoided (Cummings and Hatton, 2003). Practically, transplanting early on after acute stress has subsided (7 days was sufficient to ensure settlement in previously overturned sediment, Chapter 2 & 3) and transplanting in the correct orientation ("green", algae-covered side up), ideally during mild weather conditions (avoiding mid-afternoon low tides in high summer) is precedent to enable quick establishment in the sediment after translocations (personal observation). The latter option (hatchery stock) has not yet been explored in New Zealand due to the lack of an *A. stutchburyi* hatchery (Cummings and Hatton, 2003; Cummings et al., 2007). So far, only wild caught (by dredge or hand-gathering) *A. stutchburyi* are available for purchase (Fisheries New Zealand, 2010). It was suggested that adults from healthy populations could be cultured in hatchery settings (Stewart, Creese and Lalwnitory, 2002) which could increase available stock for re-seeding restoration efforts as well as boost local seafood production. This alternative may however be too costly (due to time for individuals to grow to adequate size), but could be explored in future following the proposed juvenile enhancement programme below. Hatchery produced juvenile bivalves may not achieve the desired restorative outcomes due to higher mortality and because they do not contribute the same level of functionality (Marelli & Arnold 1996; Arnold 2001; Norkko et al. 2002; Thomas et al. 2021). This represents a dilemma, which becomes particularly obvious when trying to upscale to larger restoration efforts. Yet, if carefully managed and if sufficiently large and high-density beds exist locally, the transplanting of individuals can represent a viable option in large scale restoration efforts. Here I propose that future restoration approaches may utilise translocations from healthy and resilient populations which have been seeded from / are continuously supplemented by hatchery spat, thereby minimizing effects on natural populations while keeping hatchery costs low. This "juvenile enhancement programme" could provide hatchery-reared juveniles that have grown out of the bottleneck sizes of > 5mm (~ 8 months) to restore beds from which adults were taken.

The translocation of adult individuals is still considered the most feasible technique for stock and site enhancement, as already reproductively active individuals are translocated, that have higher survival chances than smaller clams (Stewart, Creese and Lalwnitory, 2002), and which can ideally replenish the local population through reproduction (Cummings et al., 2010). We know that transplanted *A. stutchburyi* can survive, however, their ability to grow, reproduce and establish new populations has yet to be assessed (Marsden and Adkins, 2010), which I encourage for future trials.

I showed that recruitment can be successful after an acute disturbance (defaunation). Given the positive effect of *A. stutchburyi* on the sediment properties (Chapter 2), and the inhibition of competing early colonisers (Chapter 3), the re-establishment of patches with higher *A. stutchburyi* densities (Chapter 4) may have positive cascading effects on conspecific recruitment. Yet, recruitment events alone may not fully drive recovery, as the long-term persistence and functional contribution of species also depend on their ability to grow to adult size and engage in within-site biotic and abiotic interactions (Whitlatch et al., 1998; Zajac, Whitlatch and Thrush, 1998; Norkko et al., 2006; Pilditch et al., 2015; Gladstone-Gallagher et al., 2019). In addition to findings from this thesis, if studies consider dispersal patterns and larval connectivity, potential restoration sites can guide restoration strategies even better, reducing repeated seeding effort at locations where natural recolonisation may occur (Lundquist, Oldman and Lewis, 2009). The arrival of larvae and the site's ability to "selfseed" should be included into further studies to increase the viability of such a restoration practice (Lundquist et al., 2004; Lundquist, Pilditch and Cummings, 2004; Lundquist, Oldman and Lewis, 2009).

Based on findings from Chapter 3 where < 10mm *A. stutchburyi* recruitment was slowed after the acute disturbance compared to juvenile numbers in ambient plots, the transplantation of *A. stutchburyi* spat (<5mm) for restoration may not be suitable. This corroborates previous evidence from the U.S. that enhancement by broadcasting/seeding out large numbers of unprotected spat or juvenile animals is ineffective (Peterson, Summerson and Huber, 1995; Marelli and Arnold, 1996). Higher risk for predation (Stewart, Creese and Lalwnitory, 2002; Thomas et al., 2021) and various lethal and sublethal effects of environmental conditions, like temperature increases, affect juveniles more than adults (Salmond and Wing, 2022; Stenman et al., unpublished data). This also applies to translocations across a gradient of mud stress, as larger *A. stutchbury*i individuals have been shown to be less affected by fine sediment deposition compared to smaller conspecifics (Lohrer, Thrush and Gibbs, 2004). Therefore, it seems prudent to use robust adults to establish structure in the community (Chapter 3) and remediate the habitat (Chapters 2 & 4), providing possible facilitatory effects for recruitment and later arrivals. Once established, there may be potential for additions of juveniles to further accelerate recovery (Macfarlane, 1998).

Austrovenus stutchburyi should be a priority in the management of the country's coastal ecosystems as they are a taonga species, a cultural and spiritual heritage of Aotearoa (Marsden and Adkins, 2010) and not just an important food source. Firstly, good management and conservation are crucial. Thinking further, translocation fits within a wider management environment where catchment management, development and fisheries are important aspects for consideration. The potential restoration areas should be informed by the knowledge of the Kaitiaki Roopu of the place (Cummings and Hatton, 2003). By selecting historic sites, the local stressor levels can be evaluated to inform restoration developments.

5.3.1 What is needed for restoration success

Restoration won't succeed if the habitat remains inhospitable - even if species are introduced successfully. For future field trials, more contaminated sites can offer valuable insights and should be included for transplantations, provided that the level of contamination is known and other stressors, such as reduced oxygen levels or increased sediment loads, do not co-occur (Norkko et al., 2005; Hewitt and Norkko, 2007). Yet, it is paramount that runoff from land and pollution reaching the estuary is managed actively, or stakeholders in the catchment are directly involved in the restoration programmes for beneficial collaborations. Management frameworks are required that link ecosystem functioning with resilience and create holistic approaches to understanding, managing, and conserving natural environments (Elliott et al., 2007). Therefore, further evaluation of the success of *A. stutchburyi* bed restoration over time can extend our knowledge on the suitability of this species for active restoration of degraded estuarine systems in the future such as by using management tools like the Recovery Wheel (proposed by Gann et al., 2019 explained in Fitzsimons et al., 2019).

Restoration efforts worldwide are becoming more reliant on high-technology including aquaculture, drones, automation, AI, robotics and remote sensing. It will be critical for working with clams that large-scale restoration efforts are making use of those tools by simultaneously preserving the integrity of existing populations. Given their habitat and the need to preserve intact sandflats, mainly non-destructive methods can be applied here, and a lot of effort might still need to be put into manual work (extraction of large clams, effective translocations etc.). Restoration work is only successful if done in collaboration, where the Mātauranga Māori (Māori traditional knowledge) of local tāngata whenua (people of the land) is paramount to build upon. As successful restoration is labour intensive and will likely be carried out by community groups, these efforts need long-term commitment and monitoring (Cummings and Hatton, 2003). This is important to land on similar goals and expectations as to the outcome of the restoration project, which influences decision making processes along the way (Fitzsimons et al., 2019). Including tāngata whenua/ iwi/ hapū, representatives from councils, Ministry of Fisheries (MFish), Department of Conservation (DoC), NIWA, MAF Biosecurity, universities, and members of the local community into restoration action will ensure that restoration sites are maintained and monitored (a guide for community groups offers further reading and key considerations for effective *A. stutchburyi* translocations, Cummings et al., 2010). Furthermore, we depend on reaching young minds to be passionate for a better future of our natural environment. In the light of rapidly degrading ecosystems, conservation optimism and positive stories about successful restoration can be critical to inspire hope in future generations (Adams, Whitfield and Van Niekerk, 2020; Goodall and Abrams, 2021). This thesis contributes to a tiny piece of the puzzle in how we can improve ecosystem restoration for a better future of our coasts.

Walking into the sandflat on an outgoing tide at Tuapiro Point, February 2022.

References

Adams, J.B., Whitfield, A.K. and Van Niekerk, L., 2020. A socio-ecological systems approach towards future research for the restoration, conservation and management of southern African estuaries. *African Journal of Aquatic Science*, 45(1–2), pp.231–241.

Adams, S.M., 2005. Assessing cause and effect of multiple stressors on marine systems. In: *Marine Pollution Bulletin*. pp.649–657.

Aguirre, J.D., Bollard-Breen, B., Cameron, M., Constantine, R., Duffy, C.A.J., Dunphy, B., Hart, K., Hewitt, J.E., Jarvis, R.M., Jeffs, A., Kahui-McConnell, R., Kawharu, M., Liggins, L., Lohrer, A.M., Middleton, I., Oldman, J., Sewell, M.A., Smith, A.N.H., Thomas, D.B., Tuckey, B., Vaughan, M. and Wilson, R., 2016. Loved to pieces: Toward the sustainable management of the Waitematā Harbour and Hauraki Gulf. *Regional Studies in Marine Science*, 8, pp.220–233.

Aller, R.C., 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chemical Geology*, pp.331–345.

Amato, E.D., Simpson, S.L., Remaili, T.M., Spadaro, D.A., Jarolimek, C.V. and Jolley, D.F., 2016. Assessing the effects of bioturbation on metal bioavailability in contaminated sediments by diffusive gradients in thin films (DGT). *Environ. Sci.Technol.*, 50(6), pp.3055–3064.

Anderson, M., Gorley, R.N. and Clarke, K.R., 2008. *PERMANOVA+ for PRIMER user manual*. Plymouth, United Kingdom: Primer-E Ltd.

Angelini, C., Altieri, A.H., Silliman, B.R. and Bertness, M.D., 2011. Interactions among Foundation Species and Their Consequences for Community Organization, Biodiversity, and Conservation. *BioScience*, [online] 61(10), pp.782–789.

Angelini, C., Griffin, J.N., Van De Koppel, J., Lamers, L.P.M., Smolders, A.J.P., Derksen-Hooijberg, M., Van Der Heide, T. and Silliman, B.R., 2016. A keystone mutualism underpins resilience of a coastal ecosystem to drought. *Nature Communications*, 7.

ANZECC, 2000. Australian and New Zealand guidelines for fresh and marine water quality. *Australian and New Zealand Environment and Conservation Council and Agriculture and Resource Management Council of Australia and New Zealand,* Canberra, 1, 1-314.

Arar, E.J. and Collins, G.B., 1997. *Method 445.0 - In Vitro Determination of Chlorophyll a and Pheophytin a in Marine and Freshwater Algae by Fluorescence*. (p. 22). Cincinnati: United States Environmental Protection Agency, Office of Research and Development, National Exposure Research Laboratory.

ARC, 2004. *Blueprint for monitoring urban receiving environments*. Auckland, New Zealand.

Arnold, W.S., 2001. Bivalve enhancement and restoration strategies in Florida, U.S.A. *Hydrobiologia*, 465, pp.7–19.

Aronson, J. and Van Andel, J., 2012. Restoration Ecology and the Path to Sustainability. *Restoration Ecology: The New Frontier*, pp.293–304.

Aronson, J. and Le Floc'h, E., 1996. Vital landscape attributes: Missing tools for restoration ecology. *Restoration Ecology*, 4(4), pp.377–387.

Aubry, A. and Elliott, M., 2006. The use of environmental integrative indicators to assess seabed disturbance in estuaries and coasts: Application to the Humber Estuary, UK. *Marine Pollution Bulletin*, 53(1), pp.175–185.

Azouzi, L., Bourget, E. and Borcard, D., 2002. Spatial variation in the intertidal bivalve *Macoma balthica*: biotic variables in relation to density and abiotic factors. *Marine Ecology Progress Series*, *234*, 159-170.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. and Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. *Ecological Monographs*, *81*(2), 169-193.

Bayraktarov, E., Saunders, M.I., Abdullah, S., Mills, M., Beher, J., Possingham, H.P., Mumby, P.J. and Lovelock, C.E., 2016. The cost and feasibility of marine coastal restoration. *Ecological Applications*, 26(4), pp.1055–1074.

Beal, B.F., 2006. Relative importance of predation and intraspecific competition in regulating growth and survival of juveniles of the soft-shell clam, Mya arenaria L., at several spatial scales. *Journal of Experimental Marine Biology and Ecology*, 336(1), pp.1–17.

Belley, R. and Snelgrove, P.V.R., 2016. Relative contributions of biodiversity and environment to benthic ecosystem functioning. *Frontiers in Marine Science*, 3.

Benjamin, E.D., Handley, S.J., Hale, R., Toone, T.A., Jeffs, A. and Hillman, J.R., 2022. Biodiversity associated with restored small-scale mussel habitats has restoration decision implications. *Biodiversity and Conservation*, 31(11), pp.2833–2855.

Benthotage, C., Schulz, K.G., Cole, V.J. and Benkendorff, K., 2022. Water quality and the health of remnant leaf oyster (*Isognomon ephippium*) populations in four Australian estuaries. *Science of the Total Environment*, 826.

Berkenbusch, Katrin. and Neubauer, P., 2016. *Intertidal shellfish monitoring in the northern North Island region, 2015-16*. Ministry for Primary Industries.

Beukema, J.J., Flach, E.C., Dekker, R. and Starink, M., 1999. A long-term study of the recovery of the macrozoobenthos on large defaunated plots on a tidal flat in the Wadden Sea. *Journal of Sea Research*, 42, pp.235–254.

Bianchi, T.S., Dawson, R. and Sawangwong, P., 1988. The effects of macrobenthic deposit-feeding on the degradation of chloropigments in sandy sediments. *J Exp Mar Biol Ecol*, 122, pp.243–255.

Bishop, M. and Kelaher, B., 2007. Impacts of detrital enrichment on estuarine assemblages: disentangling effects of frequency and intensity of disturbance. *Marine Ecology Progress Series*, *341*, 25-36.

Bolam, S.G., Fernandes, T.F. and Huxham, A.M., 2002. Diversity, biomass, and ecosystem processes in the marine benthos. *Ecological Monographs*, 72(4), pp.599–615.

Borja, Á., Dauer, D.M., Elliott, M. and Simenstad, C.A., 2010. Medium-and Long-term Recovery of Estuarine and Coastal Ecosystems: Patterns, Rates and Restoration Effectiveness. *Estuaries and Coasts*, 33(6), pp.1249–1260.

Boscolo, R., Cornello, M. and Giovanardi, O., 2003. Condition index and air survival time to compare three kinds of Manila clam *Tapes philippinarum* (Adams & Reeve) farming systems. *Aquaculture International*, 11(3), pp.243–254.

Bremner, J., Rogers, S. I., & Frid, C. L. J. (2006). Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators*, 6(3), 609-622.

Broszeit, S., Hattam, C. and Beaumont, N., 2016. Bioremediation of waste under ocean acidification: Reviewing the role of Mytilus edulis. *Marine Pollution Bulletin*, 103(1–2), pp.5–14.

Bryan, G.W., Langston, W.J. and Langston, J., 1992. Bioavailability, accumulation and effects of heavy metals in sediments with special reference to United Kingdom estuaries: a review. *Environmental Pollution*, 76, pp.89–131.

Bryant, V., Newbery, D.M., Mclusky, D.S. and Campbell, R., 1985. Effect of temperature and salinity on the toxicity of nickel and zinc to two estuarine invertebrates (Corophium volutator, Macoma balthica). *Mar Ecol Prog Ser*, 24, pp.139–153.

Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F. and Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: Conflicts and opportunities. *Trends in Ecology and Evolution,* 26(10), 541-549.

Bulmer, R.H., Schwendenmann, L., Lohrer, A.M. and Lundquist, C.J., 2017. Sediment carbon and nutrient fluxes from cleared and intact temperate mangrove ecosystems and adjacent sandflats. *Science of the Total Environment*, 599–600, pp.1874–1884.

Byers, J.E. and Grabowski, J.H., 2014. Soft-Sediment Communities. In: *Marine community ecology and conservation*. pp.227–249.

Byrne, P.A. and O'Halloran, J., 2001. The role of bivalve molluscs as tools in estuarine sediment toxicity testing: a review. *Hydrobiologia*, *465*(1), 209-217.

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of applied ecology,* 48(5), 1079-1087.

Carmichael, R.H., Walton, W. and Clark, H., 2012. Bivalve-enhanced nitrogen removal from coastal estuaries. *Canadian Journal of Fisheries and Aquatic Sciences*, 69(7), pp.1131–1149.

Caswell, B.A., Paine, M. and Frid, C.L.J., 2018. Seafloor ecological functioning over two decades of organic enrichment. *Marine Pollution Bulletin*, 136, pp.212–229.

CCREM, 1987. *Canadian water quality guidelines*. Ontario.

Chapin III, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. and Tilman, D., 1997. Biotic control over the functioning of ecosystems. *Science*, 277, pp.500–504.

Chariton, A.A., Roach, A.C., Simpson, S.L. and Batley, G.E., 2010. Influence of the choice of physical and chemistry variables on interpreting patterns of sediment contaminants and their relationships with estuarine macrobenthic communities. *Marine and Freshwater Research*, 61(10), pp.1109–1122.

Christianen, M.J.A., Middelburg, J.J., Holthuijsen, S.J., Jouta, J., Compton, T.J., van der Heide, T., Piersma, T., Sinninghe Damsté, J.S., van der Veer, H.W., Schouten, S. and Olff, H., 2017. Benthic primary producers are key to sustain the Wadden Sea food web: stable carbon isotope analysis at landscape scale. *Ecology*, 98(6), pp.1498–1512.

Clark, D.E., Stephenson, F., Hewitt, J.E., Ellis, J.I., Zaiko, A., Berthelsen, A., Bulmer, R.H. and Pilditch, C.A., 2021. Influence of land-derived stressors and environmental variability on compositional turnover and diversity of estuarine benthic communities. *Marine Ecology Progress Series*, 666, pp.1–18.

Clarke, K.R. and Warwick, R.M., 1994. Similarity-based testing for community pattern: the two-way layout with no replication. *Marine Biology*, *118*(1), 167-176.

van Colen, C., Montserrat, F., Verbist, K., Vincx, M., Steyaert, M., Vanaverbeke, J., Herman, P.M.J., Degraer, S. and Ysebaert, T., 2009. Tidal flat nematode responses to hypoxia and subsequent macrofauna-mediated alterations of sediment properties. *Marine Ecology Progress Series*, 381, pp.189–197.

van Colen, C., Montserrat, F., Vincx, M., Herman, P.M.J., Ysebaert, T. and Degraer, S., 2008. Macrobenthic recovery from hypoxia in an estuarine tidal mudflat. *Marine Ecology Progress Series*, 372, pp.31–42.

van Colen, C., Rossi, F., Montserrat, F., Andersson, M.G.I., Gribsholt, B., Herman, P.M.J., Degraer, S., Vincx, M., Ysebaert, T. and Middelburg, J.J., 2012. Organism-Sediment Interactions Govern Post-Hypoxia Recovery of Ecosystem Functioning. *PLoS ONE*, 7(11).

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S.J., Kubiszewski, I., Farber, S. and Turner, R.K., 2014. Changes in the global value of ecosystem services. *Global Environmental Change*, 26(1), pp.152–158.

Crain, C., Kroeker, K. and Halpern, B., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol Lett* , 11, pp.1304–1315.

Cummings, V., 2006. Giving our estuaries a helping hand: restoring shellfish beds in Whangarei Harbour. *Water & Atmosphere*, *14*(1), 10-11.

Cummings, V. and Hatton, S., 2003. Towards the long term enhancement of shellfish beds in the Whangarei Harbour Towards the long term enhancement of shellfish beds in the Whangarei Harbour Part One: Identifying suitable habitat and methodologies for reseeding. *NIWA Client Report HAM2003-042*. Prepared for Northland Regional Council.

Cummings, V., Heweitt, J., Halliday, J. and Mackay, G., 2007. Optimizing the success of *Austrovenus stutchburyi* restoration: Preliminary investigations in a New Zealand estuary. *Journal of Shellfish Research*, 26(1), pp.89–100.

Cummings, V., May, K., Hewitt, J., Roper, D., Williams, E. and Quinn, J., 2010. *Restoring shellfish beds to harbours and estuaries A guide for community groups*. Wellington, New Zealand.

Cummings, V., Thrush, S., Hewitt, J., Norkko, A. and Pickermere, S., 2003. Terrestrial deposits on intertidal sandflats: sediment characteristics as indicators of habitat suitability for recolonising macrofauna. *Marine Ecology Progress Series*, *253*, 39-54.

Cummings, V.J., Pridmore, R.D., Thrush, S.F. and Hewitt, J.E., 1993. Emergence and floating behaviours of post-settlement juveniles of *Macomona liliana* (Bivalvia: Tellinacea). *Mar. Behav. Physiol.*, 24(1), pp.25–32.

Cummings, V.J., Pridmore, R.D., Thrush, S.F. and Hewitt, J.E., 1995. Post-settlement movement by intertidal benthic macroinvertebrates: Do common New Zealand species drift in the water column? *New Zealand Journal of Marine and Freshwater Research*, 29(1), pp.59–67.

Cussioli, M.C., Bryan, K.R., Pilditch, C.A. and De Lange, W.P., 2015. Dispersal of dredging plumes in Tauranga Harbour, New Zealand: A field study. *Australian Coasts and Ports 2015 Conference*, pp.222–228.

Dame, R.F., Zingmark, R.G. and Haskin, E., 1984. Oyster reefs as processors of estuarine materials. *Journal of Experimental Marine Biology and Ecology*, 83(3), pp.239–247.

Damodaran, D.A., 2024. Designing marine infrastructure to restore native shellfish. *Australian Zoologist*, 43(4), pp.663–675.

Davenport, J. and Chen, X., 1987. A comparison of methods for the assessment of condition in the mussel (Mytilus edulis L.). *Journal of Molluscan Studies*, 53(3), pp.293–297.

Davies-Colley, R.J. and Healy, T.R., 1978. Sediment and hydrodynamics of the Tauranga entrance to Tauranga harbour. *New Zealand Journal of Marine and Freshwater Research*, 12(3), pp.225–236.

Deb, S., Guyondet, T., Coffin, M.R.S., Barrell, J. and van den Heuvel, M., 2025. Effect of ecosystem stressors on biogeochemical processes and bivalve-mediated bioremediation approaches for estuary resilience. *Estuarine, Coastal and Shelf Science*, 323.

Deng, F., Ma, Y., Li, J., Wang, Y.Z., Yan, Q.P., Yan, X.Z. and Lin, M., 2015. Archaeal community structure and response to ark shell bioturbation in typical intertidal mudflats, Southeast coast of China. *Continental Shelf Research*, 106, pp.97–106.

Diaz, R.J. and Rosenberg, R., 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and marine biology. An annual review*, 33(245), p.03.

Dittmann, S., Gunther, C.-P. and Schleier, U., 1999. *Recolonization of Tidal Flats After Disturbance*. In *The Wadden Sea Ecosystem: Stability Properties and Mechanisms* (pp. 175-192). Berlin, Heidelberg: Springer Berlin Heidelberg.

Dobbinson, S.J., Barker, M.F. and Jillett, J.B., 1989. Experimental shore level transplantation of the New Zealand cockle *Chione stutchburyi*.

Dolbeth, M., Crespo, D., Leston, S. and Solan, M., 2019. Realistic scenarios of environmental disturbance lead to functionally important changes in benthic species-environment interactions. *Marine Environmental Research*, 150, p.104770.

Donaher, S.E., Baillie, C.J., Smith, C.S., Zhang, Y.S., Albright, A., Trackenberg, S.N., Wellman, E.H., Woodard, N. and Gittman, R.K., 2021. Bivalve facilitation mediates seagrass recovery from physical disturbance in a temperate estuary. *Ecosphere*, 12(11).

Douglas, E.J., Hewitt, J., Lohrer, A.M. and Stephenson, F., 2023. Changing intra- and interspecific interactions across sedimentary and environmental stress gradients. *Ecosphere*, 14(1).

Douglas, E.J., Pilditch, C.A., Kraan, C., Schipper, L.A., Lohrer, A.M. and Thrush, S.F., 2017. Macrofaunal Functional Diversity Provides Resilience to Nutrient Enrichment in Coastal Sediments. *Ecosystems*, 20(7), pp.1324–1336.

Drylie, T.P., Lohrer, A.M., Needham, H.R. and Pilditch, C.A., 2020. Taxonomic and functional response of estuarine benthic communities to experimental organic enrichment: Consequences for ecosystem function. *Journal of Experimental Marine Biology and Ecology*, 532.

Duarte, C.M., Agusti, S., Barbier, E., Britten, G.L., Castilla, J.C., Gattuso, J.P., Fulweiler, R.W., Hughes, T.P., Knowlton, N., Lovelock, C.E., Lotze, H.K., Predragovic, M., Poloczanska, E., Roberts, C. and Worm, B., 2020. *Rebuilding marine life*. *Nature*. *80*(7801), 39-51.

Elliott, M., Burdon, D., Hemingway, K.L. and Apitz, S.E., 2007. Estuarine, coastal and marine ecosystem restoration: Confusing management and science - A revision of concepts. *Estuarine, Coastal and Shelf Science*, *74*(3), 349-366.

Ellis, J., Clark, D., Hewitt, J., Taiapa, C., Sinner, J., Patterson, M. and McCallion, A., 2013. *Ecological survey of Tauranga harbour, MTM Report No. 13*. Manaaki Taha Moana Research Team.

Ellis, J., Nicholls, P., Craggs, R., Hofstra, D. and Hewitt, J., 2004. Effects of terrigenous sedimentation on mangrove physiology and associated macrobenthic communities. *Marine Ecology Progress Series*, *270*, 71-82.

Ellis, J.I., Clark, D., Atalah, J., Jiang, W., Taiapa, C., Patterson, M., Sinner, J. and Hewitt, J., 2017. Multiple stressor effects on marine infauna: Responses of estuarine taxa and functional traits to sedimentation, nutrient and metal loading. *Scientific Reports*, 7(1).

Ellis, J.I., Hewitt, J.E., Clark, D., Taiapa, C., Patterson, M., Sinner, J., Hardy, D. and Thrush, S.F., 2015. Assessing ecological community health in coastal estuarine systems impacted by multiple stressors. *Journal of Experimental Marine Biology and Ecology*, 473, pp.176–187.

Ellis, J.I., Norkko, A. and Thrush, S.F., 2000. Broad-scale disturbance of intertidal and shallow sublittoral soft-sediment habitats; Effects on the benthic macrofauna. *Journal of Aquatic Ecosystem Stress and Recovery*, *7*(1), 57-74.

ESRI, 2025. *ArcGIS Desktop: Release 10*.

Eyre, B.D. and Ferguson, A.J.P., 2002. Comparison of carbon production and decomposition, benthic nutrient fluxes and denitrification in seagrass, phytoplankton, benthic microalgae- and macroalgae-dominated warm-temperate Australian lagoons. *Marine Ecology Progress Series*, 229, pp.43–59.

Falkenberg, L.J., Cornet, J.E. and Joyce, P.W.S., 2024. Nature-based solutions to the management of legacy plastic pollution: Filter-feeders as bioremediation tools for coastal microplastics. *Science of the Total Environment*, 956.

Field, J.G., Clarke, K.R. and Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine ecology progress series*, 8, pp.37–52.

Fisheries New Zealand, 2010. *Cockles (COC) (Austrovenus stutchburyi) Tuangi*. Available from: https://fs.fish.govt.nz/Page.aspx?pk=22&filST=cockle. Accessed 3rd July 2025.

Fitzsimons, J., Branigan, S., Brumbaugh, R.D., McDonald, T. and zu Emergassen, P.S.E. (eds), 2019. *Restoration guidelines for shellfish reefs*. Arlington VA, USA: The Nature Conservancy.

Fitzsimons, J.A., Branigan, S., Gillies, C.L., Brumbaugh, R.D., Cheng, J., DeAngelis, B.M., Geselbracht, L., Hancock, B., Jeffs, A., McDonald, T., McLeod, I.M., Pogoda, B., Theuerkauf, S.J., Thomas, M., Westby, S. and zu Ermgassen, P.S.E., 2020. Restoring shellfish reefs: Global guidelines for practitioners and scientists. *Conservation Science and Practice*, 2(6).

Flach, E.C., 1996. The influence of the cockle, Cerastoderma edule, on the macrozoobenthic community of tidal flats in the Wadden Sea. *Marine Ecology*, 17(1–3), pp.87–98.

Ford, R.B. and Honeywill, C., 2002. Grazing on intertidal microphytobenthos by macrofauna: is pheophorbide *a* a useful marker? *Marine Ecology Progress Series*, *229*, 33-42.

Freilich, E.H., 2018. *Restoration of Mauri (Life-Force) to Ōkahu Bay: Investigation of a Community Driven Restoration Process*. Pomona Senior Theses. 196. Available from: https://scholarship.claremont.edu/pomona_theses/196. (Accessed 5th August 2025).

French McCay, D.P., Peterson, C.H., DeAlteris J. T. and Catena, J., 2003. Restoration that targets function as opposed to structure: replacing lost bivalve production and filtration. *Mar Ecol Prog Ser*. *264*, 197-212.

Friendly, M., 2002. Corrgrams: Exploratory displays for correlation matrices. *The american statistician*, *56*(4), 316-324.

Fukunaga, A. and Anderson, M.J., 2011. Bioaccumulation of copper, lead and zinc by the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. *Journal of Experimental Marine Biology and Ecology*, 396(2), pp.244–252.

Fukunaga, A., Anderson, M.J., Webster-Brown, J.G. and Ford, R.B., 2010. Individual and combined effects of heavy metals on estuarine infaunal communities. *Marine Ecology Progress Series*, 402, pp.123–136.

Gagné, F., Blaise, C., Pellerin, J., Fournier, M., Durand, M.J. and Talbot, A., 2008. Relationships between intertidal clam population and health status of the soft-shell clam Mya arenaria in the St. Lawrence Estuary and Saguenay Fjord (Québec, Canada). *Environment International*, 34(1), pp.30–43.

Gagnon, K., Rinde, E., Bengil, E.G.T., Carugati, L., Christianen, M.J.A., Danovaro, R., Gambi, C., Govers, L.L., Kipson, S., Meysick, L., Pajusalu, L., Tüney Kızılkaya, İ., van de Koppel, J., van der Heide, T., van Katwijk, M.M. and Boström, C., 2020. Facilitating foundation species: The potential for plant–bivalve interactions to improve habitat restoration success. *Journal of Applied Ecology*, *57*(6), 1161-1179.

Gallagher, E.D., Jumars, P.A. and Trueblood, D.D., 1983. Facilitation of soft-bottom succession by tube builders. *Ecology*, 64, pp.1200–1216.

Gammal, J., Hewitt, J., Gladstone-Gallagher, R., Thrush, S., Douglas, E., Lohrer, A. and Pilditch, C., 2023. Stressors Increase the Impacts of Coastal Macrofauna Biodiversity Loss on Ecosystem Multifunctionality. *Ecosystems*, *26*(3), 539-552.

Gann, G.D., McDonald, T., Walder, B., Aronson, J., Nelson, C.R., Jonson, J., Hallett, J.G., Eisenberg, C., Guariguata, M.R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K. and Dixon, K.W., 2019. International principles and standards for the practice of ecological restoration. Second edition. *Restoration Ecology*, 27(S1), pp.S1–S46.

Giles, H. and Pilditch, C.A., 2006. Effects of mussel (Perna canaliculus) biodeposit decomposition on benthic respiration and nutrient fluxes. *Marine Biology*, 150(2), pp.261–271.

Gladstone-Gallagher, R. V., Lundquist, C.J. and Pilditch, C.A., 2014. Mangrove (Avicennia marina subsp. australasica) litter production and decomposition in a temperate estuary. *New Zealand Journal of Marine and Freshwater Research*, 48(1), pp.24–37.

Gladstone-Gallagher, R. V., Pilditch, C.A., Stephenson, F. and Thrush, S.F., 2019. Linking Traits across Ecological Scales Determines Functional Resilience. *Trends in Ecology and Evolution*, *34*(12), 1080-1091.

Gonzalez, S.V., Johnston, E., Gribben, P.E. and Dafforn, K., 2019. The application of bioturbators for aquatic bioremediation: Review and meta-analysis. *Environmental Pollution*, *250*, 426-436.

Goodall, J. and Abrams, D., 2021. *The Book of Hope: A Survival Guide for an Endangered Planet*. Penguin UK.

Grant, J. and Daborn, G., 1994. *The effect of bioturbation on sediment transport on an intertidal mudflat*. *Netherlands Journal of Sea Research*, *32*(1), 63-72.

Guerra-García, J.M. and García-Gómez, J.C., 2006. Recolonization of defaunated sediments: Fine versus gross sand and dredging versus experimental trays. *Estuarine, Coastal and Shelf Science*, 68(1), pp.328–342.

Habeeb, R.L., Trebilco, J., Wotherspoon, S. and Johnson, C.R., 2005. Determining natural scales of ecological systems. *Ecological Monographs*, 75(4), pp.467–487.

Halpern, B.S., McLeod, K.L., Rosenberg, A.A. and Crowder, L.B., 2008a. Managing for cumulative impacts in ecosystem-based management through ocean zoning. *Ocean and Coastal Management*, 51(3), pp.203–211.

Halpern, B.S., Silliman, B.R., Olden, J.D., Bruno, J.P. and Bertness, M.D., 2007. *Incorporating positive interactions in aquatic restoration and conservation*. *Frontiers in Ecology and the Environment*, *5*(3), 153-160.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. and Watson, R., 2008b. A global map of human impact on marine ecosystems. *Science*, 319(5865), pp.948–952.

Harris, L.A., Hodgkins, C.L.S., Day, M.C., Austin, D., Testa, J.M., Boynton, W., Van Der Tak, L. and Chen, N.W., 2015a. Optimizing recovery of eutrophic estuaries: Impact of destratification and re-aeration on nutrient and dissolved oxygen dynamics. *Ecological Engineering*, 75, pp.470–483.

Harris, R.J., Pilditch, C.A., Hewitt, J.E., Lohrer, A.M., Colen, C. Van, Townsend, M. and Thrush, S.F., 2015b. Biotic interactions influence sediment erodibility on wave-exposed sandflats. *Source: Marine Ecology Progress Series*, 523, pp.15–30.

Heath, R.A., 1985. A review of the physical oceanography of the seas around New Zealand - 1982. . *New Zealand Journal of Marine and Freshwater Research*, 19(1), pp.79–124.

Hēnare, M., 2001. Tapu, mana, mauri, hau, wairua: A Maori philosophy of vitalism and cosmos. *Indigenous traditions and ecology: The interbeing of cosmology and community*, pp.197–221.

Hēnare, M., 2015. Tapu, mana, mauri, hau, wairua. *Indigenous spiritualities at work: Transforming the spirit of enterprise*, 77.

Hepburn, C.D., Jackson, A., Vanderburg, P., Kainamu, A. and Flack, B., 2010. Ki uta ki tai: From the mountains to the sea. Holistic approaches to customary fisheries management. In: *4th International traditional knowledge conference*. pp.142–148.

Hering, D., Borja, A., Carstensen, J., Carvalho, L., Elliott, M., Feld, C.K., Heiskanen, A.S., Johnson, R.K., Moe, J., Pont, D., Solheim, A.L. and de Bund, W. van, 2010. The European Water Framework Directive at the age of 10: A critical review of the achievements with recommendations for the future. *Science of the Total Environment*, 408(19), pp.4007–4019.

Hewitt, J. and Cummings, V., 2013. Context-dependent success of restoration of a key species, biodiversity and community composition. *Marine Ecology Progress Series*, 479, pp.63–73.

Hewitt, J., Gladstone-Gallagher, R. and Thrush, S., 2022. *Disturbance–recovery dynamics inform seafloor management for recovery*. *Frontiers in Ecology and the Environment*, *20*(10), 564-572.

Hewitt, J.E., Anderson, M.J., Hickey, C.W., Kelly, S. and Thrush, S.F., 2009. Enhancing the ecological significance of sediment contamination guidelines through integration with community analysis. *Environmental Science and Technology*, 43(6), pp.2118–2123.

Hewitt, J.E., Anderson, M.J. and Thrush, S.F., 2005. Assessing and monitoring ecological community health in marine systems. *Ecological Applications*, 15(3), pp.942–953.

Hewitt, J.E., Legendre, P., Mcardle, B.H., Thrush, S.F., Bellehumeur, C. and Lawrie, S.M., 1997. *Identifying relationships between adult and juvenile bivalves at different spatial scales*. *Journal of Experimental Marine Biology and Ecology*, *216*(1-2), 77-98.

Hewitt, J.E. and Norkko, J., 2007. Incorporating temporal variability of stressors into studies: An example using suspension-feeding bivalves and elevated suspended sediment concentrations. *Journal of Experimental Marine Biology and Ecology*, 341(1), pp.131–141.

Hewitt, J.E., Thrush, S.F., Cummings, V.J. and Pridmore, R.D., 1996. Matching patterns with processes: Predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. *Marine Ecology Progress Series*, 135(1–3), pp.57–67.

Hewitt, J.E., Thrush, S.F., Dayton, P.K. and Bonsdorff, E., 2007. The Effect of Spatial and Temporal Heterogeneity on the Design and Analysis of Empirical Studies of Scale-Dependent Systems. *Am. Nat*, 169, pp.398–408.

Hunt, H.L., Pilditch, C.A., Gladstone-Gallagher, R. V. and Lundquist, C.J., 2020. Spatial and temporal variation in the dispersal of clam populations on intertidal flats. *Journal of Experimental Marine Biology and Ecology*, 524.

Ito, M., Ito, K., Ohta, K., Hano, T., Onduka, T., Mochida, K. and Fujii, K., 2016. Evaluation of bioremediation potential of three benthic annelids in organically polluted marine sediment. *Chemosphere*, 163, pp.392–399.

Jaques, A.P., 1985. *National inventory of sources and releases of lead 1982*. Ottawa, Canada.

Jones, H.F.E., Pilditch, C.A., Bruesewitz, D.A. and Lohrer, A.M., 2011. Sedimentary environment influences the effect of an infaunal suspension feeding bivalve on estuarine ecosystem function. *PLoS ONE*, 6(10).

Jones, H.F.E., Pilditch, C.A., Hamilton, D.P. and Bryan, K.R., 2017. Impacts of a bivalve mass mortality event on an estuarine food web and bivalve grazing pressure. *New Zealand Journal of Marine and Freshwater Research*, 51(3), pp.370–392.

Jones, M., 1975. Synergistic Effects of Salinity, Temperature and Heavy Metals on Mortality and Osmoregulation in Marine and Estuarine Isopods (Crustacea). *Marine Biology*, 30, pp.13–20.

Jordan, T.E., Weller, D.E. and Pelc, C.E., 2018. Effects of Local Watershed Land Use on Water Quality in Mid-Atlantic Coastal Bays and Subestuaries of the Chesapeake Bay. *Estuaries and Coasts*, 41, pp.38–53.

De Juan, S. and Hewitt, J., 2011. Relative importance of local biotic and environmental factors versus regional factors in driving macrobenthic species richness in intertidal areas. *Marine Ecology Progress Series*, 423, pp.117–129.

De Juan, S., Thrush, S.F., Hewitt, J.E., Halliday, J. and Lohrer, A.M., 2014. Cumulative degradation in estuaries: Contribution of individual species to community recovery. *Marine Ecology Progress Series*, 510, pp.25–38.

Karlson, A., Pilditch, C.A., Probert, P.K., Leduc, D. and Savage, C., 2021. Large Infaunal Bivalves Determine Community Uptake of Macroalgal Detritus and Food Web Pathways. *Ecosystems*, 24(2), pp.384–402.

Karlson, A.M.L., Niemand, C., Savage, C. and Pilditch, C.A., 2016. Density of key-species determines efficiency of macroalgae detritus uptake by intertidal benthic communities. *PLoS ONE*, 11(7).

Karlson, K., Hulth, S., Ringdahl and Rosenberg, R., 2005. Experimental recolonisation of Baltic Sea reduced sediments: survival of benthic macrofauna and effects on nutrient cycling. *Marine Ecology Progress Series*, *294*, 35-49.

Karydis, M. and Kitsiou, D., 2013. *Marine water quality monitoring: A review*. *Marine Pollution Bulletin*, *77*(1-2), 23-36.

Kennish, M.J., 1994. Pollution in Estuaries and Coastal Marine Waters. *Journal of Coastal Research*, 27-49.

Kristensen, E., Delefosse, M., Quintana, C.O., Flindt, M.R. and Valdemarsen, T., 2014. *Influence of benthic macrofauna community shifts on ecosystem functioning in shallow estuaries*. *Frontiers in Marine Science*, *1*, 41.

Kröger, K., Gardner, J., Rowden, A. and Wear, R., 2006. Recovery of a subtidal soft-sediment macroinvertebrate assemblage following experimentally induced effects of a harmful algal bloom. *Marine Ecology Progress Series*, *326*, 85-98.

Laliberté, E., Legendre, P. and Shipley, B., 2014. Package FD: *measuring functional diversity from multiple traits, and other tools for functional ecology*. *1*, 0-12.

Lam-Gordillo, O., Baring, R. and Dittmann, S., 2020. Ecosystem functioning and functional approaches on marine macrobenthic fauna: A research synthesis towards a global consensus. *Ecological Indicators*, 115, p.106379.

Lam-Gordillo, O., Baring, R. and Dittmann, S., 2021. Taxonomic and Functional Patterns of Benthic Communities in Southern Temperate Tidal Flats. *Frontiers in Marine Science*, 8.

Lam-Gordillo, O., Hewitt, J.E., Douglas, E.J., Dudley, B.D., Holmes, S.J., Hailes, S., Carter, K., Greenfield, B., Drylie, T. and Lohrer, A.M., 2024. Climatic, oceanic, freshwater, and local environmental drivers of New Zealand estuarine macroinvertebrates. *Marine Environmental Research*, 197.

Lam-Gordillo, O., Huang, J., Barceló, A., Kent, J., Mosley, L.M., Welsh, D.T., Simpson, S.L. and Dittmann, S., 2022a. Restoration of benthic macrofauna promotes biogeochemical remediation of hostile sediments; An in situ transplantation experiment in a eutrophic estuarine-hypersaline lagoon system. *Science of the Total Environment*, 833.

Lam-Gordillo, O., Lohrer, A.M., Hewitt, J. and Dittmann, S., 2023. NZTD - The New Zealand Trait Database for shallow-water marine benthic invertebrates. *Scientific Data*, 10(1).

Lam-Gordillo, O., Mosley, L.M., Simpson, S.L., Welsh, D.T. and Dittmann, S., 2022b. Loss of benthic macrofauna functional traits correlates with changes in sediment biogeochemistry along an extreme salinity gradient in the Coorong lagoon, Australia. *Marine Pollution Bulletin*, 174.

Landner, L. and Reuther, R., 2004. *Metals in society and in the environment: A critical review of current knowledge on fluxes, speciation, bioavailability and risk for adverse effects of copper, chromium, nickel and zinc*. Springer, Netherlands.

Larcombe, M.F., 1971. *The ecology, population dynamics and energetics of some soft shore molluscs.* PhD Thesis. University of Auckland.

Lelieveld, S.D., Pilditch, C.A. and Green, M.O., 2004. Effects of deposit-feeding bivalve (*Macomona liliana*) density on intertidal sediment stability. *New Zealand Journal of Marine and Freshwater Research*, 38(1), pp.115–128.

Lenihan, H.S., Peterson, C., Kim, S., Conlan, K., Fairey, R., McDonald, C., Gabrowski, J. and Oliver, J., 2003. Variation in marine benthic community composition allows discrimination of multiple stressors. *Marine Ecology Progress Series*, *261*, 63-73.

Lenihan, H.S., Peterson, C.H., Miller, R.J., Kayal, M. and Potoski, M., 2018. Biotic disturbance mitigates effects of multiple stressors in a marine benthic community. *Ecosphere*, 9(6).

Levin, L.A., Boesch, D.F., Covich, A., Dahm, C., Erséus, C., Ewel, K.C., Kneib, R.T., Moldenke, A., Palmer, M.A., Snelgrove, P., Strayer, D. and Weslawski, J.M., 2001. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems*, *4*(5), 430-451.

Liang, S., Li, H., Liang, J., Liu, H., Wang, X., Chen, L., Gao, L., Qi, J. and Guo, Y., 2024. Synergistic effects of bivalve and microalgae co-cultivation on carbon dynamics and water quality. *Marine Environmental Research*, 201.

Lock, K. and Leslie, S., 2007. *New Zealand's quota management system: a history of the first 20 years. Motu Working Paper 07-02.*

Lohrer, A., Thrush, S., Hweitt, J., Berkenbusch, K., Ahrens, M. and Cummings, V., 2004. Terrestrially derived sediment: response of marine macrobenthic communities to thin terrigenous deposits. *Marine Ecology Progress Series*, *273*, 121-138.

Lohrer, A.M., Chiaroni, L.D., Hewitt, J.E. and Thrush, S.F., 2008. Biogenic disturbance determines invasion success in a subtidal soft-sediment system. *Ecology*, 89(5), pp.1299–1307.

Lohrer, A.M., Halliday, N.J., Thrush, S.F., Hewitt, J.E. and Rodil, I.F., 2010. Ecosystem functioning in a disturbance-recovery context: Contribution of macrofauna to primary production and nutrient release on intertidal sandflats. *Journal of Experimental Marine Biology and Ecology*, 390(1), pp.6–13.

Lohrer, A.M., Hewitt, J.E., Hailes, S.F., Thrush, S.F., Ahrens, M. and Halliday, J., 2011. Contamination on sandflats and the decoupling of linked ecological functions. *Austral Ecology*, 36(4), pp.378–388.

Lohrer, A.M., Rodil, I.F., Townsend, M., Chiaroni, L.D., Hewitt, J.E. and Thrush, S.F., 2013. Biogenic habitat transitions influence facilitation in a marine soft-sediment ecosystem. *Ecology*, 94(1), pp.136–145.

Lohrer, A.M., Thrush, S.F. and Gibbs, M.M., 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature*, 431(7012), pp.1092–1095.

Lohrer, A.M., Townsend, M., Rodil, I.F., Hewitt, J.E. and Thrush, S.F., 2012. Detecting shifts in ecosystem functioning: The decoupling of fundamental relationships with increased pollutant stress on sandflats. *Marine Pollution Bulletin*, 64(12), pp.2761–2769.

Long, E.R., Macdonald, D.D., Smith, S.L. and Calder, F.D., 1995. Incidence of adverse biological effects within ranges of chemical concentrations in marine and estuarine sediments. *Environmental management*, 19(1), pp.81–97.

Loreau, M., Naeem, S., Inchausti, P. and Bengtsson, J., 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science*, 294(5543), 804-808.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H. and Jackson, J.B.C., 2006. Depletion degradation, and recovery potential of estuaries and coastal seas. *Science*, 312(5781), pp.1806–1809.

De Luca-Abbott, S., 2001. Biomarkers of Sublethal Stress in the Soft-sediment Bivalve *Austrovenus stutchburyi* Exposed in-situ to Contaminated Sediment in an Urban New Zealand Harbour. *Marine pollution bulletin*, *42*(10), 817-825.

De Luca-Abbott, S.B., 2000. *Effects of contaminants on Austrovenus stutchburyi - using biomarkers to detect sublethal stress*. Doctoral thesis, University of Auckland.

Lukwambe, B., Nicholaus, R., Zhao, L., Yang, W., Zhu, J. and Zheng, Z., 2020. Microbial community and interspecies interaction during grazing of ark shell bivalve (Scapharca subcrenata) in a full-scale bioremediation system of mariculture effluents. *Marine Environmental Research*, 158.

Lundquist, C.J., Oldman, J.W. and Lewis, M.J., 2009. Predicting suitability of cockle *austrovenus stutchburyi* restoration sites using hydrodynamic models of larval dispersal. *New Zealand Journal of Marine and Freshwater Research*, 43(3), pp.735–748.

Lundquist, C.J., Pilditch, C.A. and Cummings, V.J., 2004. Behaviour controls post-settlement dispersal by the juvenile bivalves *Austrovenus stutchburyi* and *Macomona liliana*. *Journal of Experimental Marine Biology and Ecology*, 306(1), pp.51–74.

Lundquist, C.J., Thrush, S.F., Oldman, J.W. and Senior, A.K., 2004. Limited transport and recolonization potential in shallow tidal estuaries. *Limnology and Oceanography*, 49(2), pp.386–395.

Luoma, S.N. and Rainbow, P.S., 2008. *Metal contamination in aquatic environments: science and lateral management*. Cambridge: Cambridge University Press.

Ma, Y., Hu, A., Yu, C.P., Yan, Q., Yan, X., Wang, Y., Deng, F. and Xiong, H., 2015. Response of microbial communities to bioturbation by artificially introducing macrobenthos to mudflat sediments for in situ bioremediation in a typical semi-enclosed bay, southeast China. *Marine Pollution Bulletin*, 94(1–2), pp.114–122.

Macfarlane, S.L., 1998. The evolution of a municipal quahog (hardclam), *Mercenaria mercenaria* management program, a 20-year history: 1975-1995. *Journal of Shellfish Research*, 17(4), pp.1015–1036.

Macleod, C.K., Moltschaniwskyj, N.A. and Crawford, C.M., 2008. Ecological and functional changes associated with long-term recovery from organic enrichment. *Marine Ecology Progress Series*, 365, pp.17–24.

Malle, K.G., 1992. Zinc in the environment. *Zeitschrift Fur Wasser- Und Abwasser-Forschung-Journal for Water and Wastewater Research-Acta Hydrochimica Et Hydrobiologica*, 20, pp.196–204.

Marelli, D.C. and Arnold, W.S., 1996. Growth and mortality of transplanted juvenile hard clams, Mercenaria mercenaria, in the northern Indian River Lagoon, Florida. *Journal of Shellfiih Research*, 15(3), pp.709–713.

Marsden, I.D. and Adkins, S.C., 2010. Current status of cockle bed restoration in New Zealand. *Aquaculture International*, 18(1), pp.83–97.

Marsden, I.D. and Rainbow, P.S., 2004. Does the accumulation of trace metals in crustaceans affect their ecology - The amphipod example? *Journal of Experimental Marine Biology and Ecology*, 300(1–2), pp.373–408.

Marsden, I.D., Smith, B.D. and Rainbow, P.S., 2014. Effects of environmental and physiological variables on the accumulated concentrations of trace metals in the New Zealand cockle *Austrovenus stutchburyi*. *Science of the Total Environment*, 470–471, pp.324–339.

Martin, T.D., Creed, J.T. and Brockhoff, C.A., 1994. Method 200.2, Revision 2.8: Sample Preparation Procedure for Spectrochemical Determination of Total Recoverable Elements. In: C.K. Smoley, ed. *Methods for the Determination of Metals in Environmental Samples*. Cincinnati, OH: USEPA. pp.15–24.

Mccarthy, A., Hepburn, C., Scott, N., Schweikert, K., Turner, R. and Moller, H., 2013. Local people see and care most? Severe depletion of inshore fisheries and its consequences for Māori communities in New Zealand. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(3), pp.369–390.

McKinnon, J., 1996. Studies of the Age, Growth and Shell Increment Patterns in the New Zealand Cockle (*Austrovenus stutchburyi*). Doctoral thesis, University of Otago.

McLeod, I.M., zu Ermgassen, P.S.E., Gillies, C.L., Hancock, B., Humphries, A., Westby, S.R., Quan, W., Allison, S. and Debney, A., 2019. Can Bivalve Habitat Restoration Improve Degraded Estuaries? In: *Coasts and Estuaries: The Future*. Elsevier. pp.427–442.

McLusky, D.S. and Elliott, M., 2004. *The Estuarine Ecosystem: Ecology, Threats and Management*. Oxford: Oxford University Press.

Mead, H., 2003. *Tīkanga Māori: Living by Māori values*. Huia.

Meadows, P.S. and Tait, J., 1989. Modification of sediment permeability and shear strength by two burrowing invertebrates. *Marine Biology*, 101, pp.75–82.

Meadows, P.S., Tait, J. and Hussain, S.A., 1990. Effects of estuarine infauna on sediment stability and particle sedimentation. *Hydrobiologia*, 190, pp.263–266.

Meysman, F.J.R., Middelburg, J.J. and Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology and Evolution*, *21*(12), 688-695.

Middelburg, J.J., 2018. Reviews and syntheses: To the bottom of carbon processing at the seafloor. *Biogeosciences*, *15*(2), 413-427.

Miller, D.C., Geider, R.J. and Macintyre, H.L., 1996. Microphytobenthos: The Ecological Role of the 'Secret Garden' of Unvegetated, Shallow-Water Marine Habitats. II. Role in Sediment Stability and Shallow-Water Food Webs. *Estuaries*, *19*(2), 202-212.

Miller, L.P. and Gaylord, B., 2007. Barriers to flow: The effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. *Journal of Experimental Marine Biology and Ecology*, 344(2), pp.215–228.

Miranda, A., Voltolina, D., Izaguirre-Fierro, G., Osuna-López, I. and Sandoval, I., 2009. Removal of suspended solids from the effluents of a shrimp farm by the blood ark Anadara tuberculosa (Sowerby 1833). . *Hydrobiologica*, 19, pp.173–176.

Montserrat, F., Van Colen, C., Degraer, S., Ysebaert, T. and Herman, P.M.J., 2008. Benthic community-mediated sediment dynamics. *Marine Ecology Progress Series*, 372, pp.43–59.

Morgan, T.K.K.B., 2006. Waiora and cultural identity: Water quality assessment using the Mauri Model. *AlterNative: An International Journal of Indigenous Peoples*, 3(1), pp.42–67.

Morris, L. and Keough, M., 2003. Variation in the response of intertidal infaunal invertebrates to nutrient additions: field manipulations at two sites within Port Phillip Bay, Australia.

Morton, J.E. and Miller, M.C., 1973. *The New Zealand Sea Shore*. 2nd Edition ed. London: Collins.

Needham, H.R., Pilditch, C.A., Lohrer, A.M. and Thrush, S.F., 2011. Context-Specific Bioturbation Mediates Changes to Ecosystem Functioning. *Ecosystems*, 14(7), pp. 1096-1109.

Newell, R.I.E., Cornwell, J.C. and Owens, M.S., 2002. Influence of simulated bivalve biodeposition and microphytobenthos on sediment nitrogen dynamics: A laboratory study. *Limnology and Oceanography*, 47(5), pp.1367–1379.

Nicholaus, R., Lukwambe, B., Zhao, L., Yang, W., Zhu, J. and Zheng, Z., 2019. Bioturbation of blood clam Tegillarca granosa on benthic nutrient fluxes and microbial community in an aquaculture wastewater treatment system. *International Biodeterioration and Biodegradation*, 142, pp.73–82.

Nieves-Soto, M., Enriquez-Ocaña, F., Piña-Valdez, P., Maeda-Martínez, A.N., Almodóvar-Cebreros, J.R. and Acosta-Salmón, H., 2011. Is the mangrove cockle Anadara tuberculosa a candidate for effluent bioremediation? Energy budgets under combined conditions of temperature and salinity. *Aquaculture*, 318(3–4), pp.434–438.

Nixon, S.W., 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia*, 41(1), pp.199–219.

Norkko, A., Rosenberg, R., Thrush, S.F. and Whitlatch, R.B., 2006. Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. In: *Journal of Experimental Marine Biology and Ecology*. pp.195–207.

Norkko, A., Thrush, S.F., Hewitt, J.E., Cummings, V.J., Norkko, J., Ellis, J.I., Funnell, G.A., Schultz, D. and MacDonald, I., 2002. Smothering of estuarine sandflats by terrigenous clay: The role of wind-wave disturbance and bioturbation in site-dependent macrofaunal recovery. *Marine Ecology Progress Series*, 234, pp.23–41.

Norkko, A., Villnäs, A., Norkko, J., Valanko, S. and Pilditch, C.A., 2013. Size matters: Implications of the loss of large individuals for ecosystem function. *Scientific Reports*, 3, pp.1–7.

Norkko, J., Gammal, J., Hewitt, J.E., Josefson, A.B., Carstensen, J. and Norkko, A., 2015. Seafloor Ecosystem Function Relationships: In Situ Patterns of Change Across Gradients of Increasing Hypoxic Stress. *Ecosystems*, 18(8), pp.1424–1439.

Norkko, J., Norkko, A., Thrush, S.F., Valanko, S. and Suurkuukka, H., 2010. Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in soft-sediment communities. *Marine Ecology Progress Series*, 413, pp.253–266.

Norkko, J., Pilditch, C.A., Gammal, J., Rosenberg, R., Enemar, A., Magnusson, M., Granberg, M.E., Lindgren, J.F., Agrenius, S. and Norkko, A., 2019. Ecosystem functioning along gradients of increasing hypoxia and changing soft-sediment community types. *Journal of Sea Research*, 153, pp.1–43.

Norkko, J., Reed, D.C., Timmermann, K., Norkko, A., Gustafsson, B.G., Bonsdorff, E., Slomp, C.P., Carstensen, J. and Conley, D.J., 2012. A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology*, 18(2), pp.422–434.

Norkko, J. and Thrush, S.F., 2006. Ecophysiology in environmental impact assessment: Implications of spatial differences in seasonal variability of bivalve condition. *Marine Ecology Progress Series*, 326, pp.175–186.

Norkko, Pilditch, Thrush and Wells, 2005. Effects of food availability and hypoxia on bivalves: the value of using multiple parameters to measure bivalve condition in environmental studies. *Marine ecology Progress series*, *298*, 205-218.

Norling, P. and Kautsky, N., 2007. Structural and functional effects of Mytilus edulis on diversity of associated species and ecosystem functioning. *Marine Ecology Progress Series*, 351, pp.163–175.

O'Brien, S.A., Dehling, D.M. and Tylianakis, J.M., 2022. The recovery of functional diversity with restoration. *Ecology*, 103(3).

O'Meara, T., Gibbs, E. and Thrush, S.F., 2018. Rapid organic matter assay of organic matter degradation across depth gradients within marine sediments. *Methods in Ecology and Evolution*, 9(2), pp.245–253.

O'Meara, T.A., Hewitt, J.E., Thrush, S.F., Douglas, E.J. and Lohrer, A.M., 2020. Denitrification and the Role of Macrofauna Across Estuarine Gradients in Nutrient and Sediment Loading. *Estuaries and Coasts*, *43*(6), 1394-1405.

O'Meara, T.A., Hillman, J.R. and Thrush, S.F., 2017. Rising tides, cumulative impacts and cascading changes to estuarine ecosystem functions. *Scientific Reports*, 7(1), pp.1–7.

Van Der Oost, R., Beyer, J. and Vermeulen, N.P.E., 2003. Fish bioaccumulation and biomarkers in environmental risk assessment: a review. *Environmental Toxicology and Pharmacology*, 13, pp.57–149.

Ormerod, S.J., 2003. Restoration in applied ecology: Editor's introduction. *Journal of Applied Ecology*, 40(1), pp.44–50.

Our Land and Water National Science Challenge, 2023. *The Tīmata Method: A low-cost way to retire farmland into native forest*. Available from: https://ourlandandwater.nz/outputs/the-timata-method-a-low-cost-way-to-retire-farmland-into-native-forest/ (Accessed on 20 February 2025).

Overton, K., Dempster, T., Swearer, S.E., Morris, R.L. and Barrett, L.T., 2024. Predictors of outplanted marine bivalve survival in restoration: A review and synthesis. *Journal of Applied Ecology*, *61*(12), 2884-2896.

Park, S., 2004. *Aspects of mangrove distribution and abundance in Tauranga Harbour.*

Peake, B.M., Marsden, I.D. and Bryan, A.M., 2006. Spatial and temporal variations in trace metal concentrations in the Cockle, *Austrovenus Stutchburyi* from Otago, New Zealand. *Environmental Monitoring and Assessment*, 115(1–3), pp.119–144.

Pearson, T.H. and Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology - An Annual Review*, 16, pp.229–311.

Peña-Messina, E., Martinez-Cordoba, L.E., Bückle-Ramirez, L.F., Segovia-Quintero, M.A. and Zertuche-Gonzalez, J.A., 2009. A preliminary evaluation of physiological filtration variables for Crassostrea corteziensis (Hertlein, 1951) and *Anadara tuberculosa* (Sowerby, 1833) in shrimp aquaculture effluents. . *Aquaculture Research*, 40, pp.1750–1758.

Petersen, J.K., Saurel, C., Nielsen, P. and Timmermann, K., 2015. The use of shellfish for eutrophication control. *Aquaculture International*, 24(3), pp.857–878.

Peterson, C.H., Summerson, H.C. and Huber, J., 1995. Replenishment of hard clam stocks using hatchery seed: combined importance of bottom type, seed size, planting season, and density. *J Shell Res* , 14, pp.293–300.

Pilditch, C.A., Valanko, S., Norkko, J. and Norkko, A., 2015. Post-settlement dispersal: The neglected link in maintenance of soft-sediment biodiversity. *Biology Letters*, 11(2).

Pillay, D. and Branch, G.M., 2011. Bioengineering effects of burrowing thalassinidean shrimps on marine soft-bottom ecosystems. In: *Oceanography and Marine Biology: An Annual Review*. CRC Press. pp.137–191.

Powell, A.W.B., 1979. *New Zealand Mollusca: Marine, Land and Freshwater Snails*. Washington: Collins.

Pratt, D.R., Lohrer, A.M., Pilditch, C.A. and Thrush, S.F., 2014. Changes in Ecosystem Function Across Sedimentary Gradients in Estuaries. *Ecosystems*, 17(1), pp.182–194.

Pratt, D.R., Lohrer, A.M., Thrush, S.F., Hewitt, J.E., Townsend, M., Cartner, K., Pilditch, C.A., Harris, R.J., Van Colen, C. and Rodil, I.F., 2015. Detecting subtle shifts in ecosystem functioning in a dynamic estuarine environment. *PLoS ONE*, 10(7), pp.1–16.

Pratt, D.R., Pilditch, C.A., Lohrer, A.M. and Thrush, S.F., 2013. The effects of short-term increases in turbidity on sandflat microphytobenthic productivity and nutrient fluxes. *Journal of Sea Research*, 92, pp.170–177.

Pridmore, R.D., Thrush, S.F., Hewitt, J.E. and Roper, D.S., 1990. Macrobenthic community composition of six intertidal sandflats in manukau harbour, new zealand. *New Zealand Journal of Marine and Freshwater Research*, 24(1), pp.81–96.

Pridmore, R.D., Thrush, S.F., Wilcock, R.J., Smith, T.J., Hewitt, J.E. and Cummings, V.J., 1991. Effect of the organochlorine pesticide Technical Chlordane on the population structure of suspension and deposit feeding bivalves. *Marine Ecology Progress Series*, 76, pp.261–271.

Queirós, A. M., Birchenough, S. N., Bremner, J., Godbold, J. A., Parker, R. E., Romero-Ramirez, A., ... & Widdicombe, S. (2013). A bioturbation classification of European marine infaunal invertebrates. *Ecology and evolution*, 3(11), 3958-3985.

R Core Team, 2024. *R: A Language and Environment for Statistical Computing*.

Ravit, B., Cooper, K., Buckley, B., Comi, M. and Mccandlish, E., 2014. Improving management support tools for reintroducing bivalve species (Eastern oyster [*Crassostrea virginica* Gmelin]) in urban estuaries. *Integrated Environmental Assessment and Management*, 10(4), pp.555–565.

Reeves, S.E., Renzi, J.J., Fobert, E.K., Silliman, B.R., Hancock, B. and Gillies, C.L., 2020. *Facilitating Better Outcomes: How Positive Species Interactions Can Improve Oyster Reef Restoration*. *Frontiers in Marine Science*, *7*, 656.

Reiss, J., Bridle, J.R., Montoya, J.M. and Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in ecology & evolution*, 24(9), pp.505–514.

Remaili, T., Simpson, S.L. and Jolley, D.F., 2017. Effect of enhanced bioturbation intensities on the toxicity assessment of legacy-contaminated sediments. *Environ. Pollut.*, 226, pp.335–345.

Renzi, J.J., He, Q. and Silliman, B.R., 2019. Harnessing positive species interactions to enhance coastal wetland restoration. *Frontiers in Ecology and Evolution, 7, 131.*

Rhoads, D.C. and Boyer, L.F., 1982. The Effects of Marine Benthos on Physical Properties of Sediments A Successional Perspective. In *Animal-sediment relations: The biogenic alteration of sediments* (pp. 3-52). Boston, MA: Springer US.

Robb, C.K., 2014. Assessing the impact of human activities on British Columbia’s estuaries. *PLoS ONE*, 9(6).

Rodil, I.F., Lohrer, A.M., Hewitt, J.E., Townsend, M., Thrush, S.F. and Carbines, M., 2013. Tracking environmental stress gradients using three biotic integrity indices: Advantages of a locally-developed traits-based approach. *Ecological Indicators*, 34, pp.560–570.

Roper, D.S., Pridmore, R.D. and Thrush, S.F., 1992. Recruitment to the macrobenthos of *Macomona liliana* (Bivalvia: Tellinidae) in Manukau harbour, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 26(3–4), pp.385–392.

Rossi, R., Gribsholt, B., Middelburg, J.J. and Heip, C., 2008. Context-dependent effects of suspension feeding on intertidal ecosystem functioning. *Marine Ecology Progress Series*, 354, pp.47–57.

Rynkowski, L., Ellis, J.I., Needham, H.R. and Pilditch, C.A., 2025. A systematic review and meta-analysis of the cumulative effects of multiple stressors on marine bivalves. *Marine Biology*, 172(7), p.96.

Salmond, N.H. and Wing, S.R., 2022. Sub-lethal and lethal effects of chronic ammonia exposure and hypoxia on a New Zealand bivalve. *Journal of Experimental Marine Biology and Ecology*, 549.

Sandwell, D.R., Pilditch, C.A. and Lohrer, A.M., 2009. Density dependent effects of an infaunal suspension-feeding bivalve *(Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. *Journal of Experimental Marine Biology and Ecology*, 373(1), pp.16–25.

Savage, C., Thrush, S.F., Lohrer, A.M. and Hewitt, J.E., 2012. Ecosystem services transcend boundaries: Estuaries provide resource subsidies and influence functional diversity in coastal benthic communities. *PLoS ONE*, 7(8).

Scheffer, M., Carpenter, S.R., Foley, Jonathan, A., Folke, C. and Walker, B., 2001. Catastrophic shifts in ecosstems. *Nature*, 413.

Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., Van De Koppel, J., Van De Leemput, I.A., Levin, S.A., Van Nes, E.H., Pascual, M. and Vandermeer, J., 2012. Anticipating Critical Transitions. *Science*, [online] 338, pp.334–348.

Schenone, S. and Thrush, S.F., 2022. Scaling-up ecosystem functions of coastal heterogeneous sediments: testing practices using high resolution data. *Landscape Ecology*, 37(6), pp.1603–1614.

Schneider, C.A., Rasband, W.S. and Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), pp.671–675.

Sea, M.A., Hillman, J.R. and Thrush, S.F., 2022. Enhancing multiple scales of seafloor biodiversity with mussel restoration. *Scientific Reports*, 12(1).

Searles, A.R., Gipson, E.E., Walters, L.J. and Cook, G.S., 2022. Oyster reef restoration facilitates the recovery of macroinvertebrate abundance, diversity, and composition in estuarine communities. *Scientific Reports*, 12(1).

Shen, H., Jiang, G., Wan, X., Li, H., Qiao, Y., Thrush, S. and He, P., 2017. Response of the microbial community to bioturbation by benthic macrofauna on intertidal flats. *Journal of Experimental Marine Biology and Ecology*, 488, pp.44–51.

Shen, H., Thrush, S.F., Wan, X., Li, H., Qiao, Y., Jiang, G., Sun, R., Wang, L.B. and He, P., 2016. Optimization of hard clams, polychaetes, physical disturbance and denitrifying bacteria of removing nutrients in marine sediment. *Marine Pollution Bulletin*, 110(1), pp.86–92.

Shull, D.H., 1997. Mechanisms of infaunal polychaete dispersal and colonization in an intertidal sandflat. *Journal of Marine Research*, 55, 153-179.

Silliman, B.R., Angelini, C., Krause, G., Saunders, M.I., Smith, C.S., Valdez, S.R., McLean, J.E.T., Paxton, A.B., Heide, T. van der and Abelson, A., 2023. Editorial: Marine ecosystem restoration (MER) – a call for a more inclusive paradigm. *Frontiers in Marine Science*, 10.

Silliman, B.R., Hensel, M.J.S., Gibert, J.P., Daleo, P., Smith, C.S., Wieczynski, D.J., Angelini, C., Paxton, A.B., Adler, A.M., Zhang, Y.S., Altieri, A.H., Palmer, T.M., Jones, H.P., Gittman, R.K., Griffin, J.N., O'Connor, M.I., van de Koppel, J., Poulsen, J.R., Rietkerk, M., He, Q., Bertness, M.D., van der Heide, T. and Valdez, S.R., 2024. Harnessing ecological theory to enhance ecosystem restoration. *Current Biology*, 34(9), R418–R434.

Singer, J., Anderson, J., Ledbetter, M., McCave, I., Jones, K. and Wright, R., 1988. An assessment of analytical techniques for the size analysis of fine-grained sediments. *Journal of Sedimentary Research, Journal of Sedimentary Petrology* , 58, pp.534–543.

Sinner, J., Clark, D., Ellis, J., Roberts, B., Jiang, W., Goodwin, E., Hale, L., Rolleston, S., Patterson, M., Hardy, D., Prouse, E. and Brown, S., 2011. *Health of Te Awanui Tauranga Harbour*. Palmerston North.

Smaal, A.C., Ferreira, J.G., Grant, J., Petersen, J.K. and Strand, Ø., 2019. *Goods and Services of Marine Bivalves*. Springer, Cham, Switzerland.

Smaal, A.C. and Haas, H.A., 1997. Seston dynamics and food availability on mussel and cockle beds. *Estuarine, Coastal and Shelf Science*, 45(2), pp.247–259.

Snelgrove, P.V.R., 1997. The Importance of Marine Sediment Biodiversity in Ecosystem Processes. *Ambio*, 26(8), pp.578–583.

Snelgrove, P.V.R., Thrush, S.F., Wall, D.H. and Norkko, A., 2014. Real world biodiversity-ecosystem functioning: A seafloor perspective. *Trends in Ecology and Evolution*, 29(7), pp. 398-405.

Soissons, L.M., Gomes da Conceiçâo, T., Bastiaan, J., van Dalen, J., Ysebaert, T., Herman, P.M.J., Cozzoli, F. and Bouma, T.J., 2019. Sandification vs. muddification of tidal flats by benthic organisms: A flume study. *Estuarine, Coastal and Shelf Science*, 228.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M. and Ruesink, J.L., 2004. Extinction and ecosystem function in the marine benthos. *Science 306:* pp.1177–1180.

Stenman, M., Needham, H., Gladstone-Gallagher, R.V., Ellis, J.I., Douglas, E., Lohrer, A. and Pilditch, C.A., *in review at Scientific Reports*. Short-term sublethal heat stress impairs growth of the New Zealand cockle, *Austrovenus stutchburyi*.

Stephenson, F., Gladstone-Gallagher, R. V., Bulmer, R.H., Thrush, S.F. and Hewitt, J.E., 2022. Inclusion of biotic variables improves predictions of environmental niche models. *Diversity and Distributions*, 28(7), pp.1373–1390.

Stephenson, R.L. and Chanley, P.E., 1979. Larval development of the cockle *chione stutchburyi* (Bivalvia: Veneridae) reared in the laboratory. *New Zealand Journal of Zoology*, 6(4), pp.553–559.

Stewart, M.J., 2005. *Ecological effects associated with urban development on populations of the New Zealand cockle (Austrovenus stutchburyi)*. Doctoral thesis, University of Auckland.

Stewart, M.J., Creese, R.G. and Lalwnitory, L.M., 2002. *Transplants of intertidal shellfish for enhancement of depleted populations: Preliminary trials with the New Zealand little neck clam*. [online] *Journal of Shellfish Research*, 21(1), pp. 21-27.

Tay, H.W., Bryan, K.R., Pilditch, C.A., Park, S. and Hamilton, D.P., 2012. Variations in nutrient concentrations at different time scales in two shallow tidally dominated estuaries. *Marine and Freshwater Research*, 63(2), pp.95–109.

Taylor, M.D., 1999. *The influence of environmental factors on reproduction and recruitment of Macomona liliana (Class: Bivalvia) in Manukau Harbour, New Zealand.* Doctoral thesis, Auckland University.

Tett, P., Gowen, R., Mills, D., Fernandes, T., Gilpin, L., Huxham, M., Kennington, K., Read, P., Service, M., Wilkinson, M. and Malcolm, S., 2007. Defining and detecting undesirable disturbance in the context of marine eutrophication. *Marine Pollution Bulletin*, 55(1–6), pp.282–297.

Thistle, D., 1981. Natural Physical Disturbances and Communities of Marine Soft Bottoms. *Mar. Ecol. Prog. Ser*, 6, pp.223–228.

Thomas, S., Pilditch, C.A., Thrush, S.F., Federico Baltar, &, Crawshaw, J.A., Thomson, B. and Savage, C., 2021. Does the Size Structure of Venerid Clam Populations Affect Ecosystem Functions on Intertidal Sandflats? *Estuaries and Coasts* (44), pp. 242-252.

Thomas, S., Pilditch, C.A., Thrush, S.F. and Savage, C., 2022. Ecosystem function responses to nutrient enrichment mediated by mud content in soft sediment habitats. *New Zealand Journal of Marine and Freshwater Research*, 56(3), pp.491–508.

Thomson, T., Ellis, J.I., Fusi, M., Prinz, N., Lundquist, C.J., Bury, S.J., Shankar, U., Cary, S.C. and Pilditch, C.A., 2024. Effects of catchment land use on temperate mangrove forests. *Science of the Total Environment*, 940.

Thrush, S., Pridmore, R.D. and Hewitt, J.E., 1994. Impacts on soft-sediment macrofauna: the effects of spatial variations on temporal trends. *Ecological Applications*. 4(1), pp.31-41.

Thrush, S., Townsend, M., Hewitt, J., Davies, K., Lohrer, A., Lundquist, C. and Cartner, K., 2013a. The many uses and values of estuarine ecosystems. In: In Dymond JR ed, ed. *Ecosystem services in New Zealand – conditions and trends*. Lincoln, New Zealand: Manaaki Whenua Press.

Thrush, S.F., 1999. Complex role of predators in structuring soft-sediment macrobenthic communities: Implications of changes in spatial scale for experimental studies. *Austral Ecology*, 24(4), pp.344–354.

Thrush, S.F., Halliday, J., Hewitt, J.E. and Lohrer, A.M., 2008a. The effects of habitat loss, fragmentation, and community homogenization on resilience in estuaries. *Ecological Applications*, 18(1), pp.12–21.

Thrush, S.F., Hewitt, J.E., Cummings, V.J., Green, M.O., Funnell, G.A. and Wilkinson, M.R., 2000. The generality of field experiments: Interactions between local and broad-scale processes. *Ecology*, 81(2), pp.399–415.

Thrush, S.F., Hewitt, J.E., Dayton, P.K., Coco, G., Lohrer, A.M., Norkko, A., Norkko, J. and Chiantore, M., 2009. Forecasting the limits of resilience: Integrating empirical research with theory. *Proceedings of the Royal Society B: Biological Sciences*, 276(1617), pp. 3209-3217.

Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C. and Norkko, A., 2006. Functional role of large organisms in intertidal communities: Community effects and ecosystem function. *Ecosystems*, 9(6), pp.1029–1040.

Thrush, S.F., Hewitt, J.E., Gladstone-Gallagher, R. V., Savage, C., Lundquist, C., O’Meara, T., Vieillard, A., Hillman, J.R., Mangan, S., Douglas, E.J., Clark, D.E., Lohrer, A.M. and Pilditch, C., 2021. Cumulative stressors reduce the self-regulating capacity of coastal ecosystems. *Ecological Applications*, 31(1).

Thrush, S.F., Hewitt, J.E., Hickey, C.W. and Kelly, S., 2008b. Multiple stressor effects identified from species abundance distributions: Interactions between urban contaminants and species habitat relationships. *Journal of Experimental Marine Biology and Ecology*, 366(1–2), pp.160–168.

Thrush, S.F., Hewitt, J.E., Kraan, C., Lohrer, A.M., Pilditch, C.A. and Douglas, E., 2017. Changes in the location of biodiversity– ecosystem function hot spots across the seafloor landscape with increasing sediment nutrient loading. *Proceedings of the Royal Society B: Biological Sciences*, 284(1852).

Thrush, S.F., Hewitt, J.E., Lohrer, A.M. and Chiaroni, L.D., 2013b. When small changes matter: The role of cross-scale interactions between habitat and ecological connectivity in recovery. *Ecological Applications*, 23(1), pp.226–238.

Thrush, SF., Hewitt, JE., Norkko, A., Cummings, VJ. and Funnell, GA., 2003. Macrobenthic recovery processes following catastrophic sedimentation on estuarine sandflats. *Ecological Applications*, 13(5), pp.1433–1455.

Thrush, S.F., Hewitt, J.E., Parkes, S., Lohrer, A.M., Pilditch, C., Woodin, S.A., Wethey, D.S., Chiantore, M., Asnaghi, V., De Juan, S., Kraan, C., Rodil, I., Savage, C. and Van Colen, C., 2014. Experimenting with ecosystem interaction networks in search of threshold potentials in real-world marine ecosystems. *Ecology*, pp. 1451-1457.

Thrush, S.F., Hewitt, J.E., Pridmore, R.D. and Cummings, V.J., 1996a. Adult/juvenile interactions of infaunal bivalve: contrasting outcomes in different habitats. *Mar Ecol Prog Ser*, 132, pp.83–92.

Thrush, S.F., Lundquist, C.J. and Hewitt, J.E., 2005. Spatial and Temporal Scales of Disturbance to the Seafloor: A Generalized Framework for Active Habitat Management. *American Fisheries Society Symposium*, 41, pp.639–649.

Thrush, S.F., Pridmore, R.D., Hewitt, J.E. and Cummings, V.J., 1992. *Adult infauna as facilitators of colonization on intertidal sandflats*. *Mar. Biol. EcoL*, pp. 253-265.

Thrush, S.F., Whitlatch, R.B., Pridmore, R.D., Hewitt, J.E., Cummings, V.J. and Wilkinson, M.R., 1996b. Scale-dependent recolonization: the role of sediment stability in a dynamic sandflat habitat . *Ecology* , 77(8), pp.2472–2487.

Tremblay, L.A., Clark, D., Sinner, J. and Ellis, J.I., 2017. Integration of community structure data reveals observable effects below sediment guideline thresholds in a large estuary. *Environmental Science: Processes and Impacts*, 19(9), pp.1134–1141.

Tricklebank, K.A., Grace, R. V. and Pilditch, C.A., 2021. Decadal population dynamics of an intertidal bivalve (*Austrovenus stutchburyi*) bed: pre- and post- a mass mortality event. *New Zealand Journal of Marine and Freshwater Research*, 55(2), pp.352–374.

Turner, S.J., Grant, J., Pridmore, R.D., Hewitt, J.E., Wilkinson, M.R., Hume, T.M. and Morrisey, D.J., 1997. Bedload and water-column transport and colonization processes by post-settlement benthic macrofauna: Does infaunal density matter? *Journal of Experimental Marine Biology and Ecology*, 216, pp.51–75.

USEPA, 1976. *Quality criteria for water. Office of Planning and Water*. Washington DC. EPA-440-9-76-023.

Venter, O., Pillay, D. and Prayag, K., 2020. Water filtration by burrowing sandprawns provides novel insights on endobenthic engineering and solutions for eutrophication. *Scientific Reports*, 10(1).

Volkenborn, N., Meile, C., Polerecky, L., Pilditch, C.A., Norkko, A., Norkko, J., Hewitt, J.E., Thrush, S.F., Wethey, D.S. and Woodin, S.A., 2012. Intermittent bioirrigation and oxygen dynamics in permeable sediments: An experimental and modeling study of three tellinid bivalves. *Journal of Marine Research*. 70(6).

Waltham, N.J., Elliott, M., Lee, S.Y., Lovelock, C., Duarte, C.M., Buelow, C., Simenstad, C., Nagelkerken, I., Claassens, L., Wen, C.K.C., Barletta, M., Connolly, R.M., Gillies, C., Mitsch, W.J., Ogburn, M.B., Purandare, J., Possingham, H. and Sheaves, M., 2020. UN Decade on Ecosystem Restoration 2021–2030—What Chance for Success in Restoring Coastal Ecosystems? *Frontiers in Marine Science*, 7, pp.1–5.

Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* , 30, pp.377–392.

Whitlatch, R. and Zajac, R., 1985. Biotic interactions among estuarine infaunal opportunistic species. *Marine Ecology Progress Series*, 21, pp.299–311.

Whitlatch, R.B., Hines, A.H., Thrush, S.F., Hewitt, J.E. and Cummings, V., 1997. Benthic faunal responses to variations in patch density and patch size of a suspension-feeding bivalve. *Journal of Experimental Marine Biology and Ecology*. pp. 171-189.

Whitlatch, R.B., Lohrer, A.M., Thrush, S.F., Pridmore, R.D., Hewitt, E., Cummings, V. 1 and Zajac, & R.N., 1998. Scale-dependent benthic recolonization dynamics: life stage-based dispersal and demographic consequences. *J. Recruitment. Colonization and Physical-Chemical Forcing in Marine Biological Systems*. pp. 217-226.

Widdicombe, S., Austen, M.C., Kendall, M.A., Warwick, R.M. and Jones, M.B., 2000. Bioturbation as a mechanism for setting and maintaining levels of diversity in subtidal macrobenthic communities. *Hydrobiologia*. pp. 369-377.

Wilcock, R.J., Pridmore, R.D., Thrush, S.F., Cummings, V.J., Hewitt, J.E. and Smith, T.J., 1993. Bioaccumulation and elimination of chlordane by selected intertidal benthic fauna. *Environmental Toxicology and Chemistry*, 12(4), pp.733–742.

Williams, B.G. and Pilditch, C.A., 1997. The Entrainment of Persistent Tidal Rhythmicity in a Filter-Feeding Bivalve Using Cycles of Food Availability. *Journal of Biological Rhythms*. Vol. 12(2), pp. 173-181.

Woodin, S.A., 1976. Adult-larval interactions in dense faunal assemblages: patterns of abundance. *J. Mar. Res.*, 34, pp.25–41.

Woodin, S.A. and Jackson, J.B.C., 1979. Interphyletic competition among marine benthos. *American Zoologist*, 19(4), pp.1029–1043.

Woodin, S.A., Volkenborn, N., Pilditch, C.A., Lohrer, A.M., Wethey, D.S., Hewitt, J.E. and Thrush, S.F., 2016. Same pattern, different mechanism: Locking onto the role of key species in seafloor ecosystem process. *Scientific Reports*, 6.

Woodin, S.A., Wethey, D.S., Hewitt, J.E. and Thrush, S.F., 2012. Small scale terrestrial clay deposits on intertidal sandflats: Behavioral changes and productivity reduction. *Journal of Experimental Marine Biology and Ecology*, 413, pp.184–191.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. and Watson, R., 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, 314.

Wrede, A., Andresen, H., Asmus, R., Wiltshire, K.H. and Brey, T., 2019. Macrofaunal irrigation traits enhance predictability of nutrient fluxes across the sediment-water interface. *Marine Ecology Progress Series*, 632, pp.27–42.

Yeoh, L.H., Thrush, S.F., Hewitt, J.E. and Gladstone-Gallagher, R. V., 2024. The effect of adult cockles, *Austrovenus stutchburyi*, on sediment transport. *Journal of Experimental Marine Biology and Ecology*, 570.

Zajac, R., Whitlatch, R. and Thrush, S., 1998. Recolonization and succession in soft-sediment infaunal communities: The spatial scale of controlling factors. *Hydrobiologia*, 375(376), pp.227–240.

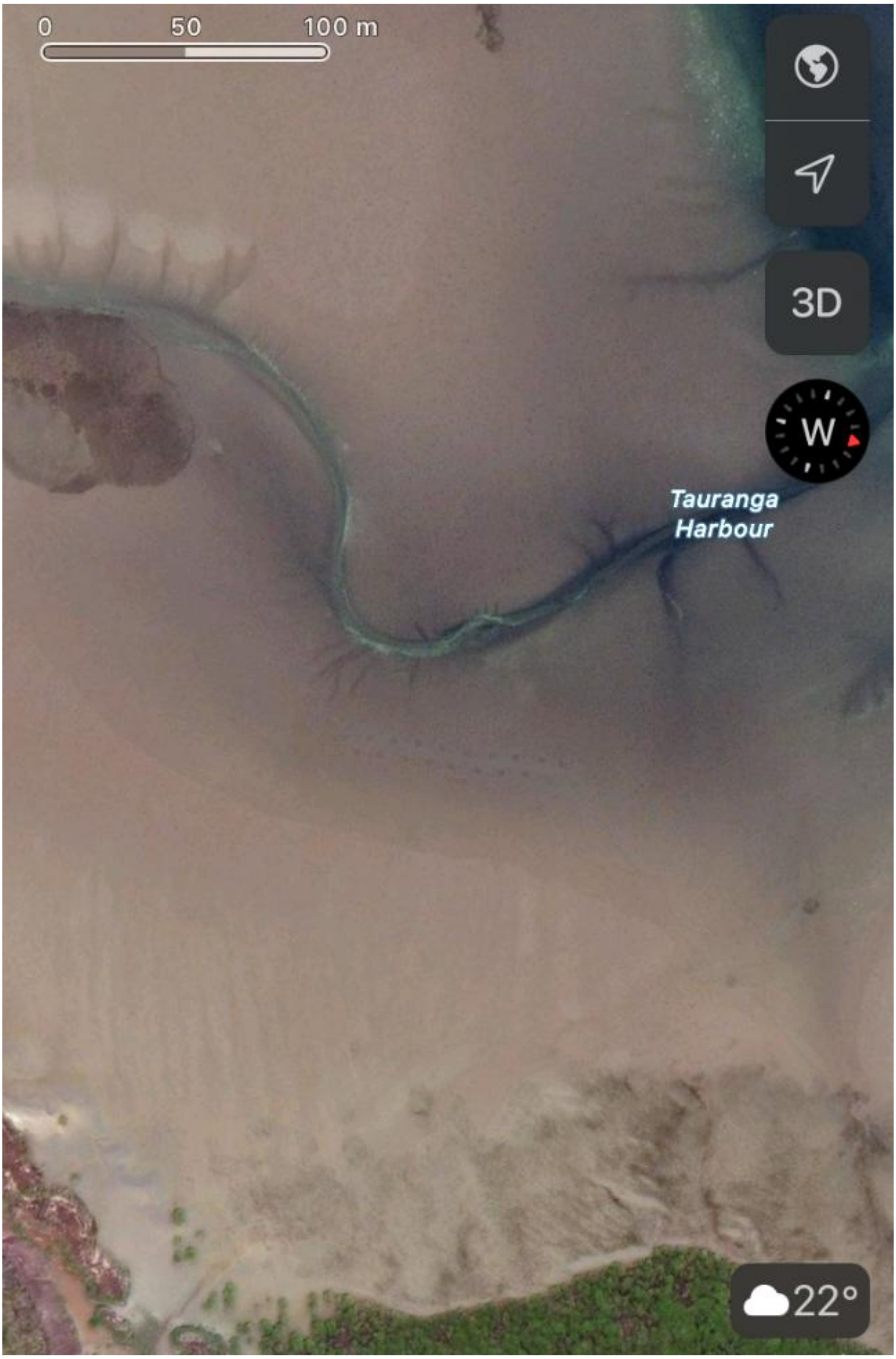
Zeng, Y. and Yang, H., 2021. Review of molluscan bivalve condition index calculations and application in Northern Quahogs *Mercenaria mercenaria*. *Aquaculture research*, 52(1), pp.23–36.

Zhang, Y.S., Cioffi, W.R., Cope, R., Daleo, P., Heywood, E., Hoyt, C., Smith, C.S. and Silliman, B.R., 2018. A global synthesis reveals gaps in coastal habitat restoration research. *Sustainability (Switzerland)*, 10(4).

Zhao, L., Zheng, Y., Nicholaus, R., Lukwambe, B., Zhu, J., Yang, W. and Zheng, Z., 2019. Bioturbation by the razor clam *Sinonovacula constricta* affects benthic nutrient fluxes in aquaculture wastewater treatment ecosystems. *Aquaculture Environment Interactions*, 11, pp.87–96.

Zhu, Q.-Z., Yin, X., Taubner, H., Wendt, J., Friedrich, M.W., Elvert, M., Hinrichs, K.-U. and Middelburg, J.J., 2024. Secondary production and priming reshape the organic matter composition in marine sediments. *Sci. Adv*, 10, p.8096.

zu Ermgassen, P.S.E., Thurstan, R.H., Corrales, J., Alleway, H., Carranza, A., Dankers, N., DeAngelis, B., Hancock, B., Kent, F., McLeod, I., Pogoda, B., Liu, Q. and Sanderson, W.G., 2020. The benefits of bivalve reef restoration: A global synthesis of underrepresented species. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(11), pp.2050–2065.



Experimental plots visible from Google and Apple Maps zoomed into Tuapiro Estuary (2021 – 2022)

Appendices

Appendix I: Ethics statement

Liaison with iwi representatives from Ngāti Te Wai of Ngai te Rangi and Ngāti Ranginui and the Tauranga Moana Customary Fisheries Trust ensured appropriate site selection and continuous engagement with the project. This study complied with all existing legislation governing animal welfare and field-based experiments. Animal ethics approval/permits were not sought as benthic invertebrate fauna manipulated/sampled in this study are exempt from the Animal Welfare Act 1999. After consultation with the Bay of Plenty Regional Council permits were not required for the in-situ faunal manipulations. The collection of benthic fauna was undertaken with a Ministry of Fisheries Special Permit (698) Client Number 8770024.

Appendix II: Supplementary material Chapter 2

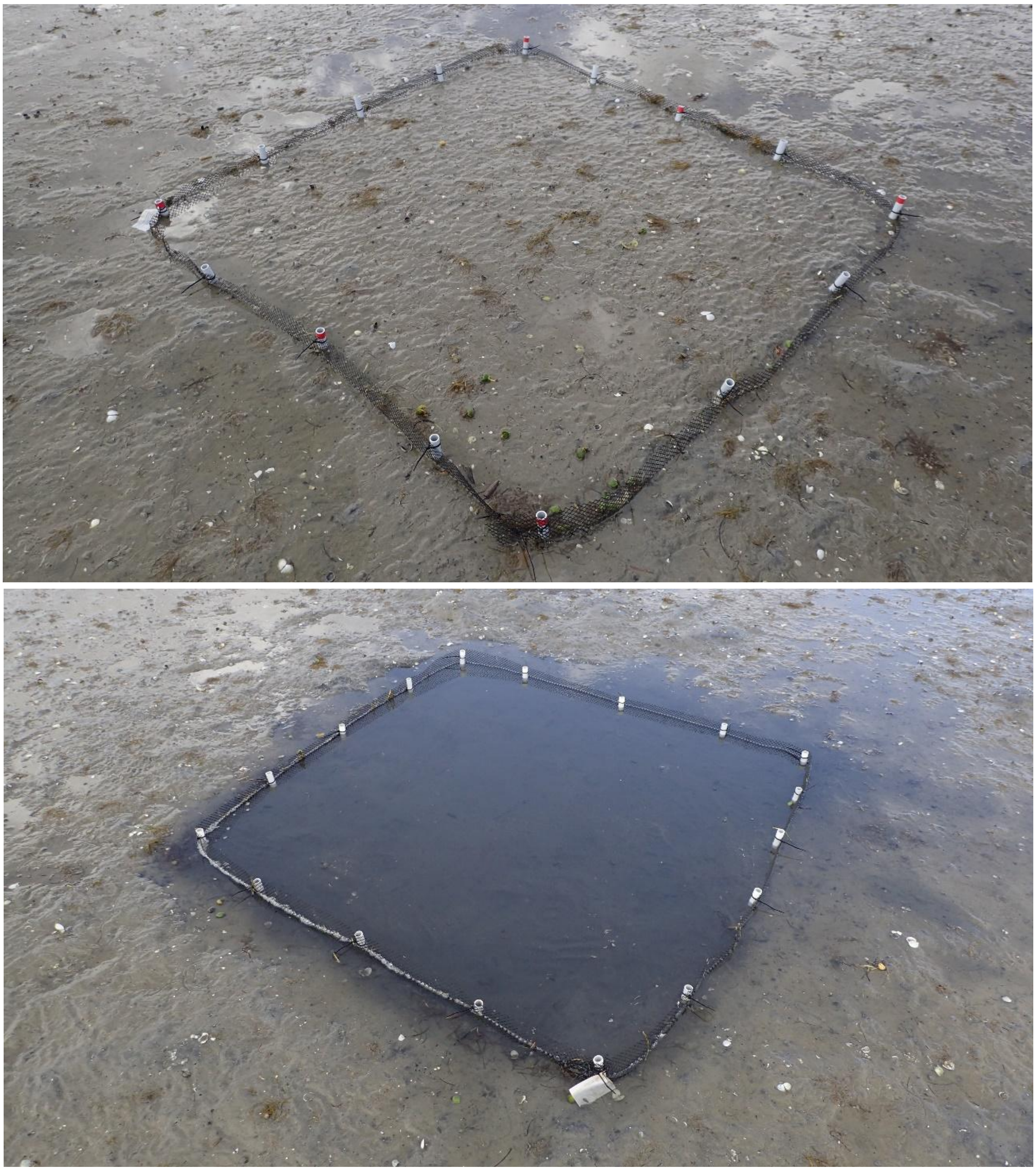


Figure A2.1 Experimental plots **(A)** directly after fencing of ambient plots and **(B)** after defaunation.

Table A2.1 Mean values for environmental variables measured during sampling at the water-seafloor interface 20, 81, and 389 d after addition of large bivalves. Measurements are presented as means ± 1 SD from two consecutive incubation days. The range is given in parentheses.

Time after addition of bivalves (d)	**PAR Seafloor (μmol photons m^{-2} s^{-1})**	**Ambient water temperature (°C)**	**Salinity**
d 20	722 ± 164 (219-913)	23.3 (22.6 - 24)	31.19 (30.1 - 32.3)
d 81	161 ± 123 (23-571)	18 (17.5 - 18.5)	32.75 (32.7 - 32.8)
d 389	735 ± 190 (314-1025)	24.4 (23 - 25.4)	34.5 (34 - 35)

Appendix III: Supplementary material Chapter 3

Table A3.1. List of the functional traits and trait modalities selected based on their effect on nutrient cycling and sediment transport (Lam-Gordillo, Baring and Dittmann, 2020; Lam-Gordillo et al., 2022b).

Trait	**Trait modalities**
Bioturbation	Biodiffusor
	Bioirrigator
	No bioturbation
	Surface modifier
Body size	Large (>20 mm)
	Medium (5–20 mm)
	Small (0.5–5 mm)
Feeding mode	Deposit feeder
	Filter/suspension
	Grazer/scraper
	Omnivore
	Predator
	Scavenger/opportunist
	Sub-surface deposit feeder
Living habit	Attached/sessile
	Burrower
	Free living/surface crawler
	Parasite / Commensal
	Tube dwelling
Morphology	Hard
	Hard exoskeleton
	Hard shell
	Irregular
	Round
	Soft/fragile
	Vermiform
Sediment position	Attached
	Bentho-pelagic
	Epibenthic
	Crevices, stones, shells
	Deeper than 3 cm
	Surface shallow <3 cm
Sediment stabilisation	Destabiliser
	None
	Stabiliser

Table A3.2 Mean values (± 1 SD) for sediment variables 20, 81, and 389 d after addition of large bivalves. ND = no disturbance/ intact sediments, D = defaunation/ no addition of bivalves, +ML = defaunation + addition of *M. liliana*, +AS = defaunation + addition of *A. stutchburyi*, +ASML = defaunation + addition of both species.

		Treatments				
Variable	**Time from defaunation**	**ND**	**D**	**+ML**	**+AS**	**+ASML**
Median grain size (µm)	d 20	178.25 ± 5.11	173.13 ± 6.45	176.25 ± 5.04	172.13 ± 5.79	171.25 ± 3.75
	d 81	174.13 ± 9.12	163.63 ± 9.03	165.50 ± 4.24	163.50 ± 6.42	165.13 ± 3.47
	d 389	188.38 ± 8.58	187.25 ± 10.74	186.75 ± 4.09	185.38 ± 2.32	184.00 ± 4.51
Mud content < 63 µm (%)	d 20	8.39 ± 1.21	9.02 ± 2.23	8.36 ± 1.05	8.50 ± 0.96	9.47 ± 1.92
	d 81	10.34 ± 1.88	14.99 ± 2.67	13.85 ± 0.34	14.19 ± 2.03	12.95 ± 0.91
	d 389	7.95 ± 1.18	10.74 ± 0.94	10.13 ± 0.52	8.93 ± 1.04	9.87 ± 0.51
Organic matter content (%)	d 20	2.16 ± 0.19	2.38 ± 0.26	2.21 ± 0.13	2.38 ± 0.18	2.40 ± 0.21
	d 81	2.39 ± 0.30	3.00 ± 0.22	2.93 ± 0.32	2.93 ± 0.20	2.89 ± 0.23
	d 389	2.33 ± 0.15	2.71 ± 0.11	2.72 ± 0.16	2.80 ± 0.40	2.61 ± 0.10
Chlorophyll *a* (µg g dw^{-1})	d 20	9.27 ± 0.32	5.99 ± 2.49	4.77 ± 0.45	4.96 ± 1.89	5.49 ± 0.81
	d 81	10.24 ± 0.55	9.31 ± 1.37	9.53 ± 1.44	10.17 ± 1.10	9.71 ± 1.00
	d 389	12.01 ± 1.16	12.78 ± 1.26	13.09 ± 0.37	13.74 ± 0.96	13.44 ± 0.58
Phaeophytin (µg g dw^{-1})	d 20	0.49 ± 0.48	1.29 ± 0.45	1.31 ± 0.02	1.29 ± 1.41	1.58 ± 0.42
	d 81	0.82 ± 0.25	1.42 ± 0.16	1.38 ± 0.36	1.20 ± 0.29	1.35 ± 0.53
	d 389	0.24 ± 0.09	0.60 ± 0.16	0.55 ± 0.16	0.44 ± 0.04	0.44 ± 0.24
Ratio chl *a*:phaeo	d 20	23.47 ± 21.15	4.67 ± 0.91	3.63 ± 0.34	3.30 ± 2.07	3.66 ± 1.12
	d 81	13.42 ± 4.12	6.57 ± 0.93	7.11 ± 1.53	8.81 ± 1.90	7.86 ± 2.43
	d 389	54.77 ± 20.36	22.16 ± 5.03	24.96 ± 5.86	31.46 ± 3.13	37.13 ± 17.43

Table A3.3 Average size and density (per core) of *Macomona liliana* and *Austrovenus stutchburyi* across treatments and time (d 20, d 81, d 389) (± standard deviation, * indicates only one replicate for size average). Size categories are adults (>20 mm for *M. liliana* and >18mm for *A. stutchburyi*), pre-adults (19.9 – 10mm and 17.9 – 10mm) and juveniles (< 10 mm shell length). Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi;* +ASML = defaunation + addition of both species.

	Macomona liliana					***Austrovenus stutchburyi***				
	Average size (mm)					**Average size (mm)**				
	ND	**D**	**+ML**	**+AS**	**+ASML**	**ND**	**D**	**+ML**	**+AS**	**+ASML**
day 20	15.0 ± 7.7	13.1 ± 3.9	25.8 ± 4.2	15.8 ± 8.3	19.6 ± 8.3	10.1 ± 5.9	11.6 ± 7.8	3.3 *	24.5 ± 5.8	24.1 ± 5.9
day 81	15.6 ± 7.9	3.8 ± 5.7	9.8 ± 10.6	2.9 ± 4.5	10.7 ± 12.7	9.6 ± 6.5	4.8 ± 6.5	2.6 ± 3.9	18.0 ± 12.4	16.6 ± 11.3
day 389	14.1 ± 8.2	11.5 ± 6.7	11.1 ± 8.3	8.7 ± 5.0	11.7± 9.2	7.3 ± 6.0	3.5 ± 3.2	3.5 ± 1.7	8.2 ± 9.5	11.9 ± 11.0
	Average Density (ind core^{-1})		**Total**			**Average Density (ind core^{-1})**		**Total**		
	ND	**D**	**+ML**	**+AS**	**+ASML**	**ND**	**D**	**+ML**	**+AS**	**+ASML**
day 20	10.75 ± 0.5	2.25 ± 1.5	3.25 ± 0.96	1.75 ± 1.5	4.0 ± 0.82	12.0 ± 8.21	0.75 ± 1.5	0.25 ± 0.5	12.0 ± 2.94	12.5 ± 3.0
day 81	9.25 ± 0.96	7.0 ± 3.74	7.5 ± 1.0	8.0 ± 4.42	9.5 ± 3.32	12.5 ± 5.69	5.75 ± 2.99	2.75 ± 1.71	15.75 ± 5.38	13.67 ± 9.07
day 389	7.5 ± 1.73	6.75 ± 1.5	7.75 ± 1.71	6.5 ± 2.65	7.0 ± 0.82	13.75 ± 9.74	8.0 ± 3.74	5.25 ± 1.89	9.0 ± 4.0	10.75 ± 0.96
			Adult					**Adult**		
day 20	3.75 ± 0.96	0.25 ± 0.5	3.0 ± 0.82	0.75 ± 0.96	2.5 ± 1.0	3.5 ± 3.0	0.25 ± 0.5	0.0 ± 0.0	11.25 ± 3.86	11.5 ± 2.65
day 81	2.75 ± 0.96	0.25 ± 0.5	2.5 ± 0.58	0.25 ± 0.5	3.0 ± 0.82	3.5 ± 2.38	1.0 ± 1.41	0.0 ± 0.0	10.25 ± 3.77	10.0 ± 6.48
day 389	2.25 ± 0.5	1.5 ± 0.58	1.75 ± 0.96	0.25 ± 0.5	2.0 ± 0.82	2.75 ± 1.71	0.25 ± 0.5	0.0 ± 0.0	2.0 ± 1.63	4.5 ± 3.0
			Pre-adults					**Pre-adults**		
day 20	3.75 ± 2.75	1.5 ± 1.0	0.25 ± 0.5	0.5 ± 1.0	1.0 ± 0.82	3.0 ± 1.63	0.25 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.0
day 81	4.25 ± 2.06	1.25 ± 1.89	0.5 ± 0.58	0.5 ± 0.58	0.5 ± 0.58	2.75 ± 1.5	0.25 ± 0.5	0.25 ± 0.5	0.5 ± 0.58	0.0 ± 0.0
day 389	3.25 ± 1.89	1.5 ± 1.0	0.5 ± 0.58	3.0 ± 2.45	0.25 ± 0.5	1.75 ± 2.22	0.25 ± 0.5	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.58
			Juvenile					**Juvenile**		
day 20	3.25 ± 2.5	0.5 ± 1.0	0.0 ± 0.0	0.5 ± 0.58	0.5 ± 0.58	5.5 ± 5.07	0.25 ± 0.5	0.25 ± 0.5	0.75 ± 0.96	0.5 ± 0.58
day 81	2.25 ± 2.06	5.5 ± 3.79	4.5 ± 0.58	7.25 ± 4.11	6.0 ± 2.45	6.25 ± 2.99	4.5 ± 1.91	2.5 ± 1.29	5.0 ± 1.41	5.25 ± 3.1
day 389	2.0 ± 1.41	3.75 ± 2.22	5.5 ± 2.08	3.25 ± 1.5	4.75 ± 1.26	9.25 ± 7.37	7.5 ± 3.87	5.25 ± 1.89	7.0 ± 2.83	5.75 ± 2.63

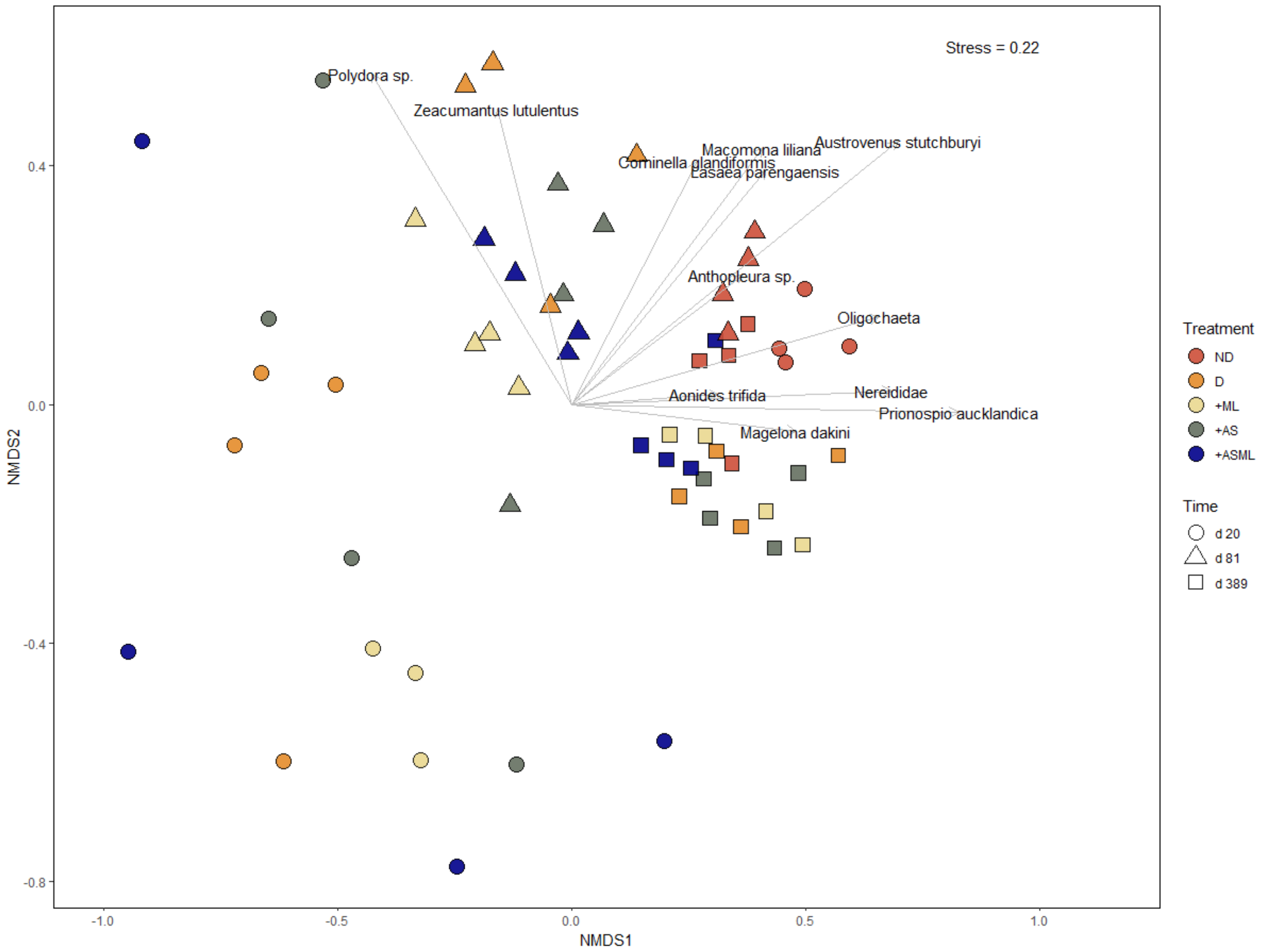


Figure A3.1 Non-metric multidimensional scaling (NMDS) plot showing dissimilarities of five treatments over three time points (d 20, d 81, d 389). The ten most important taxa identified by SIMPER analysis and *M. liliana* and *A. stutchburyi* are overlayed. Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species.

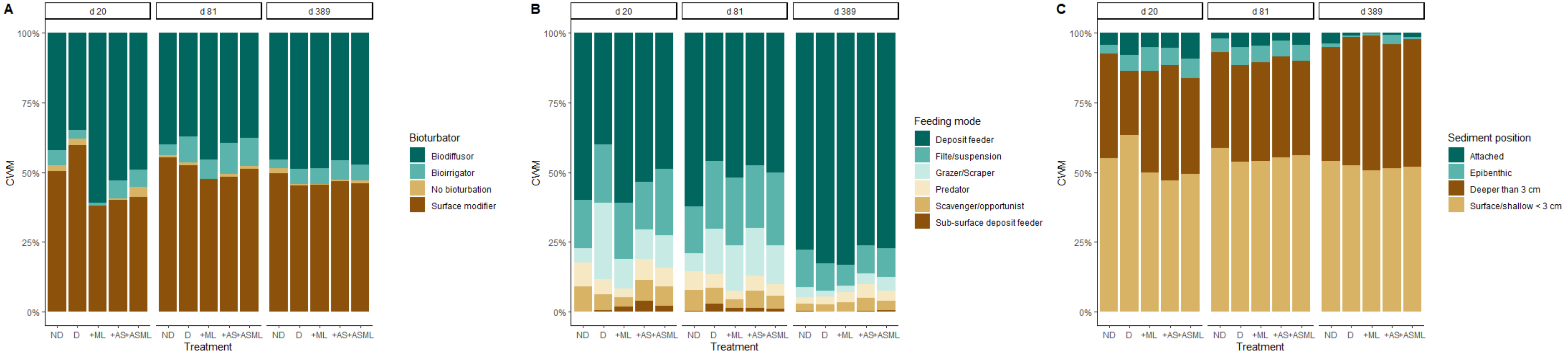


Figure A3.2 Remaining three summaries of community weighted means (CMW) of seven chosen trait values and associated trait modalities across time (d 20, d 81, d 389). **(A)** Bioturbation, **(B)** Feeding monde, **(C)** Sediment position. Treatments*:* ND = no disturbance, intact sediments, D = defaunation, no addition of bivalves, +ML = defaunation + addition of *Macomona liliana*, +AS = defaunation + addition of *Austrovenus stutchburyi*, +ASML = defaunation + addition of both species.

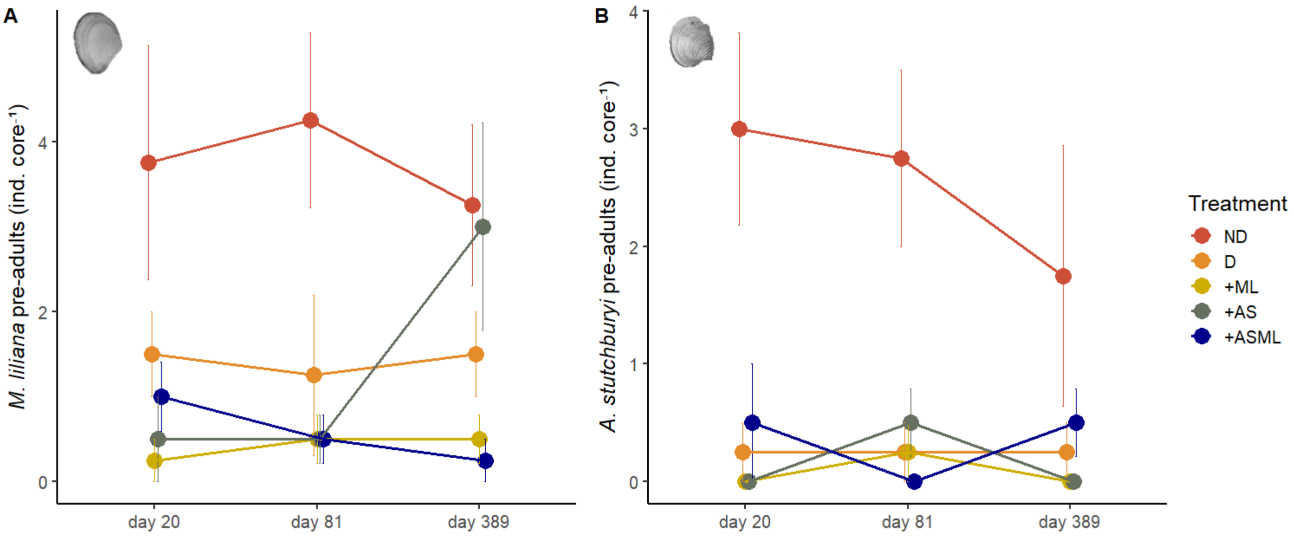


Figure A3.3 Mean densities (± standard error) of bivalve pre-adults for **(A)** *M. liliana* (10-19.9 mm), and **(B)** *A. stutchburyi* (10-17.9 mm) per core across treatments over time (d 20, d 81, d 389) from macrofauna cores. Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species.

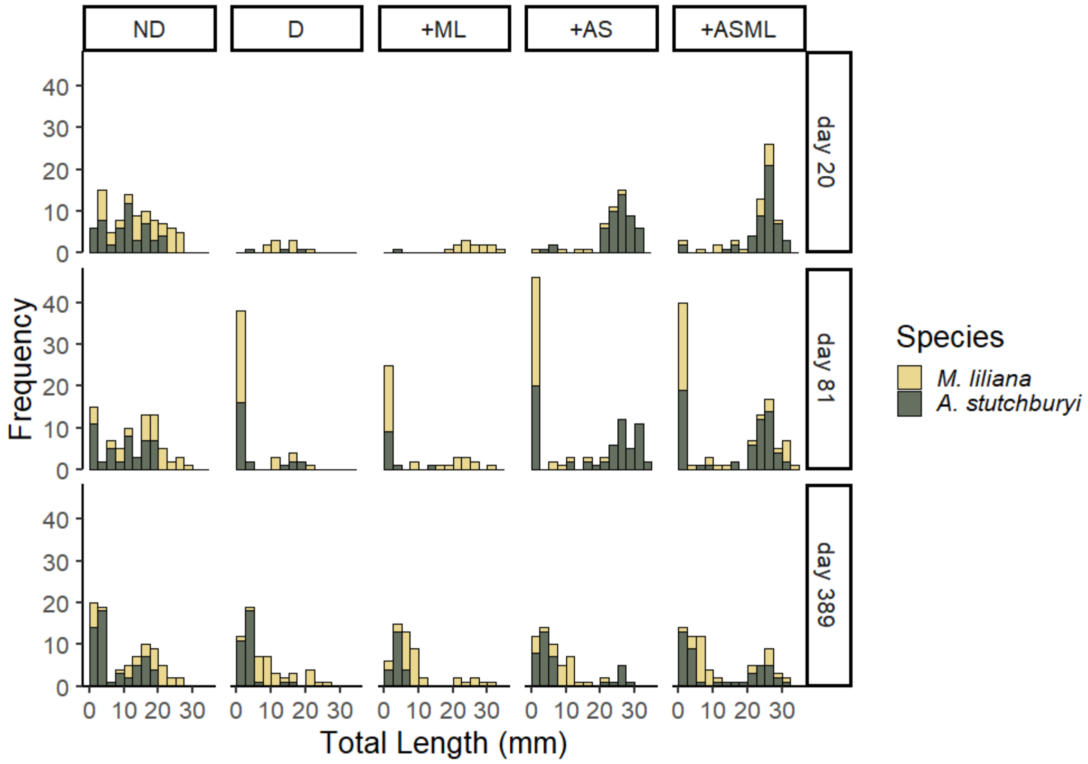


Figure A3.4 Total size frequency distribution of *M. liliana* and *A. stutchburyi* across treatments from four replicate macrofauna cores (all sizes included) across time (d 20, d 81, d 389). Treatments: ND = no disturbance, intact sediments; D = defaunation, no addition of bivalves; +ML = defaunation + addition of *Macomona liliana*; +AS = defaunation + addition of *Austrovenus stutchburyi*; +ASML = defaunation + addition of both species.

Appendix IV: Supplementary material Chapter 4

Table A4.1 Location names, exact site GPS locations, health categories based on Ellis et al. (2013) and this study across chosen site within Tauranga Harbour.

	Code	GPS Location Latitude	Longitude	Health Category Ellis et al. (2013)	Health Category this study
Source Sites					
Athenree	ATH	-37.45367803	175.96891201101243	1	2.3
Tuapiro Point	TUAP	-37.487138	175.95602600835264	2	2.3
Waikareao Entrance	REA	-37.666069	176.16035400889814	2	2.3
Translocation Sites					
Bowentown	BOW	-37.45159102	175.97196101211011	2	2.1
Moana Rd/Tanners Point	MOA	-37.47762403	175.94524302519858	2	1.5
Tuapiro Estuary	TUAE	-37.49111798	175.9511670190841	3	3.4
Uretara Estuary	URE	-37.53538901	175.93743201345205	5	3.4
Ōmokoroa	OMO	-37.637551	176.03424701839685	5	3.6
Te Puna	PUN	-37.65772004	176.05399402789772	4	3.6
Matua	MAT	-37.673519	176.11350101418793	3	2.4
Waimapu	WAI	-37.70575	176.16808333333333	3	2.8
Rangataua Bay	RAN	-37.70776	176.22111199423671	4	2.9

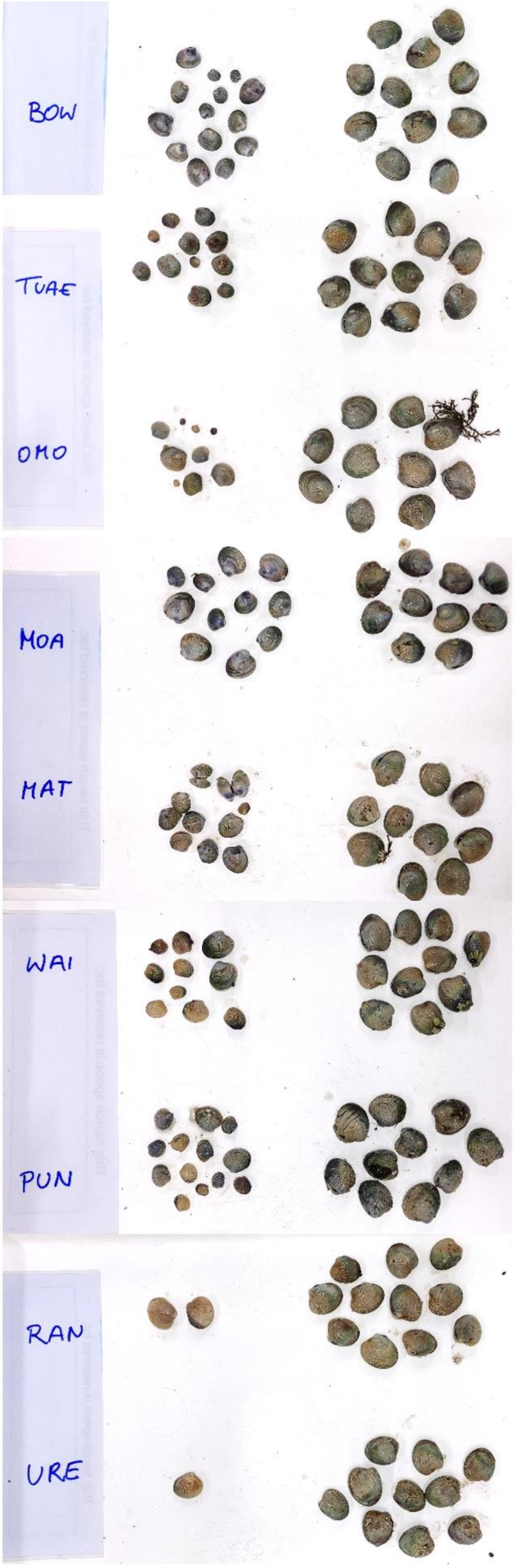


Figure A4.1 Approximately ten representative *A. stutchburyi* for all sites from ambient sites (left) and corresponding translocation sites (right) showing different sizes and colouring between treatments. Less individuals can be shown for sites RAN and URE due to low ambient densities after processing of collected individuals.

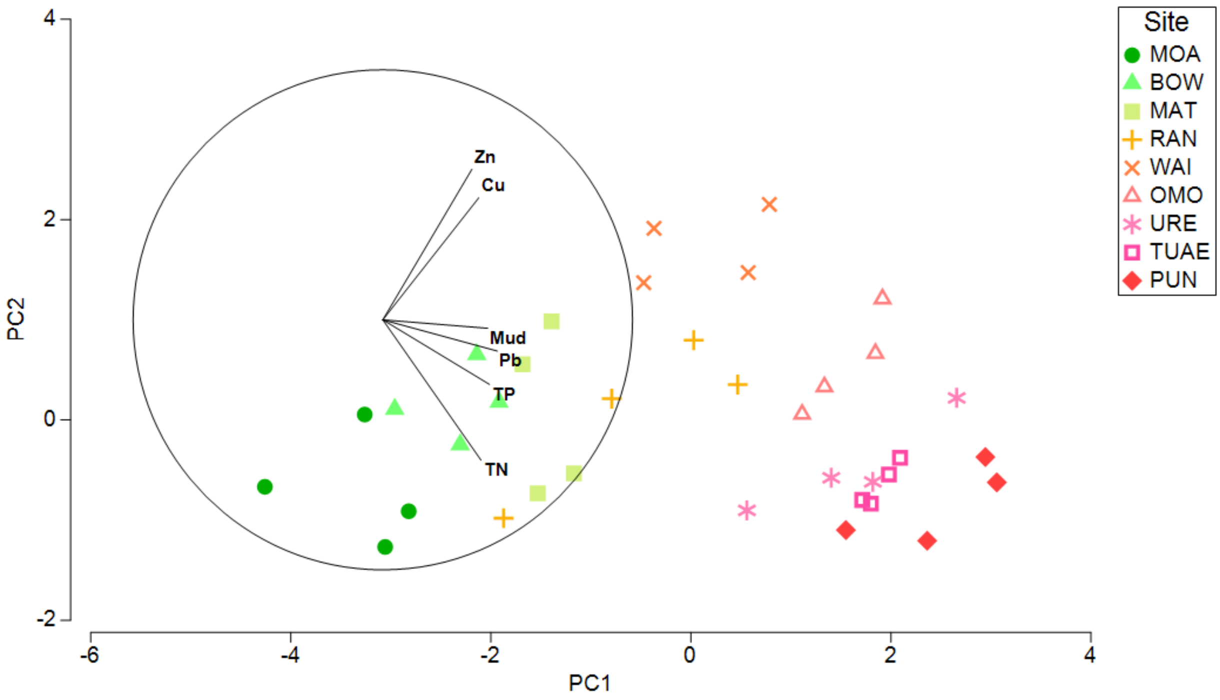


Figure A4.2 PCA plot showing ambient sites based on their levels of contamination (mud content, total nitrogen (TN), total phosphorus (TP), copper (Cu), lead (Pb), and zinc (Zn)). The PC1 score explained 69.4% of the variance and was used to assign a stressor gradient.

Table A4.2 Temperature data from 5 cm depth across a 3-month period showing mean temperature and standard deviation, median, minimum and maximum temperatures recorded.

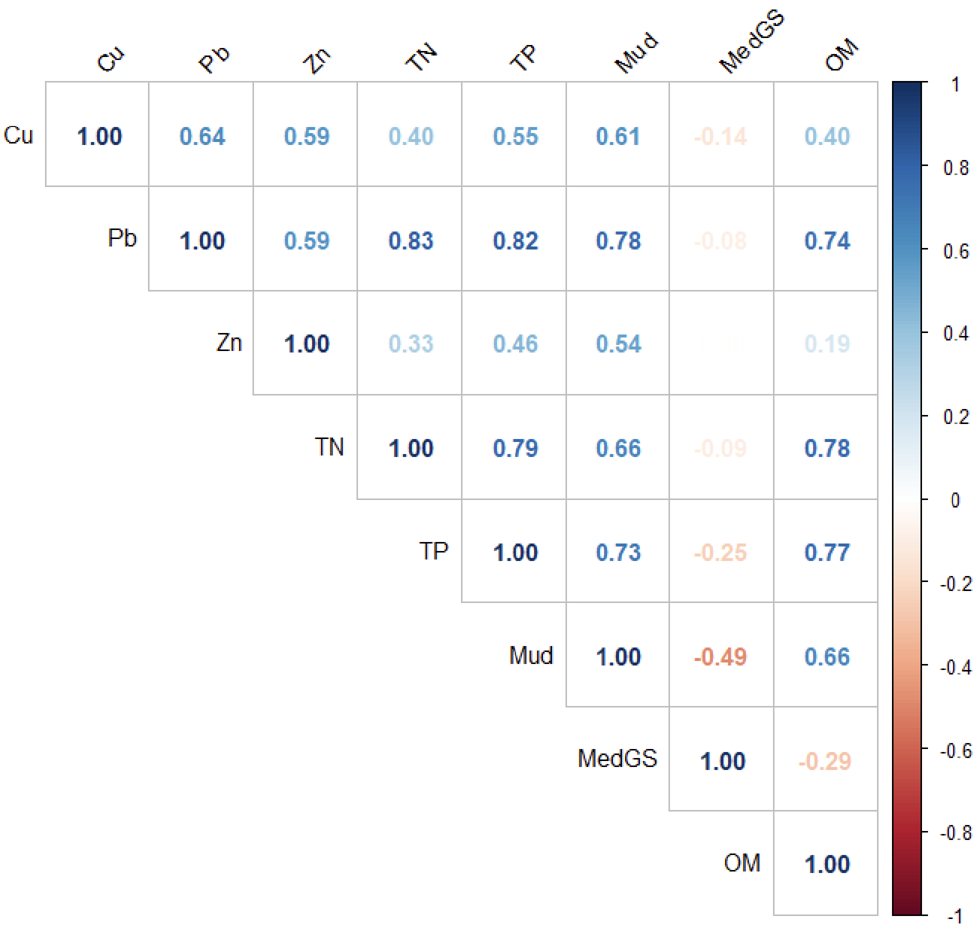
Site	**Mean temperature (°C)**	**SD**	**Median temperature (°C)**	**Min temperature (°C)**	**Max temperature (°C)**
BOW	20.65	2.16	20.6	13.7	31.0
MOA	20.72	2.32	20.7	13.4	30.1
TUAE	20.71	2.49	20.6	14.5	30.7
URE	20.66	2.14	20.3	13.6	31.4
KAT	20.83	2.44	20.7	14.5	32.4
OMO	21.14	2.38	20.9	15.7	29.8
PUN	20.67	2.07	20.5	13.0	31.2
MAT	20.32	2.36	20.1	11.7	32.6
WAI	20.68	2.61	20.7	13.7	29.8
RAN	20.56	1.98	20.4	13.3	30.3

Table A4.3 Summary of sediment properties of treatments per site after three months. The data represent the mean ±1 SD due to pooled samples (n=4).

Sites				**Sediment properties**		
Source		**Median grain size (µm)**	**Organic matter content (%)**	**Chlorophyll *a* (µg g dw^{-1})**	**Phaeophytin (µg g dw^{-1})**	**Ratio chl *a*:phaeo**
ATH		281.00 ± 15.38	1.40 ± 0.12	11.89 ± 1.69	1.28 ± 0.38	9.71 ± 2.24
TUAP		160.00 ± 1.41	2.65 ± 0.24	13.85 ± 0.69	2.03 ± 1.11	8.96 ± 5.70
REA		180.75 ± 5.12	2.61 ± 0.07	19.94 ± 2.02	3.34 ± 0.87	5.65 ± 1.17
Translocation	**Treatment**					
BOW	A	210 ± 8.27	1.73 ± 0.06	9.98 ± 1.95	1.96 ± 0.53	5.54 ± 2.33
	+AS	226 ± 11.70	1.66 ± 0.16	11.45 ± 1.60	1.89 ± 0.49	6.39 ± 1.85
MOA	A	175 ± 3.87	2.38 ± 0.19	15.37 ± 0.62	0.98 ± 0.76	29.09 ± 24.57
	+AS	174 ± 6.99	2.45 ± 0.14	15.04 ± 2.70	1.65 ± 0.60	10.32 ± 4.46
TUAE	A	151 ± 9.26	3.50 ± 0.19	17.79 ± 0.45	4.06 ± 0.94	4.53 ± 0.87
	+AS	143 ± 5.03	3.79 ± 0.38	19.48 ± 1.49	4.16 ± 0.92	4.92 ± 1.46
URE	A	258 ± 72.06	3.73 ± 0.71	18.46 ± 2.11	3.87 ± 2.42	9.46 ± 10.70
	+AS	246 ± 40.56	3.95 ± 0.48	19.60 ± 1.40	3.88 ± 1.04	5.37 ± 1.66
OMO	A	149 ± 21.67	2.97 ± 0.07	15.78 ± 0.85	3.12 ± 0.73	5.25 ± 1.12
	+AS	213 ± 62.32	3.17 ± 0.49	16.64 ± 2.06	2.65 ± 0.45	6.53 ± 1.93
PUN	A	200 ± 50.69	3.26 ± 0.17	18.88 ± 2.29	3.64 ± 1.09	5.56 ± 1.70
	+AS	228 ± 35.86	3.19 ± 0.33	18.22 ± 1.49	3.34 ± 0.51	5.51 ± 0.54
MAT	A	391 ± 10.21	2.33 ± 0.10	28.61 ± 4.65	1.18 ± 0.68	31.50 ± 17.97
	+AS	411 ± 35.91	2.36 ± 0.17	27.62 ± 8.65	1.12 ± 0.58	35.17 ± 34.23
WAI	A	233 ± 11.50	2.05 ± 0.10	16.85 ± 1.18	2.99 ± 0.73	5.85 ± 1.29
	+AS	214 ± 20.83	2.20 ± 0.14	16.99 ± 1.21	3.14 ± 1.24	6.16 ± 2.52
RAN	A	250 ± 35.14	3.55 ± 1.56	21.94 ± 3.23	1.12 ± 0.63	24.18 ± 11.38
	+AS	253 ± 37.97	2.66 ± 0.18	22.20 ± 2.03	0.87 ± 0.36	30.94 ± 18.52

Table A4.4 Mean tissue heavy metal burdens in ambient and transplanted *A. stutchburyi* after 3 months and on day of sourcing (d 0).

	Copper			Lead			Zinc		
Site	Sediment (µg g^{-1})	Ambient (µg g^{-1} DW)	Transplant (µg g^{-1} DW)	Sediment (µg g^{-1})	Ambient (µg g^{-1} DW)	Transplant (µg g^{-1} DW)	Sediment (µg g^{-1})	Ambient (µg g^{-1} DW)	Transplant (µg g^{-1} DW)
BOW	0.42 ± 0.18	6.03 ± 0.57	4.87 ± 0.56	1.53 ± 0.10	0.20 ± 0.10	0.06 ± 0.08	8.08 ± 0.55	71.71 ± 9.68	62.48 ± 12.69
MOA	0.08 ± 0.10	7.83 ± 1.38	3.94 ± 1.07	1.25 ± 0.06	0.24 ± 0.24	0.08 ± 0.06	6.18 ± 0.91	73.25 ± 6.91	63.53 ± 6.41
TUAE	0.99 ± 0.09	7.06 ± 2.47	3.40 ± 0.33	2.53 ± 0.17	0.32 ± 0.11	0.03 ± 0.06	12.7 ± 1.57	76.94 ± 7.06	72.22 ± 10.56
URE	1.00 ± 0.34	5.92 ± 2.02	4.62 ± 1.50	3.18 ± 0.61	0.35 ± 0.13	0.01 ± 0.01	11.68 ± 1.84	97.74 ± 13.99	73.52 ± 13.24
OMO	0.80 ± 0.25	6.15 ± 3.85	3.07 ± 1.00	2.65 ± 0.19	0.40 ± 0.19	0.04 ± 0.05	18.90 ± 2.92	97.62 ± 26.68	63.06 ± 23.22
PUN	0.70 ± 0.20	7.13 ± 1.46	9.35 ± 3.12	3.45 ± 0.42	0.26 ± 0.13	0.01 ± 0.02	17.48 ± 4.80	91.42 ± 8.02	75.11 ± 7.88
MAT	0.37 ± 0.08	7.12 ± 2.78	5.78 ± 0.58	1.95 ± 0.17	0.41 ± 0.17	0.13 ± 0.11	13 ± 3.91	89.24 ± 19.90	76.55 ± 8.64
WAI	1.14 ± 0.26	8.90 ± 3.88	5.04 ± 1.83	1.93 ± 0.21	0.49 ± 0.15	0.24 ± 0.31	19.33 ± 5.69	91.64 ± 11.96	71.14 ± 11.71
RAN	0.77 ± 0.26	6.36 ± 0.44	5.94 ± 0.89	2.05 ± 0.33	0.25 ± 0.08	0.09 ± 0.08	10.88 ± 4.87	88.48 ± 8.49	88.91 ± 23.65
Source									
ATH	0.32 ± 0.15	4.79 ± 0.34		1.62 ± 0.06	0.15 ± 0.13		11.62 ± 3.17	71.19 ± 4.05	
REA	0.60 ± 0.18	6.96 ± 1.27		2.02 ± 0.11	0.18 ± 0.09		13.39 ± 5.16	91.65 ± 15.73	
TUAP	0.34 ± 0.13	5.17 ± 2.69		1.81 ± 0.07	0.15 ± 0.07		9.20 ± 1.56	79.52 ± 10.97	



	Cu	Pb	Zn	TN	TP	Mud	MedGS	OM
Cu	1.00	0.64	0.59	0.40	0.55	0.61	-0.14	0.40
Pb		1.00	0.59	0.83	0.82	0.78	-0.08	0.74
Zn			1.00	0.33	0.46	0.54	0.00	0.19
TN				1.00	0.79	0.66	-0.09	0.78
TP					1.00	0.73	-0.25	0.77
Mud						1.00	-0.49	0.66
MedGS							1.00	-0.29
OM								1.00

Figure A4.3 Spearman rank correlations between heavy metals, nutrients and sediment variables (Copper (Cu), lead (Pb), zinc (Zn), total nitrogen (TN), total phosphorus (TP), Median grain size (MedGS), and sediment organic matter content (OM)). Values above 0.7 were considered high correlations.

Table A4.5 Summary of repeated measures PERMANOVA results on univariate measures of sediment properties. PERMANOVA tests (Euclidean distance) were performed on sediment variables as a function of site and treatment (ambient vs. translocation). Significant effects ($p < 0.05$) are indicated in bold. PERMANOVA post-hoc pairwise tests show individual effects, separately. GS = grain size; Mud = silt/clay (particles < 63 µm), OM = total organic matter content of sediment, Chl *a* = sediment chlorophyll *a* pigment content, phaeo = sediment phaeophytin concentration.

Variable	Source	df	MS	Pseudo-F	p (perm)
Mud	Site x Treatment	8	10.477	1.933	0.069
	Site	8	282.24	52.061	**< 0.001**
	Treatment	1	0.003	0.001	0.982
	Residual	54	5.421		
Med GS	Site x Treatment	8	1307.4	1.173	0.336
	Site	8	43165	38.725	**< 0.001**
	Treatment	1	1901.4	1.706	0.197
	Residual	54	1114.6		
OM	Site x Treatment	8	0.248	1.136	0.357
	Site	8	4.165	19.073	**0.001**
	Treatment	1	0.001	0.005	0.942
	Residual	54	0.218		
Chl *a*	Site x Treatment	8	1.814	0.219	0.987
	Site	8	184.7	22.296	**< 0.001**
	Treatment	1	2.850	0.344	0.573
	Residual	54	8.284		
Phaeo	Site x Treatment	8	0.217	0.248	0.982
	Site	8	11.626	13.306	**< 0.001**
	Treatment	1	0.004	0.005	0.948
	Residual	54	0.874		

Table A4.6 Summary of repeated measures PERMANOVA results on univariate proxies for ecosystem productivity. PERMANOVA tests (Euclidean distance) were performed as a function of site and treatment (ambient vs. translocation). To account for repeated measures, plot was assigned as random factor nested within treatment. Significant effects ($p < 0.05$) are indicated in bold. In the instance of time × treatment interactions, p-values are not given for main effects, and PERMANOVA post-hoc pairwise tests show individual effects (for treatment), separately. SOC = sediment oxygen consumption; NPP = net primary production; CD = carbon degradation.

Variable	**Source**	**df**	**MS**	**Pseudo-F**	**p (perm)**	**Post-hoc pair-wise tests**
SOC	Site x Treatment	8	1.13E+06	0.82908	0.5723	
	Site	8	5.47E+06	4.029	**0.0016**	
	Treatment	1	1.27E+06	0.93817	0.3385	
	Residual	47	1.36E+06			
NPP	**Site x Treatment**	8	4.76E+06	2.9574	**0.0075**	RAN: A < T
	Site	8	1.80E+07	11.196		
	Treatment	1	1.09E+07	6.7946		
	Residual	50	1.61E+06			
CD	Site x Treatment	8	0.15653	1.1731	0.3401	
	Site	8	0.31215	2.3393	**0.0306**	
	Treatment	1	0.00845	0.063325	0.8071	
	Residual	54	0.13344